Interactions between Native and Nonnative Fishes of the Upper Muddy River, Nevada

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Abstract.—I investigated interactions between native and nonnative fishes in the upper Muddy River system to add insight into (1) the mechanism causing the decline of the Moapa dace *Moapa coriacea* after the introduction of the shortfin molly *Poecilia mexicana,* (2) the reason Moapa White River springfish *Crenichthys baileyi moapae* were less affected by the introduction, and (3) the reason interactions between natives is relatively benign. I investigated the hypothesis that the shortfin molly caused the decline of the Moapa dace through competition or predation on larvae, pressures not experienced by the Moapa White River springfish. Relative interspecific competition was analyzed by contrasting the ranges of spatial and dietary overlap among larval, juvenile, and adult life stages. There appeared to be moderate to low spatial overlap between the various life stages of native and nonnative fishes. Overlap in diet was highest between adult Moapa White River springfish and shortfin mollies. Laboratory experiments suggested that shortfin mollies prey vigorously upon fish larvae. In terms of spatial habitat use, Moapa White River springfish larvae were less available to adult shortfin mollies for consumption than were Moapa dace larvae. When predation on larvae is the mechanism by which nonnative fish reduce native forms, aggressiveness of the predator and the degree to which the predator overlaps in habitat with the prey may influence the degree to which a native fish population is affected.

The addition of nonnative fish species may greatly alter the structure of a native fish community (Moyle et al. 1986; Brown and Moyle 1991). Frequently, nonnative fishes replace or greatly diminish natives, and several western species are extinct or have experienced dramatic declines following the invasion of nonnative fishes (Miller et al. 1989; Moyle and Williams 1990). The mechanisms of these adverse interspecific interactions have received little attention (Moyle et al. 1986; Ross 1991).

After the upper Muddy River, Nevada, was invaded by nonnative fishes, the two native fishes, Moapa dace *Moapa coriacea* and Moapa White River springfish *Crenichthys baileyi moapae,* declined (Cross 1976). The Moapa dace declined sufficiently that it was federally listed as endangered (U.S. Department of the Interior 1973). The Moapa White River springfish also declined but less dramatically, and it is a candidate 2 species (being considered for listing as endangered or threatened; U.S. Fish and Wildlife Service 1991).

Both species are endemic to the headwaters of the Muddy River (also called the Moapa River), Clark County, Nevada, a tributary to the Colorado River system. The river originates from about 20 warm springs (31.0–32.0°C at their sources) having a combined discharge of 1.1 m^3/s (Eakin 1964). Water cools in a downstream direction. Moapa dace and Moapa White River springfish tween 26.0 and 32.0°C. They are hence relegated to the upper 2 km of the approximately 40-km river and to several small headwater tributaries (Deacon and Bradley 1972; Cross 1976; Scoppettone et al. 1992). The general area in which they occur is known as the Warm Springs area (Hubbs and Miller 1948; La Rivers 1962). Reproduction occurs year-round and is confined to the upper, spring-fed tributaries, typically within 150 m of the warmwater discharges (Scoppettone et al. 1992). In these areas, water temperatures vary between 29.0 and 32.2°C and dissolved oxygen concentrations vary between 4.1 and 6.2 mg/L, both seasonally and over 24-h periods; conductivity is about 964 μs/cm and pH is 7.5 (my unpublished data). Juveniles are found almost exclusively in the spring-fed tributaries, whereas adults are also found in the main stem (Scoppettone et al. 1992).

There is little published information pertaining to the life history of Moapa White River springfish. Other subspecies of *C. baileyi* are omnivorous and opportunistic in diet (Williams and Williams 1982) and withstand unusual extremes in temperature and dissolved oxygen (Sumner and Sargent 1940; Hubbs and Hettler 1964; Hubbs et al. 1967). White River springfish reproduce year-round, laying eggs 1.9 mm in diameter that are typically attached to aquatic vegetation (Kopec 1949; Espinosa 1968). Their daily activity patterns were studied by Deacon and Wilson (1967).

cur in the Warm Springs area but are represented by relatively few individuals. Moapa speckled dace *Rhinichthys osculus moapae* occur at the lower boundary of the Warm Springs site, and roundtail chub *Gila robusta* extend further into the area (Deacon and Bradley 1972; Cross 1976). Both are most abundant in the cooler, downstream reaches.

