Aquatic Invertebrates of Cuatro Ciénegas, Coahuila, México and Effects of Fish on Stromatolite Invertebrate Assemblages

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ABSTRACT

Aquatic Invertebrates of Cuatro Ciénegas, Coahuila, México and Effects of Fish on Stromatolite Invertebrate Assemblages

By Eric Dinger

Cuatro Ciénegas, Coahuila, México is an isolated basin in Northeastern México that contains an estimated 200 separate aquatic habitats. Although long recognized for its high diversity of fish, snails and turtles it had never been fully surveyed for aquatic insects and other aquatic invertebrates. The first part of my thesis was to develop a species list for the basin through surveys. The second part was stimulated by my observations and collections of the invertebrate assemblages upon the stromatolites of Cuatro Ciénegas.

I collected 2,549 aquatic invertebrates from eighteen habitats, and identified 136 different taxonomic groups, of which 118 were aquatic insects. The number of endemic species will be unknown until regional surveys are done. Few were found in all habitats, and 55 occurred in only one habitat type. The species presence/absence data was correlated to basic habitat type (canals, ciénegas, playa lakes, rivers, lagunas, and pozas), indicating that basic habitat type can be used to predict the invertebrate assemblages. Also, four different exotic species were collected during the survey: 1) *Melanoides tuberculata*, a Thiarid Snail; 2) *Procambarus clarkii*, a crayfish; 3) *Thiara granifera*; a Thiarid Snail just outside the basin and 4) *Corbicula sp.*, an Asiatic clam also just outside the basin. The threats posed to the native biota are still unknown for the native biota. Comparisons of Cuatro Ciénegas diversity to diversity in other desert aquatic habitats indicate that species richness is equitable.

Using cages of different mesh sizes, I selectively excluded large fish (*Cichlasoma minckleyi*) and all fish (*C. minckleyi* and the small pupfish, *Cyprinodon bifaciatus*) from oncoid stromatolites for three months. Exclusion of *C. minckleyi* and *C. bifaciatus* resulted in increased native snail densities, along with increases in Ceratopogonid densities. Shifts in invertebrate assemblages were also detected using NMDS ordination and MRRP analysis. Although there was no change in algal biomass, there does appear to be changes in algal species composition. Changes in algal species may result in the loss of stromatolite formation. This suggests that fish have an important role in structuring stromatolite invertebrates and may be explain why modern stromatolite formation persists in Cuatro Ciénegas.

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Preface

This thesis is written in a format for later publication in peer reviewed science journals. Because of this, there may be some redundancy in the two chapters. The first chapter will be submitted to the Southwestern Naturalist, while the second will be submitted to a broad, ecological journal such as Oecologia.

Chapter 1

Aquatic Invertebrates of Cuatro Ciénegas

Abstract

This is the first survey of non-gastropod aquatic invertebrates of Cuatro Ciénegas, Coahuila, México. The survey was conducted with four purposes: 1) establish a species list of aquatic invertebrates, 2) correlate species distribution with physical, chemical and biological data, 3) describe the current distribution of exotic aquatic invertebrates, and 4) determine if Cuatro Ciénegas has similar levels of invertebrate biodiversity to other arid aquatic habitats. Over 2000 invertebrates were collected from eighteen different sites and six different habitat types (canals, ciénegas, pozas, rivers, lagunas and playa lakes). I identified 136 different taxa, of which 118 were aquatic insects. No correlation was detected with physical and chemical parameters, nor was there any relation with fish assemblages. However, invertebrate assemblages did group according to habitat type. Two exotic species were found within the basin (a snail, *Melanoides tuberculata* and a crayfish, *Procambarus clarkii*). Both were known to be in the basin previously, but no new range extensions were detected. Their potential impacts are still unknown. Two other exotic species were found just outside of the basin in waterways connecting to the basin (*Corbicula sp.* and *Thiara granifera*). Literature searches of published desert aquatic invertebrate surveys showed that Cuatro Ciénegas has similar biodiversity levels of aquatic insects and invertebrates. Many invertebrates were only found at individual sites and only certain habitat types, stressing the importance of protecting all types of habitats within the basin. The high levels of biodiversity and their importance in the ecosystem suggest the need for further conservation.

Introduction

The Cuatro Ciénegas Basin in Coahuila, México was declared a protected area by the Mexican government in 1994, and is regarded as a high priority site for conservation due to its high numbers of endemic fish and snails (Contreras-Balderas 1984, Williams et al. 1989, Minckley 1992). Cuatro Ciénegas has been compared to the Galapagos Islands because of its high rate of endemism. Half of the native fish assemblage are endemic species (eight of sixteen), and close to seventy percent of the hydrobiid snails species (nine of thirteen) are endemic. Additionally, other aquatic organisms of the basin have high rates of endemics (Turtles: 75%; Crustacea: 50%) (Cole 1984, McCoy 1984). Although most of the fish, snails and turtles were thoroughly described (taxonomically and distribution, for example: Minckley 1962, Taylor 1966, Brown 1974, Itzkowitz and Minckley 1969), there has been very little work on other aquatic invertebrates.

Establishing a baseline reference on all aquatic invertebrates is important because: 1) the insects of the basin may contain similarly high rates of endemism and be an important source of biodiversity; 2) the aquatic invertebrates may be an important link in aquatic food webs to transfer energy to the higher trophic levels, 3) aquatic insect adults may be important in exporting energy to the terrestrial ecosystem and 4) conservation threats, such as water extraction, may endanger the still mostly unknown aquatic insects.

This survey has four primary goals. First, to develop a list of non-gastropod invertebrates to help provide baseline data on the biodiversity of all aquatic invertebrates within the basin. Gastropods were not included in the survey because there is a large amount of historical distribution and diversity data already in the literature. Second, to correlate species distribution with physical and chemical variables and fish assemblages.

Third, to describe the distribution of exotic invertebrates within the basin. Prior to this survey, two exotic species were known to inhabit several waterways of the basin, *Melanoides tuberculata,* the African Thiarid Snail (Thiaridae: Gastropoda) and *Procambarus clarkii*, a southeastern crayfish (Cambaridae: Decapoda) (Contreras-Arquieta 1998, Minckley, pers. communication). Both species have potential for affecting the natural ecosystems and food webs of Cuatro Ciénegas. Fourth, to compare the diversity and abundance of aquatic invertebrates to other desert aquatic ecosystems.

Methods and Materials

Study area—The study was conducted in the Cuatro Ciénegas Basin in central Coahuila, Mexico (26˚45'-27˚00'N and 102˚00'-102˚20'W). The basin is located at 740 meters above sea level between the mountain ranges of the Sierra Madre, Sierra Fragua and Sierra de San Marcos y Piños of the Chihuahuan Desert (Fig. 1). The desert receives less than 200 mm of average annual precipitation, and summertime temperatures can exceed 44˚C, while winter temperatures can drop below 0˚C (Shreve 1944).

There are over 200 aquatic habitats in the basin which I have grouped into seven categories: 1) ciénegas, 2) lagunas, 3) playa lakes, 4) pozas, 5) canals, 6) rivers, and 7) spring seeps. Ciénegas are shallow (< 1 m deep), complex heterogeneous habitats that are fed by rios or canals and generally characterized by high evaporative rates. Lagunas are spring-fed habitats that have heterogeneous bathyspheres, with shallow (less than one meter) and deep parts (up to 3 or 4 m) scattered throughout the habitat. Playa

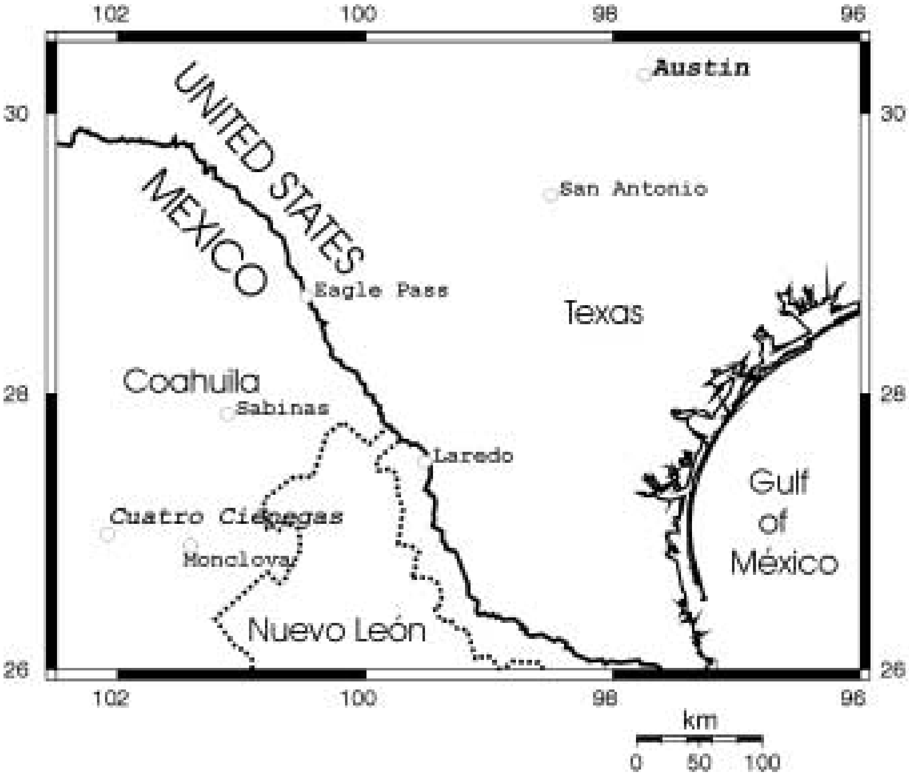

Figure 1. Location of the Cuatro Ciénegas Basin in the Mexican State of Coahuila.

lakes are large (usually several square hectares or more) habitats fed through rivers and canals that also experience high evaporation. Pozas are small, circular homogeneous habitats, usually with a central spring feeding them. Some pozas are very deep (> 18 m), but most are only 3-4 m deep. Canals are abundant throughout the basin and are usually constructed of cement, but are occasionally simple ditches in the ground. Rivers in the basin generally have high amounts of aquatic vegetation, and are almost exclusively runs and pools, with very few riffles. Spring seeps are common in some parts of the basin, but have very little in the way of standing water and are often more saturated soil than water.

Riparian vegetation includes *Salix nigra*, *Typha domingensis, Phragmites australis* and *Eleocharis sp*, and aquatic vegetation is generally *Nymphaea ampla*, but *Chara sp., Utricularia obtusa*, *Ludwigia sp.*, and *Potamogeton nodosus* are also common throughout the basin (see Pinkava [1984] for complete catalog). Algal assemblages include cyanobacteria, diatoms, and green algae, but stromatolites are also present in several of the sites. Stromatolites are rare laminated, benthic, microbial deposits found only in a few freshwater locations throughout the world. They were once the predominant life form in the Precambrian Era, but declined in abundance 570 million years ago. Modern stromatolites are formed by an algal matrix that actively precipitates calcite through biological activity, and incorporates the minerals into their structure. In Cuatro Ciénegas, different algal species create variation in morphologies ranging from oncoid stromatolites to large shelf stromatolites.

Survey methods—Eighteen sites were sampled between June 1999 and July 2000, with most of the summer collections in June and July of 1999, and winter collections in January 2000 (Table 1). Sites were chosen to encompass the seven habitat types and to include sites that have been historically sampled for fish and gastropods. Spring seeps were not sampled since they generally represent marginal habitats for aquatic insects, having very little open water suitable for insects. While these eighteen sites received intensive surveys, other sites were visited but have limited collections.