Two nonnative fishes, western mosquitofish *Gambusia affinis* and shortfin molly *Poecilia mexicana*, are established within the range of the Moapa dace and Moapa White River springfish. The western mosquitofish was already present when the Moapa dace was discovered in 1938 (Hubbs and Miller 1948), and it was the predominant species in the upper Muddy River in 1963 (Deacon and Bradley 1972). Western mosquitofish are omnivorous and formidable predators on fish larvae, sometimes replacing native fish populations (Minckley 1973; Meffe 1985). Early effects of western mosquitofish on Moapa dace are undocumented, but the dace population appeared to be stable in the early 1960s (Cross 1976). The shortfin molly, introduced in 1963 (Hubbs and Deacon 1964), was the most abundant species in the upper Muddy River in 1968 (Deacon and Bradley 1972). The Moapa dace population declined after shortfin mollies were introduced (Cross 1976). It is unlikely that the decline was caused by habitat degradation, because there had been no readily apparent physical changes in Moapa dace habitat (J. Deacon, University Nevada, personal communication). Shortfin molly and mosquitofish occur throughout the range of Moapa dace and Moapa White River springfish except for a 170-m stream reach at the south edge of the Warm Springs area and within the bounds of the Moapa National Wildlife Refuge. Little published life history information is available on the shortfin molly except that, like the western mosquitofish, it bears live young (Meffe and Snelson 1989).

In this paper I examine present niche overlap (habitat use and diet) of Moapa dace with both nonnative (shortfin molly and western mosquitofish) and native (Moapa White River springfish) species as a possible explanation for the observed decline of Moapa dace. Although overlap may suggest the potential for interspecific competition, lack of overlap may imply that it has not been an important factor—as long as that lack is not the result of intense competition that caused niche shifts (Werner and Hall 1979). I then explore the value of an overlap analysis under present conditions for identifying causes of species decline. I also conclude that shortfin mollies and western mosquitofish are more aggressive predators on fish larvae than are Moapa White River springfish and that such predation may have caused the decline of the Moapa dace population.

Methods

I define the origin of Muddy River as the confluence of South Fork Stream and Upper Muddy Stream, both of which are spring fed (Figure 1). Two other spring-fed tributaries (Muddy Spring and Refuge Stream) enter the Muddy River in the Warm Springs area, which at the time of study was largely agricultural. Several spring-fed tributaries served as irrigation ditches, some lined with concrete; up to 25% of the river flow was used for irrigation.

Established in 1979, the Moapa National Wildlife Refuge was a former swimming resort. Its spring discharge had been intermittently manipulated and chlorinated. Cumulative refuge spring flow was 0.09 m^3/s. Its primary stream channel was treated with a piscicide in 1984 to eliminate shortfin molly and western mosquitofish. Moapa dace and Moapa White River springfish were reintroduced in 1984, and they were isolated from nonnative fishes by a 75-cm-high waterfall.

Relative abundance.—I determined relative abundances of the various fishes in tributary streams where all life stages of Moapa dace and Moapa White River springfish were known to occur. Numbers of fish in these streams, used by Moapa dace for reproduction and rearing, had not previously been documented. Numbers of adult Moapa White River springfish, shortfin mollies, and western mosquitofish were calculated by mark–recapture methods, and adult Moapa dace were counted with the aid of mask and snorkel.