Qualitative invertebrate collections used different methods, depending upon the habitat type. The most efficient technique for lentic sites was the use of an O-ring net (253µm) to sweep both littoral and submerged aquatic vegetation. In soft sediments, a larger mesh size (1mm) was used to decrease sorting time. In lotic habitats, a D-frame kick net (253 µm) was used to collect invertebrates in both hard and soft substrates. Stromatolites were disaggregated and elutriated to collect specimens, while stalks of *Typha domingensis* were cut with a knife to collect invertebrates living in their leaves. All samples were visually sorted in the field and preserved in 95% ethanol. Invertebrates were identified in the lab to the lowest possible taxonomic level using keys to North American taxa (Needham and Westfall 1954, Pennak 1989, Thorp and Covich 1991, Merritt and Cummins 1995, Westfall and May 1996, Wiggins 1996).

Physio-chemical parameters (temperature, dissolved oxygen, conductivity, and pH) were measured using a portable Hydrolab Minisonde water probe. Nutrient and ionic composition samples were collected in sterile bottles, filtered through a 0.45µm membrane filter and acidified to a pH < 2.0. Laboratory analyses were run on a Technicon Auto-Analyzer II (PO_4^{-3}, NO_3^-), a Dionex DX 100 Ion Chromatograph (Cl^-, SO_4^{-2}) and a Perkin-Elmer Model 560 Atomic Absorption Spectrophotometer (Ca^{+2}, Mg^{+2}, Na^+).

Table 1. Habitats sampled during survey. All UTM coordinates are for Zone 13. * indicates not data not available. Habitat type definitions are in the text. Habitat size is on a scale from 1 to 10. Habitat code is for cross-reference to Appendix 1.

	Location (UTM Coordinates)				
Habitat Name	North	East	Habitat Type	Habitat Size	Habitat Code
Becerra	2976191.05	784293.78	Poza	9	1
Canal de La Becerra	2976730.66	186706.42	Canal	5	2
Charcos Prietos	2979912.39	198466.93	Laguna	5	3
Churince	2981039.07	191524.17	Poza	4	4
Escobedo	2977959.10	193371.82	Poza	3.5	5
Juan Santos	2978786.08	187438.56	Laguna	7	6
Las Playitas Inlet	*	*	Playa Lake	8	7
Las Playitas SE Shore	2979863.39	796817.38	Playa Lake	10	8
Los Gatitos	*	*	Cienega	3	9
Los Gatos	2977405.44	798314.24	Cienega	8	10
Los Hundidos	2979783.13	194917.32	Laguna	9	11
Mojarral Este	2981484.11	189919.88	Laguna	8	12
Mojarral Oeste	2980879.12	785725.34	Poza	5	13
Poza Azul	2969600.35	795644.73	Poza	4	14
Puente Chiquita	2981076.96	793510.97	River	5	15
Rio Garabatal	*	*	River	7	16
Seca Salada	*	*	Canal	5	17
Tio Candido	2974517.98	790796.55	Laguna	3	18

Transects were conducted to quantify physical habitat in areas with high densities of invertebrates. Because preliminary invertebrate surveys showed highest abundance and diversity along the riparian and littoral zones, transects were concentrated in these areas. Transects are representative of the habitat where the highest densities of invertebrates were found, but this is not always representative of the entire habitat. In lentic habitats, ten transects approximately ten meters apart were sampled from the edge of the habitat to eight meters. Depth and substrate type were recorded at 1m, 2m, 4m, 6m and 8m along each transect. The number of aquatic macrophytes and percent emergent vegetation were recorded for each transect. In lotic habitats, ten transects were run along a 100m longitudinal reach and recorded width, depth and substrate type at five equidistant points across the channel. Percent and type of littoral and riparian vegetation, and types of algae present were estimated.

Concurrent surveys of fish were conducted using minnow traps, seine, cast, gill and frame netting. Baited minnow traps also occasionally caught several larger invertebrate specimens. Data were recorded as presence and absence of species and are reported in Marks et al. (2001, in prep).

Because accurate habitat size is difficult to quantify without high quality aerial photographs, habitat size was qualitatively rated from (1) small to (10) large, following the technique of Minckley (1984). Small habitats were several square meters in size, while large habitats were several hectares in size (Table 1).

Statistical Analysis—The presence-absence data collected at each site were transformed into Sorenson (Bray-Curtis) distance measures, which was originally used for presence-absence data. Non-metric multidimensional scaling (NMDS) ordination was used to provide a visual summary of patterns of Sorenson (Bray-Curtis) values. NMDS ordination was chosen because it has been shown to work well by accurately portraying ecological data (McCune and Mefford 1999).

Multi-Response Permutation Procedure (MRPP) was used to assess significance of habitat types (canal, poza, ciénegas, etc.) upon invertebrate assemblages. This non-parametric test is used for detecting differences between *apriori* groups, in this case habitat type. In this test, the statistic A is a measure of effect size, where $A = 1$ indicates that samples between habitat groups are identical, and an *A* = 0 indicates that samples are heterogeneous between habitats. In other words, an *A* near 1 indicates strong grouping, while an *A* near 0 indicates weak grouping. An initial MRPP was used on all groups (canal, poza, ciénegas, etc.) at once, and if significant grouping was detected, then multiple two-way MRPPs were used to elucidate the specific differences in grouping (i.e. canal vs. poza, river vs. poza). MRPP is unable to compare groups where both members only contain two members, so not all pairwise comparisons were possible.

To test for correlations between a distance matrix of invertebrate assemblages and distance matrices of fish assemblages and physical/chemical habitat data, a Mantel test was used. The Mantel Test determines whether the correlation is stronger than expected by chance by comparing sums of observed cross products to a distribution of random cross products. Since some surveyed sites did not have a complete data set of physical habitat measurements, some survey sites were excluded from the analysis. Monte Carlo simulation (randomized permutations of the matrices) was used to test for significance. All statistical tests were done using PCORD4 software package (McCune and Mefford 1999).

Results

A total of 2,549 aquatic and semi-aquatic individual invertebrates were collected and identified in this survey. One hundred thirty-six different taxa were identified, including 118 insect taxa (Appendix A). All but 26 were found at the 18 intensively sampled sites, with others collected at sites that were only cursorily sampled. The highest species richness is found in rivers, with 94 taxa groups. Ciénegas have the lowest species richness, with only 16 taxa groups (Table 2). The site with the highest species richness was Rio Garabatal, with 48 taxa, while the site with the lowest was the inlet of Las Playitas (a playa lake habitat) where only the amphipod, *Hyalella sp.*, was found.

Among the invertebrates, very few were widespread throughout all the habitats. The only taxa found in all habitat types were Chironomidae (multiple species); Oligochaetes; *Hyalella sp.* (Taltridae: Amphipoda); and *Palaemonetes suttkusi* (Palaemonidae: Decapoda). Several were present in all but one habitat type, but most were limited to just a few, with 55 limited to only one habitat type (see Appendix A).

No new exotic invertebrate species were found in the basin, but two potentially invasive species, *Corbicula sp.* (Asiatic Clam) and *Thiara granifera* (Turban Snail) were found in Rio Salado de Nadadores, a river that connects to the basin through several canals (Table 3). The crayfish, *Procambarus clarkii* is an exotic species that has been known to be in the basin for several years, but the distribution within the basin has been unknown. No new range extensions of *Melanoides tuberculata* were found, nor were living specimens found in one habitat (Poza de la Becerra) where it was previously reported. The habitats where high densities of *M. tuberculata* were found was at the base of *Typha domingensis* in the littoral zone of Poza Churince and in the Canal de la Becerra. No specimens of *M. tuberculata* were found in the Rio Mesquites, but this is a large, expansive habitat, which makes it hard to determine if they are absent, rare, or just not present in the sections sampled.

Analysis of presence/absence data using MRPP analysis shows significant grouping of habitat types ($p = 0.002$, $A = 0.107$). These differences are apparent in the

Table 2. Numbers of different representatives of insect orders found during survey separated by habitat type. Other taxa include Amphipoda, Acarina, Hirudinea, Annelida, Decapoda, Collembola, Isopoda, Turbellaria, and Nematoda.

Habitat Type	Total no.	Coleo-ptera	Di-ptera	Ephem-eroptera	Hemi-ptera	Lepido-ptera	Megalo-ptera	Odo-nata	Tricho-ptera	Other Taxa
Canals	37	7	8	5	2	0	1	3	6	5
Ciénegas	16	1	1	2	5	0	0	1	0	6
Lagunas	38	9	3	4	1	1	0	10	1	9
Playa Lakes	22	5	1	4	0	0	1	5	0	6
Pozas	50	7	7	6	3	1	0	15	2	9
Rivers	94	16	8	10	12	1	2	20	10	15

Table 3. Known locations of invertebrate exotic species. * Rio Salado de Nadadores is immediately outside the basin, but is connected through canals.

Exotics Species		Localities Found	New Record?
Latin Name	Common Name		
Corbicula sp.	Asiatic Clam	Rio Salado de Nadadores*	Yes
Melanoides tuberculata	Turban Snail	Poza Churince	No
		Rio Mesquites	No
		Santa Tecla	No
		Canal de la Becerra	No
Procambarus clarkii	Southeastern Crayfish	Rio Garabatal	Yes
		Rio Mesquites	Yes
		Mojarral Este	Yes
Thiara granifera	Turban Snail	Rio Salado de Nadadores*	Yes

NMDS ordination (Fig. 2). There appears to be groupings for rivers, canals, and ciénegas. There is considerable intermixing and large spread of both pozas and lagunas.

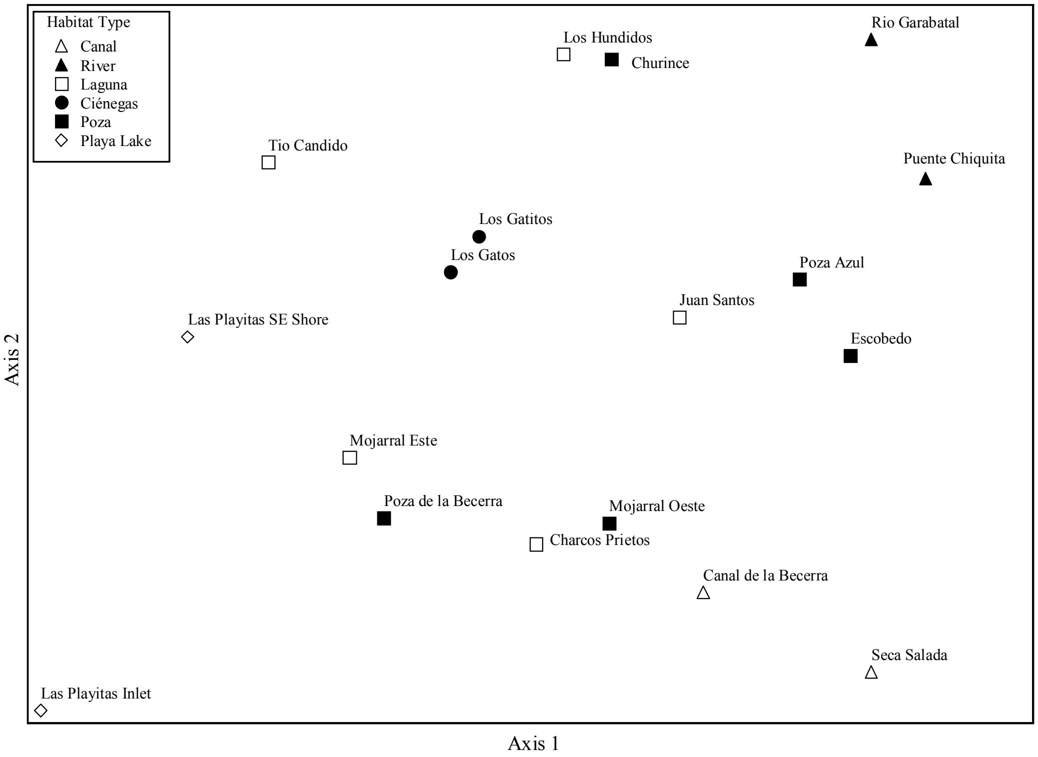

Figure 2. NMDS Ordination of invertebrate assemblages.