In summer 1984, I estimated relative abundance of adult Moapa White River springfish (>27 mm total length, TL), western mosquitofish (>20 mm TL), and shortfin mollies (>20 mm TL) in four tributaries: Refuge, Upper Apcar, Muddy Spring, and South Fork (Figure 1). Sampling occurred during 16–21 July in Upper Apcar, 18–22 July in South Fork, 23–25 July in Refuge, and 16–23 August in Muddy Spring. Estimates were made by isolating representative 10-m reaches with a 3-mm-mesh block net at each end. At least 10% of each stream's length was sampled. Fish within the reach were captured with minnow traps lined with 1-mm-mesh fiberglass screen; traps were fished overnight for 14–16 h. The upper tip of the caudal fin was clipped from each captured fish and

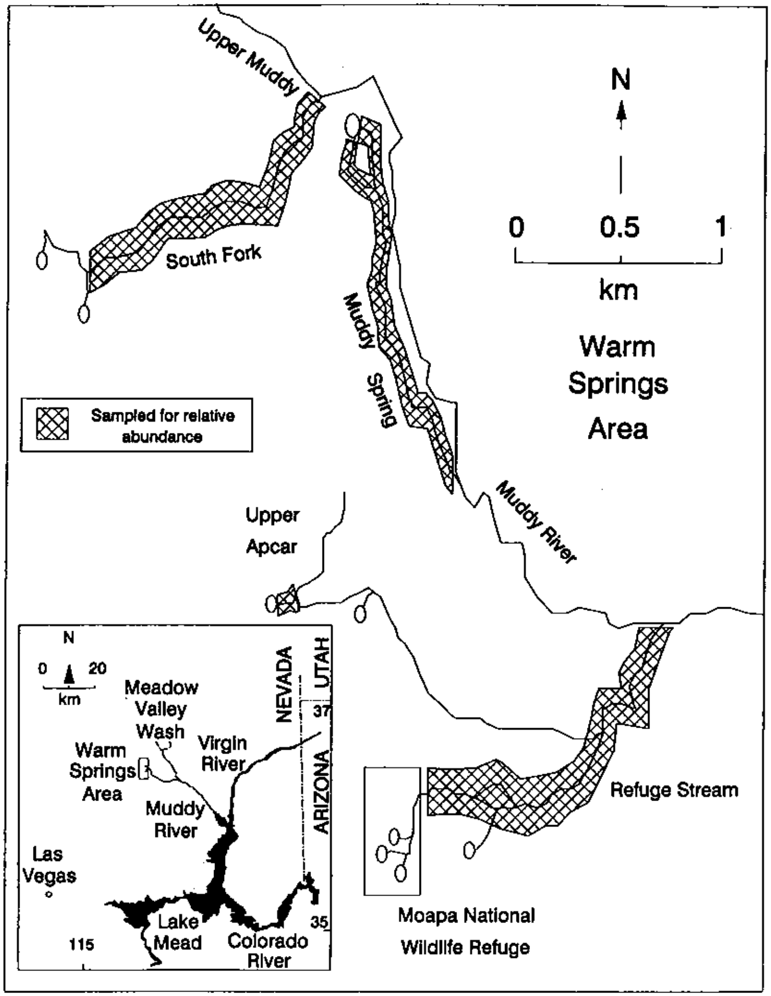

FIGURE 1.—Warm Springs, Nevada, area showing stream reaches sampled for relative abundances of adult Moapa dace, Moapa White River springfish, shortfin mollies, and western mosquitofish. Inset shows the relationship of the Muddy River and Warm Springs area to the Colorado River.

mate (Ricker 1975) was used to calculate population size from recaptures:

$$N = \frac{(M + 1)(C + 1)}{R + 1};$$

N is population number, M is the number of fish marked, C is the number of fish captured for census, and R is the number of fish recaptured.

Population estimates were made for each reach, and data were expanded to represent the entire nursery stream. At least 15% of each reach of each nursery stream was sampled.

Moapa dace did not trap reliably, so mark and recapture was unsuccessful. In December 1984, I counted adult Moapa dace with the aid of mask and snorkel. Adult fish (≥40 mm TL) were counted by snorkeling in an upstream direction. They were generally in open water and not so sensitive to my presence that they were difficult to count. As I moved upstream, displaced fish swam around and downstream from me, and were not counted twice.

Spatial overlap in microhabitat.—Spatial microhabitat use by Moapa dace and Moapa White River springfish larvae, juveniles, and adults was determined by quantifying position of the fish in the water column in terms of depth and water velocity. The same quantification was made for juvenile and adult shortfin mollies and western mosquitofish; larvae of these species were assumed to have developed internally. Substrata were sand and gravel in the main-stem upper Muddy River and primarily silt and sandy silt in tributaries. Substratum was a poor predictor of microhabitat use for adult fish, so it was not considered. Habitat use measurements were made intermittently from 1986 through 1987 and in the summer and fall of 1992. Moapa dace smaller than 15 mm TL were assumed to be larvae, and fish larger than 40 mm TL were considered adults, approximating Snyder's (1981) determination for speckled dace. Moapa White River springfish smaller than 14 mm TL were considered larvae, and those at least 27 mm, the smallest fish on which I observed spawning colors, were considered adults. Western mosquitofish and shortfin mollies were designated juveniles at sizes less than 20 mm TL and adults at sizes of 20 mm and greater.

Depth measurements included depth of the fish from the water surface (focal depth) and depth of stream at the position of the fish (total depth). Water column position (relative depth) was determined by dividing focal point depth by total depth, giving a range from 0 at the surface to 1 at the bottom. Velocity measurements were taken at or near the site where the fish was observed holding position in the water column (focal point velocity) and at 40% of the depth at the site (mean water column velocity). A Marsh-McBirney model 210[1] digital flow meter on a calibrated rod was used to measure depth and velocity.

Spatial overlap of species was calculated for adults, juveniles, and larvae; the variables used were mean velocity and position in the water column. Also used was whether the fish occurred in total water depths above or below 10 cm; this distinction helped segregate young fish from adults. These categories were selected because they best defined habitat differences between species and life stages. I followed Moyle and Vondracek (1985) and divided mean velocity into increments of 10 cm/s and relative depth into increments of 0.1. I used Schoener's (1970) model to calculate spatial overlap among upper Muddy River fishes:

$$S = 1 - 0.5\left(\sum |P_{x,i} - P_{y,i}|\right);$$

$P_{x,i}$ and $P_{y,i}$ are the proportional uses of habitat element i by species x and y. This index ranges from 0 to 1. I followed Brown and Moyle (1991) and considered values less than 0.33 as representing low overlap and values above 0.67 as indicating high overlap. I multiplied calculated values of S by 100 to obtain percent overlaps.

For each species and life history stage, I estimated niche breadths (B) in terms of mean water velocity, focal point velocity, total water column depth, and relative depth using the following formula devised by Levins (1968):

$$B = 1/\sum (P_i^2);$$

P_i is the proportion of physical variable used in each category. Categories were increments of 10 cm/s for mean and focal point velocities, 10 cm for total depth, and 0.1 for relative depth.

Introduced fishes may cause a niche shift or reduction of niche breadth (Brown and Moyle 1991; Moyle et al. 1986). I tested for an induced shift in habitat of Moapa dace and Moapa White River springfish caused by nonnative fish by contrasting habitat use by natives isolated on the Moapa National Wildlife Refuge with habitat use by natives cohabitating with shortfin mollies and western mosquitofish. Sites selected for contrast were those with discharges similar to those along the refuge stream (0.03–0.09 m^3/s). This selection included a 300-m reach immediately downstream of the isolated refuge populations (0.09 m^3/s) and a reach of Upper Apcar Stream (0.03 m^3/s). A one way analysis of variance was used to test differences expressed by adult Moapa dace and Moapa White River springfish with and without nonnatives.

Dietary overlap.—Ten adults each of Moapa dace, Moapa White River springfish, and shortfin molly were captured from each of three Upper Muddy River tributary streams representing three habitat types (glide, pool, and chute); western mosquitofish were taken only in the pool habitat. Fish were captured by seining and with unbaited minnow traps fished no longer than 10 min. All fish from a site were taken at the same time and preserved simultaneously in a 10% formalin solution. The anterior third of the gut of Moapa dace, Moapa White River springfish, and shortfin mollies and the entire gut of western mosquitofish was examined. Contents were identified with a dissecting microscope. To evaluate the relative importance of various foods, the Hynes (1950) method of numerically quantifying diet was employed and used in the same model used to determine spatial overlap. To add further insight as

[1] The use of trade names or commercial product names is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Fish and Wildlife Service.

to diet among species, food items consumed were quantified by frequency of occurrence (Windell 1971).