The post-hoc MRPP showed significant differences among lagunas and canals; lagunas and ciénegas; and between lagunas and rivers (Table 4). Although MRPP cannot make pairwise comparisons of playa lakes, ciénegas, rivers, and canals each does appear to group separately from each other.

In the Mantel Test for correlation between the matrices of invertebrate assemblages and physio-chemical measurements (Table 5), two sites had to be excluded due to missing data: Rio Garabatal and Los Gatitos. The test was not significant (p = 0.16). There was also no correlation detected between matrices of invertebrate assemblages and fish assemblages (p = 0.209).

Observation of densities during collection periods indicate little variability between summer and winter in either densities or presence and absence, but life stages of many aquatic insects (particularly odonates) vary seasonally, with later instars being found in winter months.

Due to difficulties in quantitatively sampling lotic and littoral habitats, observations on invertebrate densities were limited to qualitative estimates. Qualitative estimates of densities in the field were low throughout the year, with many taxa being represented by single individuals in the collections. Even more common insects, such as the mayfly, *Baetis sp.*, are often limited to only a few dozen animals/m^2 in some habitats. Midges (Chironomidae) and *Hyalella sp.* were abundant, but only in a few microhabitats, such as the algal mats of stromatolites, and littoral vegetation and root mats of riparian vegetation. Taxa found in the open, sedimented areas of pozas and lagunas are limited to the native hydrobiid snails and the occasional amphipod (*Hyalella sp.*), glass shrimp (*Palaemonetes suttkusi*) or Chironomidae midges.

Table 4. Post-hoc MRPP results to test for grouping of invertebrate assemblages by habitat type. Overall MRPP was significant ($p = 0.002$, $A = 0.107$). TFS indicates Too Few Sites to test. *p* values are given with *A* values in parentheses.

	Canal	Cienega	Laguna	Playa Lakes	Poza	River
Canal	-	TFS	0.043 (0.06)	TFS	0.124 (0.04)	TFS
Cienega		-	0.03 (0.06)	TFS	0.066 (0.08)	TFS
Laguna			-	0.135 (0.03)	0.43 (0.001)	0.036 (0.07)
Playa Lakes				-	0.062 (0.07)	TFS
Poza					-	0.108 (0.05)
River						-

Discussion

Cuatro Ciénegas contains a wide range of habitat types, with many types of microhabitats, so it is not unexpected that there are over 136 different invertebrates found in the basin. High species richness may also be due to the geographical location of the basin. Cuatro Ciénegas lies on the edge of neotropical and temperate climate zones, and may be a mixing point where these species may co-occur. Adding to this is the isolation and xeric conditions of the basin, which may increase diversification (Thomas et al. 1998), and hence, the species richness of the aquatic invertebrates of the basin.

Identification of endemic species that may have occurred through radiation is not easily ascertained, however, due to a lack of distributional information on aquatic insects in other parts of the Chihuahuan Desert. Published records of aquatic insects in Northeastern Mexico are limited, and often highlights the paucity of distributional records (Hurlbert and Villalobos-Figueroa 1982, Llorente-Bousquets et al. 1996). McCafferty and Lugo-Ortiz (1996) report no species records for any Ephemeroptera in Coahuila, although eleven different species were recorded in this survey. Many of these

Table 5. Water chemistry for surveyed sites. All readings were collected in June and July of 1999. Temperature, pH, conductivity and dissolved oxygen were measured in the field with a Hydrolab Minisonde water quality probe. Alkalinity is expressed in terms of $CaCO_3$. Alkalinity, nutrients and ions were analyzed in the laboratory (n = 2). ND indicates values below detection levels. * indicates data not available.

Site	Type of Habitat	Temperature (˚C)	pH	Conductivity (µS cm^{-1})	Dissolved Oxygen (mg l^{-1})	Alkalinity (mg l^{-1})
Canal de la Becerra	Canal	34.7	8.4	2658	11.0	167
Seca Salada	Canal	27.6	8.1	3156	8.5	147
Los Gatitos	Cienega	31.8	8.5	5759	8.8	*
Los Gatos	Cienega	30.3	8.5	11020	8.0	162
Charcos Prietos	Laguna	32.2	8.0	3571	7.4	152
Juan Santos	Laguna	29.5	7.5	2913	5.6	173
Los Hundidos	Laguna	25.7	7.9	4698	5.5	189
Mojarral Este	Laguna	33.3	7.3	2697	5.2	179
Tio Candido	Laguna	30.6	7.1	2425	4.3	154
Las Playitas	Playa Lake	25.3	8.5	7202	6.9	113
Las Playitas Inlet	Playa Lake	24.6	8.4	5412	7.3	114
Mojarral Oeste	Poza	33.3	7.1	2659	2.3	186
Poza Azul	Poza	28.9	7.6	2789	4.9	166
Poza Churince	Poza	29.5	7.1	2538	4.2	156
Poza de la Becerra	Poza	33.7	7.1	2584	2.9	168
Poza Escobedo	Poza	34.2	7.2	2651	2.3	184
Puente Chiquita	River	25.7	7.6	3759	6.1	178
Rio Garabatal	River	29.1	7.9	5514	7.8	183

Table 5 Continued.

	Nutrients and Ions mg l^{-1} (± SE)						
Site	NO_3^-	PO_4^{-3}	SO_4^{-2}	Ca^{+2}	Mg^{+2}	Na^+	Cl^-
Canal de la Becerra	2.24 (0.04)	*	1267 (17.5)	343 (5.5)	118 (1.0)	153 (1.0)	105 (1.0)
Seca Salada	0.50 (0.05)	ND	1329 (12.8)	376 (5.5)	118 (2.0)	183 (3.0)	113 (0.6)
Los Gatitos	*	*	*	*	*	*	*
Los Gatos	ND	0.1 (0.00)	3695 (32.3)	425 (18.5)	710 (0.0)	1123 (37.5)	494 (5.6)
Charcos Prietos	0.2 (0.15)	0.02 (0.01)	1512 (52.2)	448 (14.0)	137 (7.0)	209 (10.0)	120 (8.5)
Juan Santos	1.3 (0.06)	ND	1132 (210.1)	314 (1.5)	100 (0.5)	149 (0.5)	121 (32.3)
Los Hundidos	ND	0.02 (0.00)	1871.19 (47.1)	364.5 (139.5)	162.5 (1.5)	241 (3.0)	139.58 (1.6)
Mojarral Este	1.6 (0.00)	*	1418 (71.5)	357 (13.0)	120 (5.5)	150 (0.5)	100 (5.5)
Tio Candido	1.68 (0.02)	ND	1170 (8.0)	277 (12.5)	93 (4.0)	110 (4.5)	90 (0.5)
Las Playitas	ND	*	3133 (212.5)	596 (4.0)	357 (5.0)	445 (2.0)	266 (19.0)
Las Playitas Inlet	ND	ND	2158 (530.6)	459 (2.5)	363 (7.5)	502 (6.0)	219 (40.4)
Mojarral Oeste	1.8 (0.50)	ND	971 (485.3)	316 (3.0)	99 (0.5)	150 (6.5)	83 (*)
Poza Azul	1.14 (0.11)	ND	1282 (243.5)	305 (1.5)	102 (1.5)	154 (0.5)	121 (24.2)
Poza Churince	2.01 (0.01)	*	1209 (6.0)	321 (16.5)	105 (5.0)	135 (3.0)	98 (0.5)
Poza de la Becerra	2.1 (0.19)	*	1181 (0.5)	331 (9.5)	110 (4.0)	137 (1.0)	93 (0.5)
Poza Escobedo	1.83 (0.03)	ND	1290 (12.5)	320 (13.0)	108 (4.5)	129 (6.0)	99 (0.0)
Puente Chiquita	0.26 (0.09)	ND	1298 (243.5)	393 (52.0)	154 (2.0)	267 (13.5)	129 (19.7)
Rio Garabatal	0.43 (0.03)	ND	2174 (243.4)	457 (3.5)	303 (7.5)	505 (5.0)	272 (23.7)

species have been known to Cuatro Ciénegas researchers since the early 1960's, but had never been identified beyond the taxonomic order or reported (Minckley and Hendrickson, pers. communication). The only taxonomic groups that have been well surveyed in Coahuila are Odonates (Needham and Westfall 1954,Westfall and May 1996). Surveys outside the basin will have to be conducted to adequately describe species ranges before the true extent of endemic aquatic insects in Cuatro Ciénegas is known.

Even without these data, some hypotheses about which invertebrates in the basin are endemic can be made. More vagile insects, such as the odonates, are typically not endemic to small systems, because they are characterized by large ranges. Other insects with poor flying ability, such as Elmidae beetles, are more likely to be endemic to small geographic areas. Other invertebrates with limited dispersal are also highly endemic, such as leeches and amphipods. Indeed, Cole (1984) hypothesized that there are up to seven different species of *Hyalella sp.* (Crustacea: Amphipoda).

Invertebrate Assemblages and Habitat

While species distribution within the basin was not correlated with a matrix of environmental variables, presence and absence of invertebrates can be approximated by some habitat types. Since invertebrate distribution is often dependent upon physical and chemical conditions, this suggests that either the important variables were not measured, or the controlling variables were overshadowed by the measurement of too many, non-important variables used in the Mantel Test.

Two groups that were not significantly different (pozas and lagunas) are both lentic, spring-fed habitats. This may explain the lack of differences between invertebrate assemblages, but also suggests that differences used to define lagunas from pozas (no. of springs sources, contour of bathysphere, shoreline complexity) are unimportant in determining invertebrate assemblages.

Distribution of Exotic Species

The potential impact of *Melanoides tuberculata* (Thiaridae: Gastropoda) is still unknown. *M. tuberculata* was first sighted in 1994 by Contreras-Arquieta (1998) and has since been collected in Poza de la Becerra, Poza Churince, parts of the Rio Mesquites and Santa Tecla. My collections did not find any range expansion, and the distribution within the basin may be decreasing.

Although it would be premature to say that *M. tuberculata* is now locally extinct in Poza de la Becerra, the inability to find any living specimens suggests that there has not been any large impact on the environment of Poza de la Becerra due to extremely low numbers (or altogether absence) of individuals. While they were not found in the poza, they are dense in the Canal de la Becerra, which drains Poza de la Becerra and could potentially serve as a mechanism for dispersal of *M. tuberculata* into other habitats.

In Poza Churince, *M. tuberculata* has high densities, but are limited in their distribution to the littoral vegetation, along the edges of the poza. No individuals were collected in the soft flocculent sediments that are found in most pozas. The reason for lack of invasive success both in Churince and other pozas of the basin, especially given *M. tuberculata* success in other habitats throughout the world (e.g. Venezuela, Martinique Islands, Cuba, Louisiana, Texas, Florida, Africa among others [Dundee and Paine 1977, Madsen 1990, Perera et al. 1991, Pointier et al. 1993, 1994), could be due to competition and/or predation by fish, native gastropods or other invertebrates, or simply unsuitable habitats (e.g. water chemistry, substrate availability, or flow conditions).

The crayfish, *Procambarus clarkii*, was also collected in several sites throughout the basin, and as omnivores, have the potential to alter the natural foodwebs of Cuatro Ciénegas in multiple pathways as they have in other systems (Kershner and Lodge 1995). Their impact on the ecosystems of Cuatro Ciénegas is still unknown, but the crayfish may be more prevalent then initially thought due to their nocturnal behavior. Most crayfish collected in this survey was through the use of overnight minnow traps, which were only done at a few habitats. The distribution of crayfish in this survey is most likely an underestimate, and points to a need for a more extensive study.

Lastly, the presence of the Asiatic Clam *Corbicula sp.* and the Turban Snail *Thiara granifera* in the Rio Salado de Nadadores may be a sign of future problems in the basin of Cuatro Ciénegas.