Predation.—I compared the relative propensity of adult Moapa White River springfish, shortfin mollies, and mosquitofish to prey on fish larvae. I used larval suckers *Catostomus* sp. (9–10 mm TL) from the Truckee River, Nevada, as a surrogate for Moapa dace larvae. *Catostomus* larvae were used in lieu of Moapa dace because of their unlisted status, availability, and tendency to occupy habitat similar to that of larval Moapa dace (Moyle and Baltz 1985). Two experiments were run on 11 July and two on 22 July 1991. For each experiment, three adults each of Moapa White River springfish, shortfin molly, and western mosquitofish were used. Moapa White River springfish ranged from 1.4 to 3.8 g and 42 to 60 mm TL, shortfin mollies from 1.3 to 3.5 g and 45 to 58 mm TL, and western mosquitofish from 0.7 to 1.5 g and 39 to 50 mm TL. Test fish were captured from the upper Muddy River system 1–6 d prior to the experiment. Each experimental group received the same treatment. Tanks were 57-L aquaria. Controlled water temperature ranged from 27.5 to 30.0°C. Each adult was placed in a separate test tank and starved for 24 h prior to the experiment; then 10 sucker larvae and 5 brine shrimp *Artemia* sp. were placed in each of the nine experimental tanks and in three control tanks that contained only larvae and brine shrimp. *Artemia* were added to help determine if fish were habituated and willing to eat alternative prey if available. Remaining *Catostomus* larvae and *Artemia* were counted every 2 h over an 8-h period.

Results

Relative Abundance

Western mosquitofish adults were the least abundant nonnative fish species in the four Moapa dace reproduction or nursery reaches; densities ranged from 0.1 fish/m at Muddy Spring to 3.5 fish/m along South Fork Stream (Table 1). Shortfin molly predominated at two sites and Moapa White River springfish at the other two. Shortfin molly was the most numerous species in the entire area, numbering an estimated 37,800 adults compared with estimates of 16,600 adult Moapa White River springfish, fewer than 3,000 adult western mosquitofish, and 2,200 Moapa dace. These numerical estimates are only of populations in the tributaries in which Moapa dace are known to reproduce, not the total adult populations.

TABLE 1.—Densities of Moapa dace, Moapa White River springfish, shortfin molly, and western mosquitofish adults in four known Moapa dace nursery streams.

Species	Estimated population and 95% confidence interval	Fish/m
Refuge Stream		
Moapa dace	250	0.2
White River springfish	5,544 ± 583	3.4
Shortfin molly	16,104 ± 2,059	10.0
Western mosquitofish	Scarce	
Upper Apcar		
Moapa dace	200	1.1
White River springfish	2,979 ± 476	16.0
Shortfin molly	1,391 ± 253	7.5
Western mosquitofish	87 ± 43	0.5
South Fork		
Moapa dace	300	0.4
White River springfish	4,800 ± 925	6.3
Shortfin molly	18,700 ± 2,175	24.5
Western mosquitofish	2,650 ± 725	3.5
Muddy Spring		
Moapa dace	1,450	1.8
White River springfish	3,326 ± 1,082	4.1
Shortfin molly	1,637 ± 264	2.0
Western mosquitofish	106 ± 54	0.1

Spatial Overlap in Microhabitat

Adult Moapa dace were associated with greater mean water velocity and greater focal point velocity than their cohabitants (Table 2). They also had the greatest niche breadth for these spatial categories. Adult Moapa dace and Moapa White River springfish were more benthically oriented and in deeper water than adults of the two nonnatives. Moapa dace larvae and juveniles occurred in lower focal point water velocities than adults, in shallower water, and generally higher in the water column.