Diversity Compared to Other Desert Ecosystems

Exclusive of gastropods, the invertebrates of Cuatro Ciénegas have been anecdotally described as being “depauperate” (Minckley, pers. communication). This survey found species richness to be similar to other desert aquatic ecosystems (Table 6).

The belief that insects of Cuatro Ciénegas are depauperate may come from the low densities of most habitats. Reasons for the low densities are not understood, but several hypotheses may explain the low numbers. First, chemical conditions may limit invertebrate densities. Cuatro Ciénegas waters are characterized by high amounts of $CaSO_4$, which may negatively impact invertebrate populations. In other chemically extreme systems, however, the primary effect is to limit the diversity of invertebrates and

Table 6. Comparison of aquatic macroinvertebrates and insect surveys of arid aquatic ecosystems. * indicates data not available.

Ecosystem Name	Location	Desert	No. of macro-invertebrates	No. of insects	Reference
Colorado River and Tributaries	Northwestern Arizona, USA	Great Basin	*	42	Oberlin et al. 1999
Cuatro Ciénegas	Central Coahuila, Mexico	Chihuahuan	155	118	**Current Study**
Moapa Warm Springs	Southern Nevada, USA	Great Basin	197	*	Herbst, unpublished data
Montezuma Well	Northern Arizona, USA	Sonoran	*	~100	Blinn and Oberlin, 1995
Ruby Marsh	Northern Nevada, USA	Great Basin	250	*	Herbst, unpublished data
Sycamore Creek	Central Arizona, USA	Sonoran	*	99	Gray 1981

not the densities. Usually, the few organisms that can tolerate these conditions do extremely well and obtain high densities. Cuatro Ciénegas appears to be the converse of this however, with high diversity, but low densities.

Second, high amounts of fish predation may limit invertebrates. The fish of Cuatro Ciénegas are both diverse and abundant, and have the potential to control invertebrate densities. The eighteen different fish found in Cuatro Ciénegas includes fish that inhabit a large range of microhabitats, such as two species of mosquito fish that feed at the surface of the water column in the littoral zones, as well as omnivorous pupfish that feed on the benthos in both the littoral and profundal zones. The polymorphic cichlid, *Herichthys minckleyi*, with a molariform morph that can eat snails and a papilliform morph that eats detritus and soft-bodied invertebrates is another abundant predator of invertebrates that may limit their abundance.

Implications for Conservation

The high species richness and as yet unknown number of endemic aquatic insects and other invertebrates are yet another reason for continued protection of Cuatro Ciénegas habitats. The importance of aquatic invertebrates in transporting energy from primary producers to the higher trophic levels are still not fully known, but recent dietary studies using stable isotopes and gut analysis suggest that they are important food sources for some species of fish (Hulsey in press, Marks et al. in prep), as well as early dietary work showing that the polymorphic *Herichthys minckleyi* consume aquatic insects along with detritus and Hydrobiid snails (Smith 1982). Additional early studies of the relict box turtle, *Terrapene coahuila*, found aquatic invertebrates to be a source of nutrition for these endemic turtles (Brown 1974).

The aquatic insects may also play an important role in mitigating the effects of invasive species, such as *M. tuberculata*. So far, *M. tuberculata* has had limited success in Cuatro Ciénegas habitats, and one possible hypothesis is interspecific competition with native invertebrates, both gastropods and non-gastropods.

Also of concern is that the highest number of species was found in Rio Garabatal, a habitat that has been reported to periodically dry and recede (Hendrickson, unpublished data). The historical habitat, Laguna Garabatal, which dried sometime between 1983 and 1999, was once linked to the Rio Garabatal. The water source for the Rio Garabatal may now be the nearby Canal de la Becerra, where leakage from the cement channel and underground flow may provide the only water for the Rio. Ironically, the survival of this habitat may rely on a canal that drains other habitats.

The variety of habitats in Cuatro Ciénegas houses a diverse and large aquatic invertebrate assemblage. The diversity of habitats in size, type, water chemistry, and biological assemblages stress the need to not just protect certain habitats, but necessitate the need to preserve and protect all types of habitats in the basin, from the smallest spring seep to the largest playa lake.

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Chapter 2

The Role of Fish in Structuring Stromatolite Assemblages

Abstract

I tested the effects of fish on freshwater stromatolites in Cuatro Ciénegas, Mexico. Modern stromatolites only occur in a few habitats, but were the predominant life in the Precambrian and declined in the Phanerozoic. This decline in stromatolites has been attributed to the evolution of metazoan grazers. Oncoid stromatolites in Cuatro Ciénegas, however, can support a diverse assemblage of macroinvertebrates. I applied food chain theory to hypothesize that fish predation on invertebrates limits the grazing pressure of invertebrates, allowing modern stromatolite formation and growth. Two sizes of mesh cages (1mm and 6.35mm) were used to selectively limit fish access to stromatolites. The smallest mesh excluded all fish (the large, polymorphic cichlid *Herichthys minckleyi*; and the small pupfish, *Cyprinodon bifaciatus*) and the larger mesh excluded all fish except pupfish *C. bifaciatus*. Cages open on one side were used to determine cage effects. After six weeks of fish exclusion, no effects on invertebrate densities were detected. After three months, there was no effect on total invertebrate densities or biomass, but there were significant changes in specific taxa groups. Native Hydrobiid snails increased three-fold in the absence of total fish predation, while Ceratopogonids increased five-fold. Non-Metric Multi Dimensional Scaling ordination and Multi Response Permutation Procedure analysis of invertebrate assemblages also show differences in treatments that excluded all fish with cage controls. There was no change in algal biomass of the stromatolites, although there may be a shift in species composition. These results suggest that the fish assemblages, especially, *C. bifaciatus,* structure the invertebrate assemblages, and may be factors in determining algal communities as well.

Introduction

The decline of stromatolites (rock-like deposition of carbonates and sediments formed by algae [Lee 1999]) in the Middle Ordovician Period (roughly 570 million years ago) has been attributed to the evolution and diversification of metazoan grazers (Garrett 1970, Awramik 1971, Walter and Heys 1984). The hypothesis is that grazing by the metazoans, along with possible bioturbation, negatively affected both the algal assemblages and environmental conditions necessary for stromatolite formation and growth. Experimental work demonstrating that grazers can disrupt microbial mats support this hypothesis (Garrett 1970), but the hypothesis is principally based on the historical link between metazoan diversification and stromatolite decline, along with observations that most modern stromatolites occur in "extreme" environments which limit metazoan diversity and abundance (see Table 1 for summary of current inland stromatolite locations).

With the discovery of stromatolites in "non-extreme" environments that also harbor diverse metazoans, alternative hypotheses have been posed to explain the decline of stromatolites such as changing sedimentological conditions (Pratt 1982), changes in carbonate saturation in seawater (Grotzinger 1990), while Burne and Moore (1994) hypothesized that competition for space with other algal forms contributed as well. These hypotheses are not easily tested and overlook other possible explanations for the current co-occurrence of stromatolites and metazoans, such as complex trophic interactions and food web theory.

Application of food web theory may increase understanding of the interactions of vertebrates, invertebrates and stromatolites. Food web theory predicts that in a two

Table 1. Locations of modern inland water stromatolites. * indicates no mention of fauna in text of reference. Note that most localities are not "extreme", but generally lack data on fauna found in association with stromatolites.

Location	Country	Extreme?	Why Extreme	Invertebrates Present?	Vertebrates Present?	Remarks	Reference
Arbuckle Mountains, Oklahoma	USA	No		*	*		Chafetz et al1991
Cuatro Ciénegas	Mexico	No		Yes	Yes		Winsborough 1990
Lake Clifton	Australia	No		Yes	Yes	Marine salinities	Moore and Burne 1994
Lake Constance	Switzerland	No		*	*		Schafer and Stapf 1978
Little Conestoga Creek, Pennsylvania	USA	No		*	*	Formation of $CaCO^3$ ended in 1969 (Acid Pollution)	Golubic and Fisher 1975
Pieniny Mountains	Poland	No		*	*	Steep Spring Seep	Szulc and Smyk 1994
Shark Bay	Australia	Yes	Hypersaline	No	No		
Victoria Land	Antartica	Yes	Cold/Limited Light	*	*	Permanent Ice Cover	Wharton 1994
Yellowstone, Montana	USA	Yes	Thermal	No	No		Brock 1976

trophic level system, top-down effects of herbivory will more strongly limit primary production and algal growth than resources (Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981), whereas resources limit primary production in a three level system, since herbivory is controlled by predation from top trophic levels. Recent food web studies have showed this to be a simplified view, with complex trophic interactions and resource limitation being important components, but this is still a useful framework for investigations (Polis and Winemiller 1996). Studies have demonstrated that predators and herbivores can affect the abundance and diversity of lower trophic levels in a variety of aquatic habitats (Power et al. 1985, 1988, Threlkeld 1988, Power 1990, Martin et al. 1992, Rosemond et al. 1993, Brönmark 1994, Wootton 1995), but no studies have yet addressed trophic interactions of vertebrates, invertebrates and stromatolites.

The stromatolites of Cuatro Ciénegas, in the Chihuahuan Desert, provide an opportunity for testing the interactions between higher trophic levels and stromatolite formation and growth. Aquatic habitats of Cuatro Ciénegas support diverse but low densities of metazoan assemblages, particularly snails and insect larvae (Winsborough 1990, Dinger and Marks, in prep), whereas the fish diversity as well as abundances are high (Minckley 1984). This suggests that fish control invertebrate densities, limiting their effects on stromatolites, allowing for modern stromatolite formation (See Fig. 1 for hypothesized food web).

In this study, I examined the direct and indirect effects of fish removal upon invertebrates and stromatolitic algal biomass. I predicted that fish removal would positively increase invertebrate densities, resulting in a trophic cascade that reduces algal biomass, hindering stromatolite growth.

Methods

Study site

The study was conducted in Rio Mesquites, directly below the outflow of Poza Mojarral Este (lat 26°55’N, long 102°07’W) located in the Protected Area of Cuatro

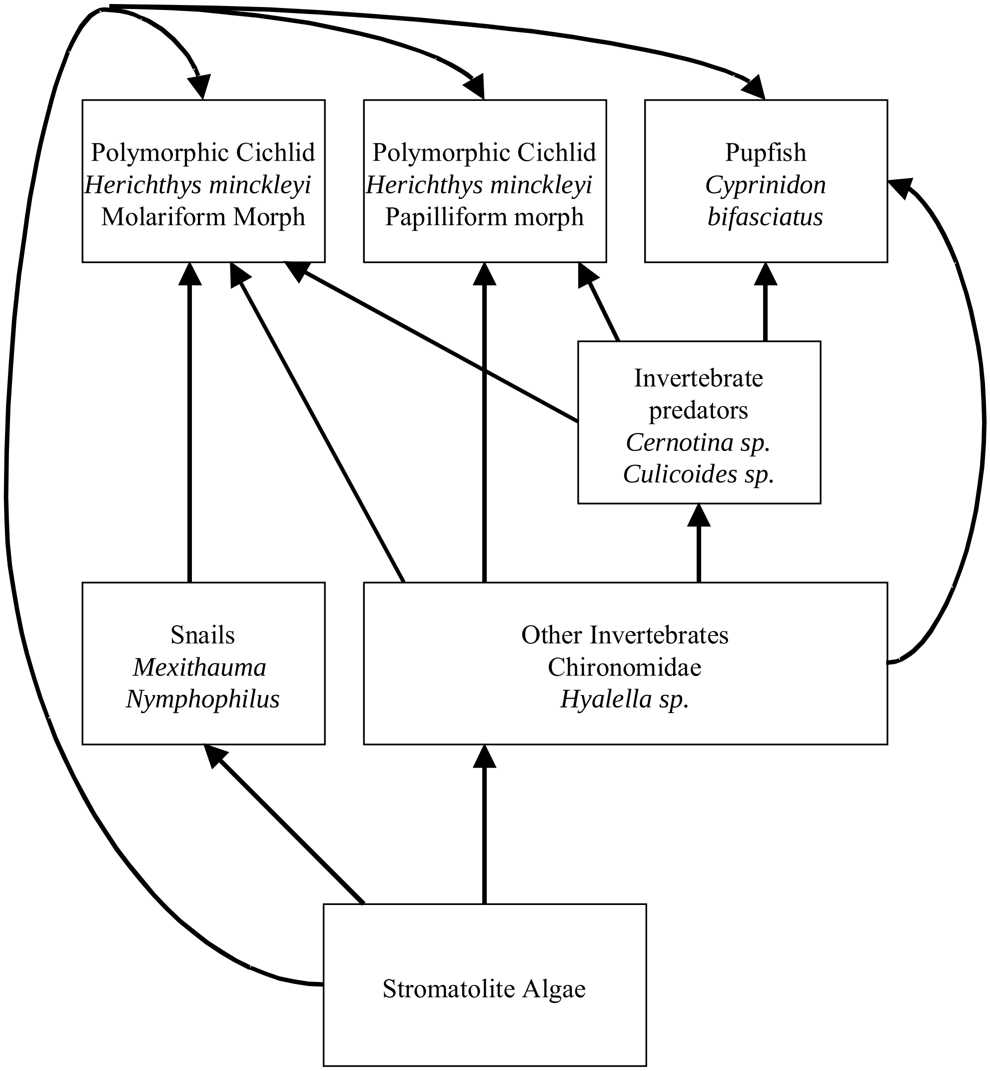

Figure 1. Hypothesized food web of Mojarral Este outflow based on personal observations and published diet studies (Smith 1982, Winsborough 1990).

Ciénegas, Coahuila, México. The basin of Cuatro Ciénegas was declared a protected area in 1994, prior to which it was used for horse grazing and fishing. Although areas of the basin are still used for livestock grazing and agriculture, Poza Mojarral Este is located in a protected visitors center monitored daily by park staff.

The arid climate of the Chihuahuan Desert is characterized by hot summers with air temperatures exceeding 44°C, while winter air temperatures can drop below 0°C (Minckley 1969). The annual rainfall of the basin is below 200mm, and is one of the driest areas of the Chihuahuan Desert (Shreve 1944).

The ions in the spring-fed water of the outflow are dominated by Ca^{2+} and SO_4^{2-}. Summertime diel changes in water temperatures range from 29°C to 32°C with dissolved oxygen values ranging from 3.5 mg/l to 6.2 mg/l. The pH ranges from 7.3 in the early morning to 7.5 in the afternoon.

The width of the outflow in the 45 m long study reach ranged from 10 to 15 m and depths ranged from 50 to 80 cm. The riparian vegetation of this reach is dominated by species of *Eleocharis*, (*E. cellulosa, E. rostellata* and *E. caribaea* [Pinkava 1974, 1984]). Flocculent sediments and *Nymphae ampla* dominate the substrate, with *N. ampla* on the edges of the channel.

High densities of oncoid stromatolites (5.8 ± 0.76 per m^2), shaped like oblong spheres with diameters ranging from 2-30 cm are found in the middle of the channel. These stromatolites of Cuatro Ciénegas are laminated, benthic, microbial carbonate deposits caused by biological activity, where the microbial components incorporate carbonate into their extracellular material. There are several different morphologies of stromatolites found within the basin, but this study used oncoid stromatolites for ease of manipulation. These stromatolites have identical morphologies and floral and faunal assemblages as the larger stromatolites in other portions of the Rio Mesquites, but are smaller and unattached (Winsborough 1990). The average diameter of stromatolites used in the experiment was 15 cm (± 0.192 SE, n=30). Algal components of the stromatolites are dominated by the green alga, *Gongrosira calcifera* Krieger, *Cyanostylon microcystoides* ; the Cyanobacteria *Homeothrix balearica* Bornet and Flahault, *Schizothrix lacustris* A. Brown; and the diatoms *Eunotia sp., Amphora katii* Selva, *Epithemia argus* Kütz, and *Gomphonema intricatum* Ehr. (Winsborough 1990).

Although 18 species of fish are found throughout Cuatro Ciénegas (Minckley 1984), only a few are found in association with oncoid stromatolites at this site. The most prevalent fish associated with stromatolites are the polymorphic cichlid *Herichthys minckleyi* and the pupfish *Cyprinidon bifaciatus*. *H. minckleyi* has two dominant morphologies in Cuatro Ciénegas, both of which occur in the study reach. One, with molariform phyrangeal dentition, can readily eat the native snails; the other, with papilliform dentition; primarily consumes algae, detritus and soft body invertebrates (Sage and Selander 1975, Smith 1982). Both *H. minckleyi* and *C. bifaciatus* have been observed "pecking" directly upon the stromatolites, as well as using the stromatolites as refuge and habitat (Winsborough 1990, Dinger pers. observation). Adult *H. minckleyi* range from 54 to 183 mm standard length (SL), whereas *C. bifaciatus* are much smaller and range from 12 to 30 mm (SL) (Hendrickson et al., unpublished data). Other fish in the study reach include the large mouth bass, *Micropterus salmoides*, the mosquito fish

Gambusia marshi, and *Cyprinella xanthicara*, but these lower density species have not been observed directly interacting with stromatolites.

Experimental design

The study was conducted from 20 June to 19 September 2000 in 20 caged exclosures (50cm X 50cm) constructed of PVC pipe framing with either Vexar mesh (6.35mm) or fiberglass hardware mesh (1mm) enclosing the sides and bottoms. We used four experimental treatments: large fish exclosure (to exclude *H. minckleyi*); total fish exclosures (to exclude *H. minckleyi* and pupfish); and cage controls for both fish exclosures. Vexar mesh excluded larger fish (primarily *H. minckleyi*), and hardware mesh excluded all fish (except for larvae and very small juveniles), including pupfish (*C. bifaciatus*). Cage controls, identical to full exclosures but open on one side, allowed access to all fish and were used to assess cage effects. Five replicates of each treatment were randomly assigned to plots throughout the river. Cages were stocked with two oncoid stromatolites (mean diameter of 15cm) haphazardly picked from the channel stromatolites bed.

The cages were kept clean of detritus and algal growth by scrubbing with a nylon brush approximately every 2 d. Observations of fishes showed no reaction to the cleaning procedure, and fish assemblages in open cages were similar to ambient conditions.

Experimental Harvest and Laboratory Analyses

Collection. —One random stromatolite from each cage was destructively sampled on 27 July 2000 (6 wk) and again at a final harvest on 19 September 2000 (3 mo). After removal, stromatolites were digitally photographed to estimate length and width (Adobe

Photoshop version 5.5), while height was measured in the field with a ruler. The average diameter for each stromatolite was calculated and used in the geometric formula for a sphere to estimate surface area.

Algal Biomass. --A 10.16cm^2 block was cut from the upper surface of each stromatolite and preserved in 10% formaldehyde. The sample was used to determine ash-free dry mass using standard methods (Greenberg et al. 1992). Samples were dried at 60˚C to constant mass (about 48 hours), weighed and then ashed for one hour at 500˚C and reweighed to the nearest 0.1 mg.

Invertebrate Assemblages and Biomass. -- Stromatolite invertebrates were collected by disaggregating each stromatolite into a five gallon bucket of water. Lighter sediments and most invertebrates were elutriated five times into a different bucket. Larger portions of the disaggregated stromatolite were visually inspected for remaining invertebrates, particularly snails. Although most snails were collected in the initial elutriations, extra care was spent to make sure that all heavier snails were collected. The elutriate was then filtered through a 253µm mesh net and preserved in 95% ethanol for laboratory sorting.

Macroinvertebrates were sorted under 8X magnification using a dissecting microscope. Specimens were identified to the lowest possible taxonomic level (usually generic level) using keys for North American invertebrates (Needham and Westfall 1954, Pennak 1989, Thorp and Covich 1991, Merritt and Cummins 1995, Westfall and May 1996, Wiggins 1996). Subsamples of macroinvertebrates (n = 5-10 for different taxa) were used to determine average biomasses for common taxonomic groups.

Statistical Analyses. —*Independent one-tailed t-tests were used to test for differences in invertebrate densities and algal biomass between fish exclosures and their respective controls (e.g. large fish exclosure and 3 sided control). One-tailed tests were based on the* apriori *hypothesis that invertebrate densities would increase in the absence of fish. Only invertebrates that were present in more than half of the treatments were analyzed.*

Differences in taxonomic composition among treatments were calculated using Sorenson (Bray-Curtis) distance measures, which is more robust for the analysis of taxonomic data (Faith et al. 1987, McCune and Mefford 1999). Prior to computing dissimilarities, abundance values for each taxon were standardized to the maximum obtained for each taxon. This standardization equalizes the potential contributions of taxa to the overall dissimilarity, so that distance measures are not dominated by highly abundant taxa.

In order to test for the significance of the treatments on the taxonomic composition, Sorenson distance measures were analyzed with Multiple Response Permutation Procedure (MRPP). This is a non-parametric procedure to test for the difference between *a priori* groups. MRPP has the advantage over discriminate analysis of not requiring assumptions about normality or homogeneity of the community data. In this test, the statistic A is a measure of effect size, where $A = 1$ indicates that samples within a group are identical but different from other groups, and an $A = 0$ indicates that samples are heterogeneous between the groups. In other words, an A near 1 indicates strong grouping, while an A near 0 indicates weak grouping. If significant grouping occurred, MRPP was used in pairwise comparisons to determine which groups were significant and which were not.

Non-metric multidimensional scaling (NMDS ordination) was used to graphically represent the invertebrate assemblage relationship. NMDS was used because it does the best possible job of maintaining the relationship between samples in low-dimensional pictures (Clarke 1993). The minimum stress in each dimension was examined and determined that a three-dimensional plot provided an adequate summary of the pattern of dissimilarities. Species averages of the eight dominant invertebrates were plotted simultaneously in the ordination space using weighted averages to determine their influence in the ordination. Significances of species averages in determining grouping were tested using indicator species analysis.

Results

Invertebrate densities.—Experimental stromatolites provided habitat for 17 different taxa of invertebrates. Commonly occurring invertebrate taxa include midges (Chironomidae), amphipods (*Hyalella sp.*), caddisflies (*Cernotina sp.*), biting midges (Ceratopogonidae), mayflies (*Caenis sp.*) and the hydrobiidae snails, *Mexithauma quadripallium* and *Nymphophilus minckleyi* (Table 2).

Other less dominant taxa include riffle beetles (Coleoptera:Elmidae), *Dorocordulia sp., Macromia caderita* (Anisoptera: Corduliidae) and *Argia sp.* (Zygoptera:Coenagrionidae). Rare taxa include *Hexatoma* (Diptera:Tipulidae), *Mexipygrus carranzae* (Gastropoda:Hydrobiidae), *Dugesia sp.* (Turbellaria), ostracods, oligochaetes, and water mites (Acarina). Many of these were more commonly associated

Table 2. P- values for one way t-tests for differences between treatments and cage controls after the 6 week sampling point and at final harvest after 3 months. * = significant at 0.05 significance level. df = 8 for all tests. - = no data.

	6 weeks		3 months	
Taxonomic Group	Large Fish Exclosure	Total Fish Exclosure	Large Fish Exclosure	Total Fish Exclosure
Caenis sp.	0.179	0.233	0.393	0.456
Cernotina sp.	0.839	0.452	0.907	0.043*
Chironomidae	0.913	0.267	0.986	0.162
Culicoides sp.	0.090	0.117	0.117	0.001*
Hyalella sp.	0.633	0.428	0.970	0.225
Hydrobiidae	0.184	0.559	0.069	0.046*
Total Invert Density	0.769	0.744	0.702	0.215
Total Invert Biomass	-	-	0.201	0.190

with the surrounding sediments, but were occasionally found on stromatolites (Dinger, pers. observation).