Spatial habitat overlap of native and nonnative fishes was moderate to nil (Table 3). Moapa dace overlap was greatest for its larvae and juveniles with shortfin molly adults (44 and 45%, respectively). Moapa White River springfish overlap was greatest for its larvae with juvenile shortfin mollies (47%).

Adult Moapa dace and Moapa White River springfish showed no significant differences in habitat use between areas where nonnative species were present or absent (all P's > 0.38). Although the sample sizes were small, the data suggest that no major shifts in habitat use have been forced on the two native species by the introduced fishes. Sample sizes were too small to test the effects on

TABLE 2.—Means (±SD) and niche breadths (*B*) for microhabitat variables associated with upper Muddy River fishes. Maximum breadth is the number of resource classes.

Statistic or life stage	Mean velocity Mean ± SD (cm/s)	*B*	Focal velocity Mean ± SD (cm/s)	*B*	Total depth Mean ± SD (cm/s)	*B*	Relative depth Mean ± SD (cm/s)	*B*	*N*
Maximum breadth		8.0		6.0		10.0		10.0	
Moapa dace									
Larvae	1.0 ± 1.2	1.0	1.6 ± 1.4	1.0	31.1 ± 19.2	4.3	0.43 ± 17.8	4.9	199
Juvenile	6.8 ± 8.0	2.0	5.9 ± 6.6	1.4	42.3 ± 24.7	6.6	0.49 ± 23.2	6.7	148
Adult	24.8 ± 16.6	4.9	14.4 ± 9.1	3.6	58.9 ± 17.9	5.3	0.82 ± 11.5	3.4	452
Moapa White River springfish									
Larvae	1.1 ± 1.4	1.0	1.2 ± 1.7	1.0	9.5 ± 7.0	2.0	0.61 ± 30.6	5.7	72
Juvenile	5.5 ± 7.0	1.9	4.2 ± 6.0	1.3	32.6 ± 21.8	6.1	0.68 ± 22.6	5.3	116
Adult	11.2 ± 10.2	2.6	6.8 ± 6.8	1.7	33.7 ± 21.9	6.5	0.75 ± 16.9	4.6	432
Shortfin molly									
Juvenile	5.1 ± 7.3	1.5	3.5 ± 5.1	1.2	24.4 ± 25.7	3.0	0.40 ± 23.1	6.8	478
Adult	10.7 ± 9.0	2.6	8.8 ± 6.7	2.1	46.8 ± 22.8	6.6	0.36 ± 20.2	6.4	843
Western mosquitofish									
Juvenile	1.6 ± 3.6	1.0	1.4 ± 2.4	1.0	15.0 ± 12.0	2.7	0.16 ± 19.4	3.2	463
Adult	3.8 ± 3.8	1.1	4.4 ± 4.0	1.1	24.0 ± 18.0	4.4	0.14 ± 16.4	2.7	311

younger life stages of the two natives, but it was my subjective evaluation that these stages were not influenced spatially by the nonnatives.

Dietary Overlap

Moapa dace, Moapa White River springfish, and shortfin mollies were captured in each of the three habitats included in the diet study, but western mosquitofish were collected only at one site. Compared with the other species, Moapa dace had few items in their alimentary canals (Table 4). Their overlap in items consumed was 24% with shortfin molly, 30% with western mosquitofish and 31% with Moapa White River springfish. Moapa White River springfish overlapped 63% with shortfin molly and 66% with western mosquitofish.

All four species exhibited some degree of omnivory. Moapa dace were the most carnivorous, containing by volume 75% invertebrates and 25% plant material and detritus. Shortfin mollies were the most herbivorous, containing 93% plant material and detritus. Moapa White River springfish, the most omnivorous, contained 61% plant material and 39% invertebrates. Moapa dace taken from the spring pool habitat, the only site from which western mosquitofish were captured, contained fewer food items than those from other habitats; two had empty guts and the remaining eight were virtually empty. The gut contents were 73% invertebrates and 27% vegetative matter. Shortfin mollies had consumed 100% vegetative matter, Moapa White River springfish 97%, and western mosquitofish 65%. Western mosquitofish was the only species to have preyed on another fish; one had consumed a young shortfin molly.

Predation

When relative predatory aggressiveness was tested among the three atheriniforms, Moapa White River springfish consumed the fewest *Ca-*

TABLE 3.—Relative spatial overlaps (100 × Schoener's *S*) of life stages of Moapa dace, Moapa White River springfish, shortfin molly, and western mosquitofish.

Interacting species	Larvae	Juveniles	Adults
Moapa dace			
Moapa White River springfish			
Larvae	23	24	9
Juveniles	19	43	23
Adults	18	39	33
Shortfin molly			
Juveniles	30	31	13
Adults	44	45	2
Western mosquitofish			
Juveniles	26	22	0
Adults	25	22	0
Moapa White River springfish			
Shortfin molly			
Juveniles	47	31	21
Adults	19	19	21
Western mosquitofish			
Juveniles	36	13	5
Adults	19	7	7

TABLE 4.—Food items consumed by cohabiting fish species in three habitat types in the Warm Springs area. Data are percentages of stomach content volume and (in parentheses) percent frequencies of occurrence. Ten adults of each species were taken at each site (western mosquitofish were present only at one site).

Food item	Moapa dace (N = 30)	Moapa White River springfish (N = 30)	Shortfin molly (N = 30)	Western mosquitofish (N = 10)
Gastropoda				
Tryonia clathrata	1 (1)	2 (5)		11 (4)
Fluminicola alvinalis		2 (5)		2 (1)
Melanoides tuberculatum				2 (1)
Oligochaeta	27 (5)			
Ostracoda		(1)		
Amphipoda				
Hyallela azteca	2 (2)	6 (9)	1 (1)	
Arachnida				
Hydracarina		(1)		
Ephemeroptera				
Tricorythodes sp.		(1)		
Odonata				
Argia sp.		2 (2)		
Hemiptera				
Pelocoris shoshone	5 (1)	(1)		5 (1)
Homoptera				
Aphiidae	9 (1)			
Trichoptera				
Pupae		4 (4)		
Dolophilodes sp.	5 (2)			
Smicridea sp.		6 (5)	4 (2)	
Nectopsyche sp.	5 (2)	1 (2)		
Lepidoptera				
Paragyractis sp.	5 (2)	1 (1)		
Coleoptera				
Elmidae (larvae)		(1)		
Stenelmis calida	1 (1)			
Dytiscidae	9 (1)			
Diptera				
Chironomidae	5 (1)	9 (9)	2 (1)	1 (1)
Muscidae			2 (1)	
Hymenoptera			1 (1)	
Atheriniformes				
Poecilia mexicana				10 (1)
Vascular plants	3 (2)	1 (3)		
Filamentous algae	19 (11)	36 (21)	45 (25)	33 (8)
Detritus	3 (3)	28 (18)	48 (26)	33 (10)

springfish took larvae in only 10 of 12 aquaria, consuming less than 15% of the total larvae available. They did, however, consume all five *Artemia* in each aquarium within the first 2 h. Predation by shortfin mollies was greater; they consumed larvae in 12 of 12 aquaria, eating 65% of the larvae available. Western mosquitofish consumed larvae in 11 of 12 aquaria and took 60% of the larvae. Except for one western mosquitofish that ate nothing, the nonnative fishes consumed all *Artemia* within 2 h.

Discussion

The hypothesis that interspecific competition between adults for microhabitat caused the decline of Moapa dace was not supported; there was virtually no overlap in microhabitat use, and examination of habitats with various combinations of species showed no clear indication of a shift in spatial habitat use caused by competition with shortfin molly and western mosquitofish. However, interspecific competition for space and food cannot be ruled out for larvae and juveniles, because there was at least moderate interspecific microhabitat overlap. Ontogenetic shifts in food items consumed by each of the four species greatly add to the complexity of determining the potential for competition, but to document such feeding shifts would require sacrifice of a larger sample of the endangered Moapa dace. Thus, the scope of this study was narrowed to focus primarily on how nonnative adults affected native forms.