At the six-week midpoint harvest, exclusion of fish did not significantly affect either total stromatolite invertebrate densities, or densities of any specific taxonomic group (i.e. snails, amphipods, etc.) (Table 2, Fig. 2). After three months, there was no significant effect of fish exclusion on total invertebrate densities (Fig. 2) or on total invertebrate biomass (Fig. 2), although the trend was for the highest total biomasses to be in treatments that excluded all fish.

While the hypothesis that fish exclusion would increase total invertebrate density was rejected, there were strong, significant effects on specific groups. Snail density (*M. quadripallium* and *N. minckleyi*) tripled in the absence of the large, endemic cichlid, *H.*

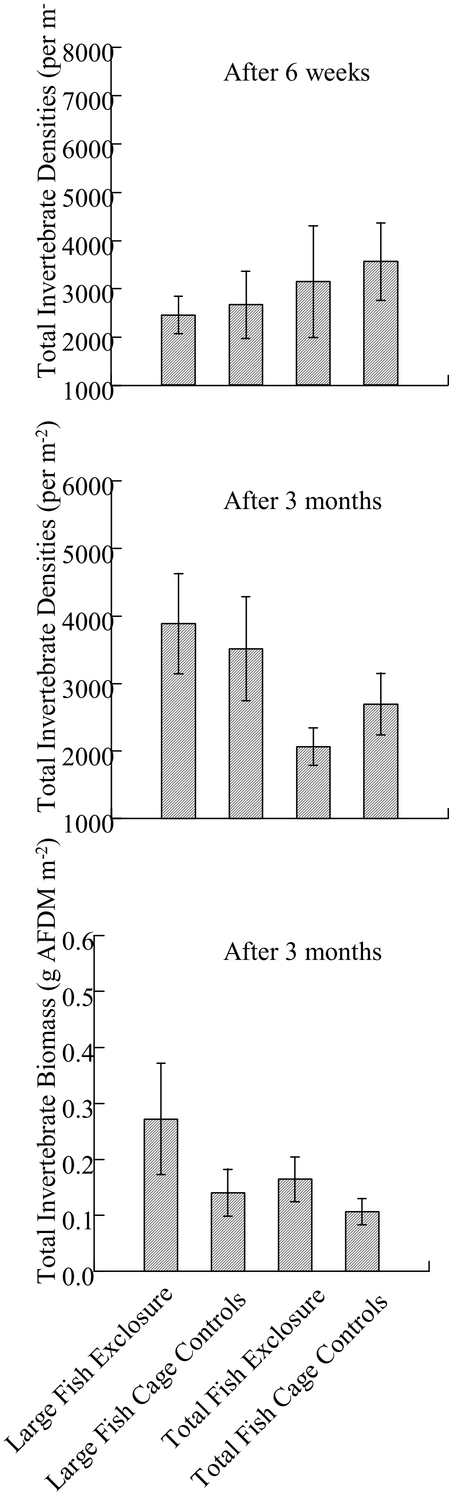

Figure 2. Mean densities and biomass of all invertebrates on stromatolites from six weeks (27 July 2000); densities only – top, and three months (19 September 2000); densities – middle; biomass – bottom. Bars = ± SE.

minckleyi, when compared to its three-sided cage control (Fig. 3). Snail densities were also higher in total fish exclosures relative to controls but were lower than when only large fish were excluded (Fig. 3). Densities of biting midges, *Culicoides sp.* and *Bezzia sp.* (Diptera: Ceratapogonidae) increased five fold in the absence of all fish predation (Fig. 3) compared to the cage control. Concurrent with the increase of ceratopogonids in the absence of fish predation was a significant decrease in the density of the predatory caddisfly, *Cernotina sp.* (Fig. 3). The two most numerically dominant taxa, (*Hyalella sp.* and Chironomidae) did not respond to experimental treatments (Table 2).

Invertebrate assemblage and biomass.—The MRPP analysis showed significant differences in taxonomic composition among the treatments ($A = 0.066$, $p = 0.015$). The differences in taxonomic composition are demonstrated in the NMDS ordination (Fig 4).

Pairwise analysis using MRPP shows that the significant grouping is found in between total fish exclusions and total fish cage controls, showing a significant change in invertebrate assemblages due to total fish exclusion (Table 3). There were also significant differences between the exclusion of all fish and exclusion of large fish. There were no significant differences between large fish exclusion and large fish cage controls. Species averages plotted on the NMDS ordination indicate that the grouping of total fish exclosures are a result of *Bezzia sp.* and *Culicoides sp.*, both ceratopogonids. Snails (*Mexithauma* and *Nymphophilus*) also appear important components of both total fish exclosures and large fish exclosures confirming t-test analyses of these species. Indicator species analysis, however, only resulted in only *Culicoides sp.* being a significant indicator of total fish exclosure (%perfect indication = 61, $p = 0.0008$).

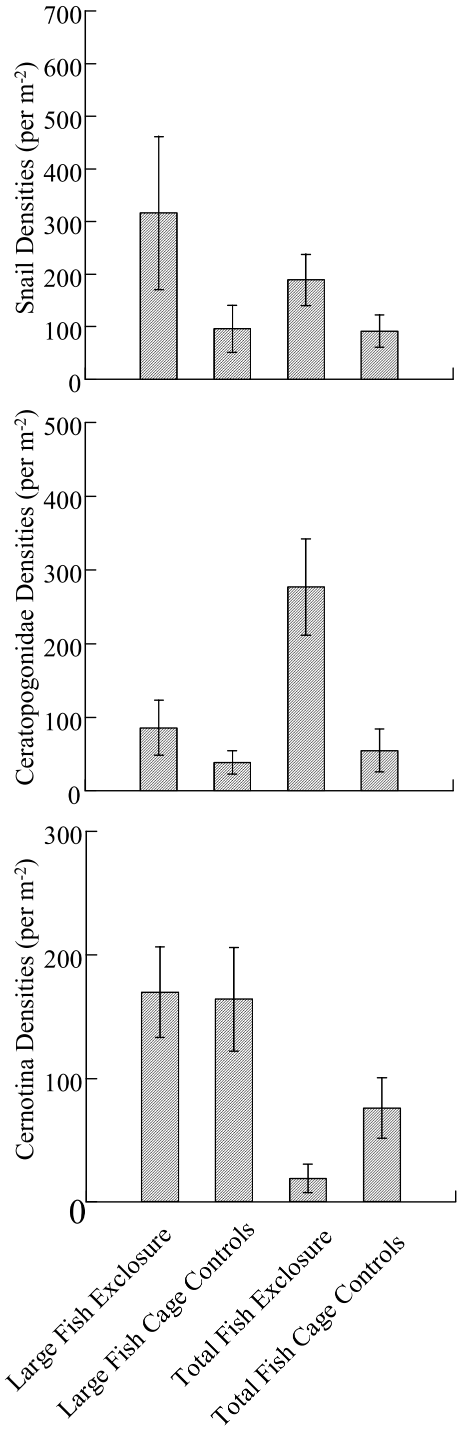

Figure 3. Mean densities of snails (top), ceratopogonids (middle) and *Cernotina sp.* (bottom) on stromatolites harvested after three months (19 September 2000). Bars = ± SE.

Table 3. Results of MRPP pairwise comparisons testing for significant differences between the groups of treatments.

Treatments Compared	*A* Statistic	*p* value
Large Fish Exclosure/Large Fish Cage Controls	-0.035	0.87
Total Fish Exclosure/Total Fish Cage Controls	0.128	0.001
Large Fish Exclosure/Total Fish Exclosure	0.052	0.05

Furthermore, changes in invertebrate assemblages were reflected in changes in percent relative biomass of species across treatments (Fig 5). The biomass is only for the eight most prevalent species, but the species not included are a very small fraction of the total. The relative biomass of snails (*M. quadripallium* and *N. minckleyi*) on ambient stromatolites and cage controls are approximately 40% but increase to 70.3% in the absence of *H. minckleyi* and 76.9% in the absence of all fish. In contrast, the relative biomass of Chironomids and amphipods (*Hyalella sp.*) decreased in the absence of fish predation.

Algal biomass.—Fish exclosure did not alter algal biomass after three months (Fig. 6). One-way t-test analysis on the effect of removing large fish was nonsignificant ($p = 0.763$). T-test on the effect of removing all fish was also nonsignificant ($p = 0.867$). Macroscopic examination of stromatolite surfaces indicates a possible shift in species assemblage.

Discussion

I did not observe the predicted trophic cascade in which fish removal increased invertebrates and decreased algal biomass, but I did, however, observe changes in species composition of invertebrates.

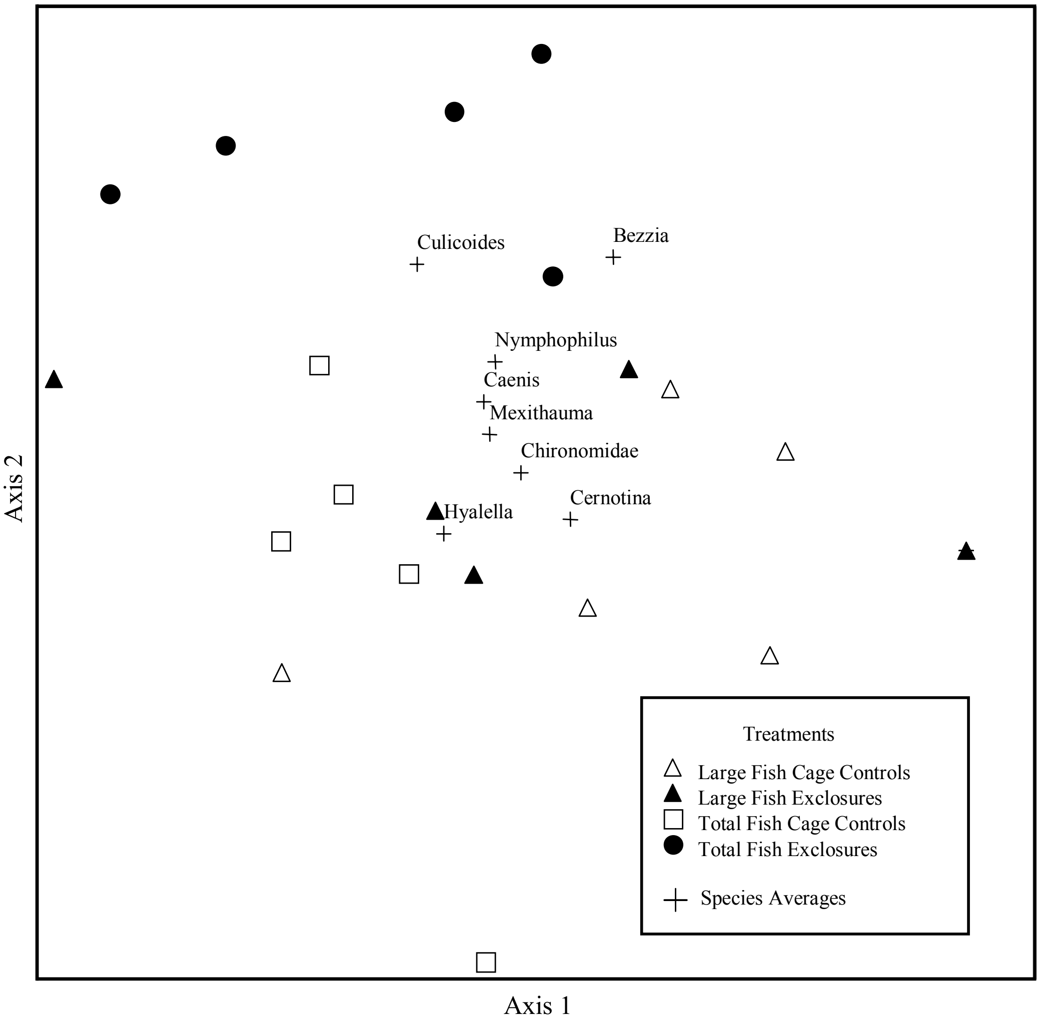

Figure 4. Non-Metric Multidimensional Scaling Ordination (NMDS) of invertebrate assemblage averages from stromatolites after three months (19 September 2000). Axes 1 and 2 provided the best representation of the ordination.

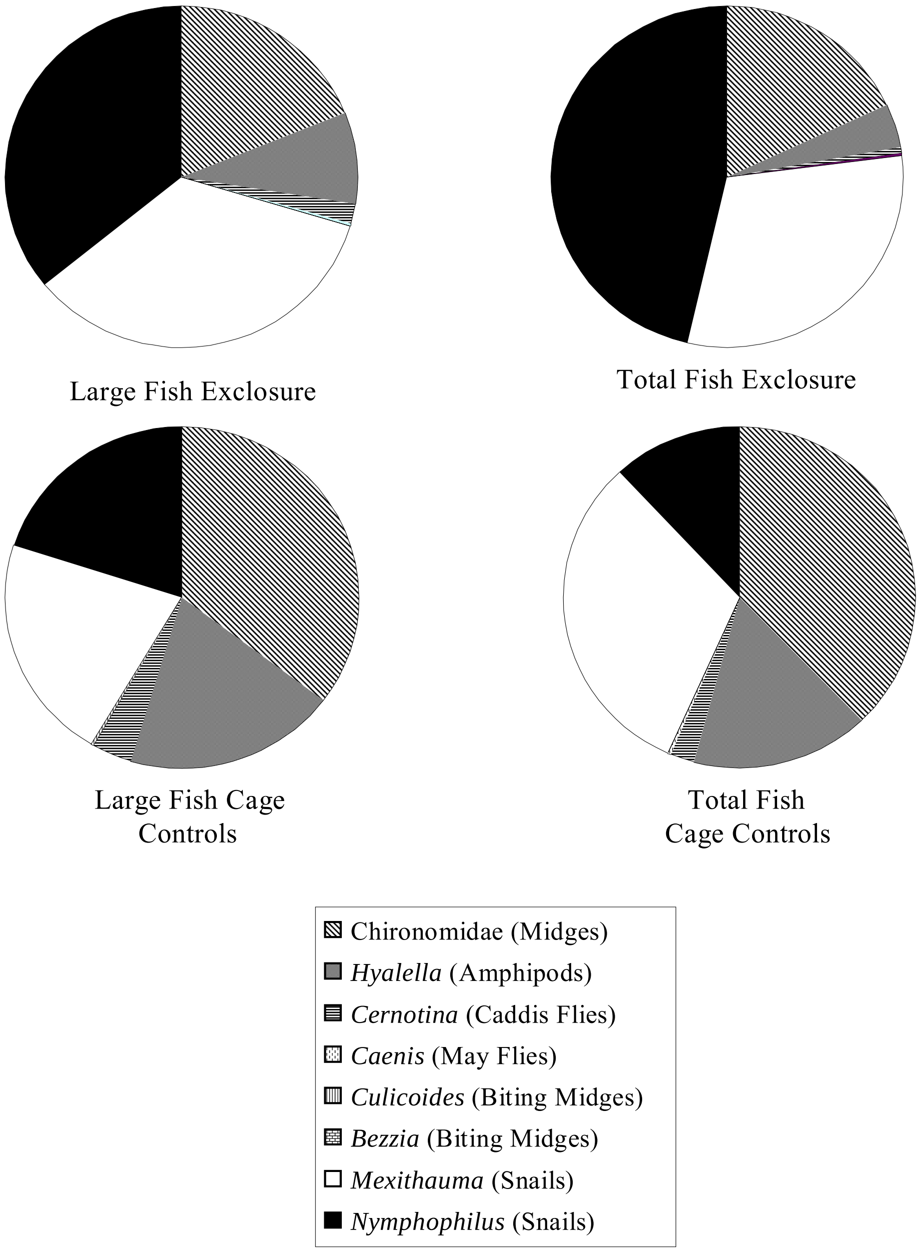

Figure 5. Mean relative biomass of invertebrates across experimental treatments after three months (19 September 2000). Note that only the eight most prominent invertebrates are included (see Table 4) since there were not enough specimens for all invertebrate taxa. These taxa represent over 97% of the relative abundance, and over 99% of the total biomass.

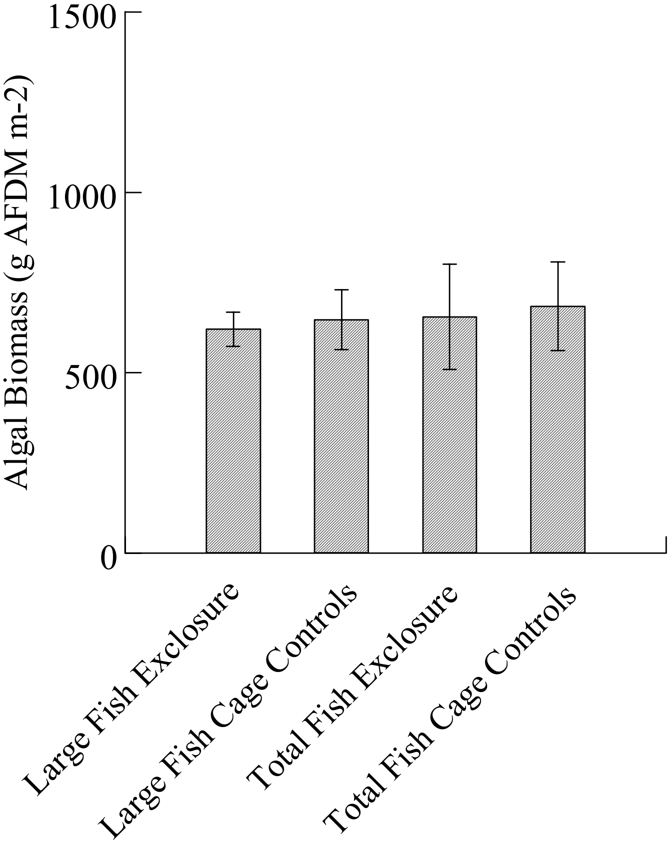

Figure 6. Algal biomass on stromatolites after three months (19 September 2000). One tailed t-tests indicates no significant differences among treatments and cage controls.

General trophic models would predict that fish removal would increase invertebrate biomass and decrease algal biomass (Hairston et al. 1960, Fretwell 1977) but experimental manipulations have had mixed results. Evidence from many freshwater systems support the trophic cascade model in fish-zooplankton-phytoplankton food webs although the strength of the response on algal biomass has varied from "strong" to "weak" (see Brett and Goldman [1996] for meta-analysis). Similarly, in stream ecosystems top predators have been shown to have strong effects in some systems, but little to no effects in others. Fish effects depend on a variety of other factors, especially when the food web linkages are between pelagic fish and benthic invertebrates and algae. For instance, Marks et al. (2000) demonstrated that the importance of fish predation is dependent on functional food chain length, which is affected by disturbance (flooding) but also that fish effects on herbivores are influenced by specific herbivore habits (i.e. highly mobile grazers versus restricted mobility grazers). Fish predation effects are also dependent upon the behavior of grazers, which can change in the presence or absence of predation (McIntosh and Townsend 1996).

Effects on Invertebrates

The exclusion of fish did not increase invertebrate densities as predicted, in part because the two most numerically dominant invertebrates (Chironomidae and *Hyalella sp.*) did not respond to experimental treatments, although fish diet data does reveal that they are a significant food item for *H. minckleyi* (Smith 1982, Hulsey pers. communication). The lack of an effect on these may be due to their specific habitats and availability of natural refuges. *Hyalella sp.* tend to congregate in the lithified crevices that are formed on the uneven surfaces of the stromatolites, which may provide an excellent refuge from fish predation. The Chironomids, additionally, form silken tubes that are enmeshed within the algal matrix of the stromatolite surface which also may provide a refuge from predation. Other studies of invertebrates with a source of refuge have also shown no fish effects (Marks et al. 2000). With these natural sources of refuge, fish predation upon these taxa may be minimal even with normally occurring high densities of fish.

Fish altered other invertebrate species, but the effect depended upon which fish species was excluded. In treatments that removed the large *H. minckleyi*, the density of the snail fauna increased, but the magnitude and significance depended also upon the presence or absence of the smaller pupfish, *C. bifaciatus*. When *C. bifaciatus* were excluded along with *H. minckleyi*, the snail density only doubled as opposed to the tripling observed when only *H. minckleyi* was excluded. Increases in snail densities with the exclusion of large *H. minckleyi* can be attributed to release from predation pressures of the molariform phenotype of *H. minckleyi,* which eats *Mexithauma*, and to a lesser degree *Nymphophilus* (Smith 1982, Hulsey, pers. comm.). The reduced increases in snail densities with the additional removal of pupfish may be due to negative interactions between snails and other invertebrates that are released from predation with the removal of pupfish. For example, our data show a five-fold increase in the biting midge, *Culicoides sp.* in pupfish exclosures. Larvae of *Culicoides* are predators and could possibly be preying either upon snail eggs, or on the snails directly. Hence, the reduced response of snail densities in the absence of all fish could be a balance between the positive effects of being released from fish predation and negative effects of increases in other invertebrates due to increased predation or competition.

An alternative hypothesis for the reduced response of snails in the absence of all fish is a potential cage effect. These treatments used a 1mm mesh size, which could reduce outside colonization of larger invertebrates, whereas the larger mesh size (6.35mm) would allow continual upward colonization through sediments, along with lateral sources of immigration. The response of snails in the absence of all fish would then represent increased reproductive success of snails in the absence of fish interference, but without immigration.

Although fish did not affect invertebrate biomass they did change invertebrate species assemblages, which may be responsible for changing the species composition of algae One of the most important of these changes may be the increase in snail densities. Although snails are a numerically small component of the invertebrate assemblage on the stromatolites (2.6% on ambient stromatolites) their importance is highlighted by their relative biomass (40.2% on ambient stromatolites). The grazing pressure of snails on stromatolites is possibly an important component in structuring the algal assemblages of oncoid stromatolites.

The lack of any effect upon any specific taxon at the six week harvest of my experiment, as well as significant effects by the end of the three month period suggest that a longer experiment may result in larger differences between treatments.

Effects on Algae

The exclusion of fish did not result in any effect on algal biomass. The lack of a detectable trophic cascade in my experiment may be the result of several factors.

First, the growth of oncoid stromatolites is slow (2-3mm of growth per year [Winsborough 1990]). Other food web manipulations of predator densities in streams have shown trophic cascades within three weeks to three months (Power et al. 1988, Threlkeld 1988, Power 1990, Marks et al. 2000). Given the slow growth of stromatolites, detecting changes in algal biomass may require longer-term experiments.

Second, both species of fish (*H. minckleyi* and *C. bifaciatus*) will "peck" at the outer layers of algae. Although the fish may be searching for invertebrates within the algal matrix, they may also be directly consuming the algae. Hence, while the removal of fish may increase grazing pressure of invertebrates, this may be offset by reduced fish herbivory on the algae. In prior studies where the top consumers are omnivorous, trophic cascades have not been observed (Pringle and Hamazaki 1998, Usio 2000). While the extent of omnivory in both pupfish and the cichlids on stromatolites is not known, dietary studies of *H. minckleyi* have revealed a wide range of stomach contents including algae, calcite, snails, and other invertebrates (Smith 1982, Hulsey unpublished data). The simultaneous direct and indirect effects of fish on intermediate consumers and primary producers may decouple a trophic cascade.