Predation on young has been identified as a mechanism by which nonnative fish replace natives (Meffe 1985). The results of my study indicate that predation on young Moapa dace by adult shortfin mollies might have contributed to the population's numerical decline. Under experimental conditions, shortfin mollies were formidable predators of fish larvae. I have seen them cannibalize their own young in aquaria and in mesocosms with ample forage, where they consumed Moapa White River springfish larvae as well (unpublished data). However, analysis of their stomach contents suggested that they tend toward herbivory in the wild. Demonstration that they prey upon Moapa dace larvae in the wild is made difficult by the current rarity of Moapa dace. Also, the sample of shortfin molly guts examined was low, and it was taken in a month (November) when Moapa dace reproduction is low (Scoppettone et al. 1992). To enhance the probability of determining their predatory potential on Moapa dace larvae, shortfin molly adults should be collected in the spring or summer, when Moapa dace recruitment is greatest.

If shortfin mollies indeed prey upon larvae in the wild, they probably would affect the Moapa dace population more than the Moapa White River springfish population. Microhabitat overlap indices for adult shortfin mollies were 44% with Moapa dace larvae but only 19% with Moapa White River springfish larvae. Moreover, 87% of Moapa dace larvae occurred in habitat used by shortfin mollies, compared with only 30% of springfish larvae. Relative vulnerability of larvae may also explain why Moapa dace declined after the introduction of shortfin molly, even though the species had not been notably affected by the arrival of western mosquitofish, a known predator of fish larvae (Minckley 1973; Moyle 1976; Meffe 1985), 25 years earlier. Larval Moapa dace showed only 25% habitat overlap with adult western mosquitofish, and 36% of them occurred in habitat used by adult mosquitofish.

My data indicate that adult Moapa dace and Moapa White River springfish probably prey very little on each other's larvae. Moapa dace adults had trivial overlap in microhabitat use with springfish larvae, and springfish adults indicated only 18% overlap with dace larvae. Furthermore, Moapa White River springfish did not appear to feed aggressively on fish larvae in aquaria.

Macrohabitat analysis added further evidence that adult shortfin mollies were a substantial force in reducing the Moapa dace population. The relatively high density of shortfin mollies in Moapa dace nursery tributaries may have intensified their predatory threat to larval dace by further enhancing the probability of encounter rates. Meffe (1984) showed that another poeciliid, Gila topminnow *Poeciliopsis occidentalis,* increased its intensity of cannibalism when its population density increased. Western mosquitofish had relatively low densities in my study area, about 10% of the number of shortfin mollies.

Although the highest number of Moapa dace adults occurred in the tributary with the lowest density of shortfin mollies, no conclusions can be drawn from this observation. Moapa dace are transients; most of the approximately 2,900 remaining adults were in the four tributaries at the time of the survey, but most adults typically occur in the upper Muddy River (Scoppettone et al. 1992).

Although there seems to be enough separation in habitat use to ensure only a small amount of interaction between Moapa dace and shortfin molly or western mosquitofish, one cannot discount the possibility that a niche shift or interactive segregation has occurred because of intense competition. Such shifts have been observed for other species (Werner and Hall 1979; Brown and Moyle 1991). The weight of evidence I have collected so far gives little support for such a shift, but it is difficult to prove such shifts without experimental introductions.

Nonnative poeciliids have caused the decline, extirpation, or extinction of several native fish populations (Cross 1976; Courtenay et al. 1985; Meffe 1985; Courtenay and Meffe 1989). When predation on larvae is the mechanism affecting native forms, analysis of relative overlap in microhabitat between the potential predator and prey may explain why one species is more affected by the introduced form than another. The approach used in this study may be useful in determining why a species is driven to extinction in one habitat while it persists in another, as has been noted for the Gila topminnow (Meffe 1985). Also, this study adds information on a subject that has received much discussion but little study, the mechanisms by which native fishes are affected by nonnatives.

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