Third, stromatolite algal growth may be primarily controlled by resources alongside top-down predation. Cuatro Ciénegas is limited in nutrients, such as PO_4, with ranges below detection limits (below 0.05 µg/l) (Marks et al. in press). Previous food web studies have shown that trophic levels are simultaneously controlled by both top-down and bottom-up effects (Power 1992, Rosemond et al. 1993, Forrester et al. 1999, Marks et al. 2001). Hence, the relative strength of bottom-up limitation may be stronger on the algae than the top-down herbivory.

Lastly, the species composition of the algal matrix of the stromatolite may be shifting. Macroscopic visual observation shows that the color and texture of the stromatolites differed depending on the treatments. In treatments that excluded fish, the algae is dull gray-green, slimy, and mucilaginous. In contrast, the stromatolites in ambient conditions are an olive-green and lack any mucilaginous texture.

Implications for Stromatolite Assemblages

Although the data for a shift in algal species composition is preliminary, it warrants future research. Because stromatolite morphology and growth depend on specific types of algae that can incorporate calcium carbonate into their structure, any shift in algal species may pose a potential threat to stromatolites. If grazing pressures shift the stromatolite algal composition to other growth forms that are grazer resistant, but are not conducive to the precipitation and binding of calcite, modern stromatolite growth would stop and become substrate for conventional algal growth. The possible fragility of stromatolite formation is highlighted by previously recorded cessation of stromatolite formation in Little Conestoga Creek, Pennsylvania (Golubić and Fisher 1975). A shift in the pH due to acid pollution halted the deposition of calcium carbonate, and formation of stromatolites stopped. Just as stromatolites depend on certain chemical conditions, they may also be dependent on the entire floral and faunal communities in their ecosystem.

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Appendix A. Aquatic invertebrates found in six different types of habitats. Numbers under habitat found refer to habitat where species was found. Keys to numbers are given in Table 2, Chapter 1. IRI = equals index of relative abundance. R = Rare, U = Uncommon, C = Common, A = Abundant

Order Family Genus species	Habitat Type Lentic Ciénega	 Laguna	 Playa	 Poza	 Lotic Canal	 River	IRI	Habitats found
Coleoptera								
Curclionidae								
nr. *Notiodes sp.*					X		R	
Dryopidae								
Helichus sp.				X		X	R	16
Dytiscidae								
nr. *Brachyvatus sp.*			X				U	
Cybister sp.		X				X	R	16,18
nr. *Hydrovatus sp.*		X		X		X	R	5,11,16
nr. *Rhantus sp.*		X					R	11
Elmidae								
Cylloepus sp.						X	U	16
Neoelmis sp.						X	R	16
nr. *Heterelmis sp.*					X	X	C	17
Hexacylloepus sp.					X	X	U	15,17
Macrelmis sp.						X	R	
Microcylloepus sp.				X		X	U	14,15,16
nr. *Neocylloepus sp.*						X	R	15
nr. *Oulimnius sp.*						X	R	15
Stenelmis sp.				X			R	14
Gyriinidae								
Gyretes sp.						X	U	15
Haliplidae								
Haliplus sp.		X	X				U	8,11
Heteroceridae								
Unknown						X	R	
Hydrochidae								
Hydrochus sp.			X				R	
Hydradenidae								
Octhebius sp.					X		R	
Hydrophilidae								
Berosus sp.		X	X		X	X	C	16

Appendix A continued.

Order Family Genus species	Habitat Type Lentic				Lotic			
	Ciénega	Laguna	Playa	Poza	Canal	River	IRI	Habitats found
Enochrus sp.		X				X	U	11,16
nr. *Helochares sp.*						X	U	16
nr. *Hydroporous sp.*		X					R	11
Laccobius sp.			X	X			C	5,8
Tropisternus sp.	X	X				X	U	6,9
Tropisternus lateralis		X			X		U	11
Lutrochidae								
Lutrochus sp.				X	X		A	5,17
Psephenidae								
Psephenus sp.				X		X	C	4,6,15
Diptera								
Ceratopogonidae								
Bezzia/Palpomyia					X	X	C	15,16,17
Probezzia sp.				X			U	2,14
Culicoides sp.					X	X	U	16,17
Chironomidae								
Various	X	X	X	X	X	X	A	All but 7
Culicidae								
Aedes sp.					X		C	
Dixidae								
Dixella sp.		X		X			R	5,6
Simuliidae								
Simulium sp.						X	A	3
Stratiomyidae								
Nemotelus sp.					X		R	
Stratiomys sp.				X	X	X	U	4,5,16
Tabanidae								
Chrysops sp.		X		X	X	X	R	4,15,18
nr. *Tabanus sp.*						X	R	
Tipulidae								
nr. *Hexatoma sp.*				X	X		R	13,17
Limonia sp.				X			R	

nr. *Limnophila sp.*						X	R	15

Appendix A continued .

Order Family Genus species	Habitat Type Lentic Ciénega	Laguna	Playa	Poza	Lotic Canal	River	IRI	Habitats found
Baetidae								
nr. *Acerpenna sp.*						X	R	15
Baetodes sp.						X	R	
Baetis sp.		X		X	X	X	C	2,3,5,6,14,15,16,17
Callibaetis sp.		X		X		X	C	4,5,6,15,16
Camelobaetidius sp.					X		U	17
Caenidae								
Caenis sp.	X	X	X	X		X	C	3,8,9,10,11,13,14,16
Ephemeridae								
Hexagenia sp.			X	X		X	A	14
Leptophebiidae								
Thraulodes sp.		X		X	X	X	U	5,6,11,14,15
Traverella sp.					X	X	U	17
Tricorythodidae								
Tricorythodes sp.	X		X	X	X	X	C	2,5,10,13,14,15,16,17
Leptohypes sp.						X	R	
Hemiptera								
Gerridae								
Metrobates sp.				X		X	U	14,15
nr. *Trepobates sp.*						X	R	16
Belostomatidae								
Abedus *nr.* vivicinussoronesis						X	U	
Belostoma sp.	X					X	U	10,16
Lethocerus sp.						X	R	16
Corixidae								
nr. *Trichocorixia sp.*	X						R	8,10
Gerridae								
nr. *Aquarius sp.*	X						R	9

Appendix A continued

Order Family Genus species	Habitat Type							
	Lentic				Lotic			
	Ciénega	Laguna	Playa	Poza	Canal	River	IRI	Habitats found
Hebridae								
Merragata nr. *hebroides*	X			X		X	U	4,9,16
Hydrometridae								
Hydrometra sp.						X	U	16
Mesoveliidae								
nr. *Mesovelia sp.*						X	R	16
Naucoridae								
Ambrysus nr. *californicus*	X	X		X	X	X	A	2,3,5,6,9,15,16,17
nr. *Cryphocricos sp.*					X		R	
nr. *Limnocoris sp.*						X	R	
Nepidae								
Ranatra sp.						X	R	
Veliidae								
Rhagovelia sp.						X	U	15
Lepidoptera								
Pyralidae								
Petrophila sp.		X		X		X	U	6,15,18
Megaloptera								
Corydalidae								
Corydalus sp.					X	X	U	13,17
Sialidae								
Sialis sp.			X			X	R	
Odonata								
Zygoptera								
Unknown				X	X	X	U	
Calopterygidae								
Hetaerina americana						X	U	15
Hetaerina titia						X	U	

Hetaerina nr. *occisa*	X	U	15

Appendix A continued

Order Family Genus species	Habitat Type Lentic Ciénega	 Laguna	 Playa	 Poza	 Lotic Canal	 River	IRI	Habitats found
Coenargrionidae								
Argia sp.						X	R	
Argia nr. *fumipennis*						X	R	16
Argia plana						X	R	
Argia pulla		X		X	X	X	A	3,4,5,11,14,16
Argia nahuana				X			R	4
Argia nr. *rhoadsi*				X			R	14
Argia nr. *sedula*						X	U	15
Argia nr. *tonto*			X				R	5
Argia translata		X		X		X	C	1,5,12,13,15
Enallagma sp.		X		X		X	C	1,5,11,14,15,16
Enallagma nr. *anna*				X			R	5
Enallagma basidens		X		X		X	C	2,4,5,6,14,16
Enallagma nr. *cyathigerum*		X		X		X	R	4,11
Enallagma nr. *dubium*				X	X		R	5,14
Enallagma nr. *durun*		X					R	11
Enallagma nr. *germinatum*				X			R	13
Hesperoagrion heterodoxum						X	R	16
Anisoptera								
Protoneuridae								
Nehallenia minuta				X			R	5
nr. *Protoneura sp.*						X	R	
Aeshnidae								
Anax nr. *junius*		X				X	R	11,15,16

Anax walsinghami		X				X	R	
Gomphidae								

Appendix A continued

Order Family Genus species	Habitat Type Lentic Ciénega	 Laguna	 Playa	 Poza	 Lotic Canal	 River	IRI	Habitats found
Erpetogomphus nr. *compositus*			X			X	C	15,16

Phyllogomphoides sp.			X	X		X	U	14,15
Progomphus borealis			X	X	X	X	U	5,14,16
Libellulidae								
nr. *Libellula quripennis*				X		X	R	
Pachydiplax nr. *longipennis*						X	R	16
Macomiinae								
Macromia nr. *caderita*	X	X	X	X		X	A	4,8,9,10,15,18
Orthoptera								
Acridadae								
Leptysma sp.						X	U	16
Trichoptera								
Helicopsychidae								
Helicopschye sp.					X		R	17
Hydrobiosidae								
Atopschye sp.						X	U	
Hydroptilidae								
Hydroptila sp.						X	U	15
Leucotrichia sp.						X	A	
Mayatrichia sp.						X	R	15
Metrichia sp.					X	X	C	16,17
Oxeytheira sp.		X				X	U	6,16
Hydropschydidae								
Leptonema sp.					X	X	C	17
Smicridea sp.					X	X	A	15,17
Leptoceridae								
Nectopschye sp.						X	U	15
nr. *Oecetis sp.*				X	X		R	17
Polycentropidae								

Appendix A continued

Order Family Genus species	Habitat Type Lentic				Lotic		IRI	Habitats found
	Ciénega	Laguna	Playa	Poza	Canal	River		
Cernotina sp.				X		X	U	4,15,16
Polyplectropus sp.					X	X	U	3,15,17

Amphipoda								
Taltridiae								
Hyalella sp. 1	X	X	X	X	X	X	A	All
Hyalella sp. 2		X				X	R	
Acarina								
Various								
Various	X	X	X	X	X	X	A	4,5,6,9,10,11,13,14, 15,16
Hirudinodiea								
Glossiphniidae								
Helobdella sp.						X	R	15,16
Helobdella nr. *fusca*						X	R	
Hirundinidae								
Unknown						X	R	15
Oligochaete								
Various								
Various	X	X	X	X	X	X	A	1,2,5,6,9,10,13,14, 15,16
Decapoda								
Palaemonidae								
Palaemonetes suttkusi	X	X	X	X	X	X	A	4,6,9,10,11,12,14, 15,16,18
Cambaridae								
Procambarus clarkii		X				X	U	16
Ostracoda								
Various								
Various	X	X	X	X		X	C	4,9,11,15,16,18
Gastropoda								
Physidae								
Physella sp.	X	X	X		X	X	U	10,11,15,16
Ancylidae								

Appendix A continued

Order Family Genus species	Habitat Type: Lentic				Habitat Type: Lotic		IRI	Habitats found
	Ciénega	Laguna	Playa	Poza	Canal	River		
nr. *Hebetancylus*				X		X	R	13,15

sp.						
Thiaridae						
Melanoides tuberculata		X		X	U	2,4
Turbellaria						
Dugesia sp.	X		X	X	C	1,3,4,6,11,12,13,15,16,17
Nematoda		X			U	
Isopoda		X			R	13