Environmental Biology of Fishes **68:** 205–214, 2003.
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Habitat use by nonnative rainbow trout, *Oncorhynchus mykiss*, and native Little Colorado spinedace, *Lepidomeda vittata*

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Received 4 January 2002 Accepted 28 July 2003

Key words: native–nonnative interactions, co-occurrence, microhabitat use

Synopsis

We evaluated overlap in microhabitat use between nonnative rainbow trout, *Oncorhynchus mykiss*, and native Little Colorado spinedace, *Lepidomeda vittata*, a federally threatened cyprinid, in natural and experimental settings. In natural settings, we also examined occurrence and microhabitat use of two other native fishes, speckled dace, *Rhinichthys osculus*, and bluehead sucker, *Catostomus discobolus*. Native species co-occurred, as did rainbow trout and bluehead sucker. However, occurrences of Little Colorado spinedace and speckled dace were not significantly correlated with occurrence of rainbow trout. Total lengths of all three native species were significantly smaller at allopatric sites than at sites sympatric with rainbow trout. Microhabitat characteristics at sites with rainbow trout did not differ from those where the other three species were found, but did differ among the native species. In laboratory experiments with Little Colorado spinedace and rainbow trout, rainbow trout used the lower depth zone most, and spinedace increased use of the lower depth zone upon addition of rainbow trout. In addition, species tended to co-occur in zones, but used cover independently of one-another, suggesting a low level of agonistic interactions. However, after addition of a high density of rainbow trout, spinedace tended to use cover less than before. We suggest that the species can coexist at low rainbow trout densities. Potential negative effects of rainbow trout on Little Colorado spinedace likely increase with increasing densities of rainbow trout, and rainbow trout likely affect smaller size classes of Little Colorado spinedace more than larger ones.

Introduction

Native–nonnative fish interactions have received much attention in the last 40 years (Miller 1961, Moyle 1976, Minckley & Deacon 1991). Introduced species can negatively affect native fish populations in at least three ways: (1) the introduced species may prey on the native species, (2) similar resource use may result in competition, or (3) resource use by the introduced species may degrade habitat and thus limit resources needed by native species.

In Arizona, trout angling is popular, and various nonnative salmonids (rainbow trout, *Oncorhynchus mykiss*, brook trout, *Salvelinus fontinalis*, brown trout, *Salmo trutta*, and cutthroat trout *O. clarki*) have been stocked since the early 1900s (Rinne & Janisch 1995). Rainbow trout have been the primary trout species stocked and are the only nonnative salmonid still stocked in high elevation streams (Rinne & Janisch 1995). This is of special concern, since rainbow trout may have contributed to the decline of Little Colorado spinedace, *Lepidomeda vittata*, a federally threatened cyprinid endemic to the Little Colorado River Basin (Figure 1; Miller 1963, Minckley & Carufel 1967, Blinn et al. 1993).

Rainbow trout may negatively affect Little Colorado spinedace populations through predation and competition. Rainbow trout are reported to prey on Little Colorado spinedace in stream enclosures (Blinn et al. 1993, Rinne & Alexander 1995). In addition, rainbow

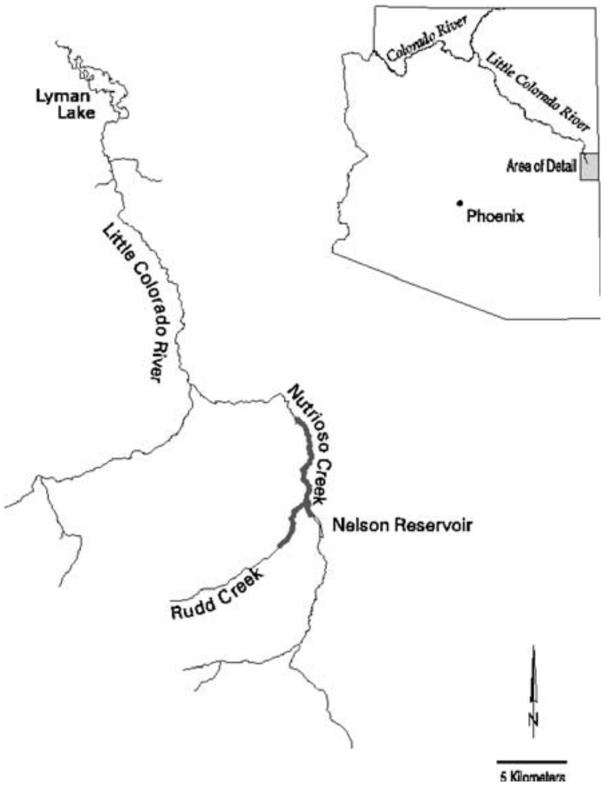

Figure 1. Map of the study area; shaded portions indicate portions of the two study streams surveyed. Nelson Reservoir is located at 34.0597° latitude and −109.1942° longitude.

trout may limit the distributions of Little Colorado spinedace (Blinn et al. 1993); in stream enclosures spinedace used undercut banks when large rainbow trout were absent, and open water when they were present. It is unclear whether this shift in habitat use was a predator-avoidance response by spinedace, or a result of interference competition.

Little Colorado spinedace are reported to be 'trout-like' in behavior, with similar habitat requirements and diet (Miller 1963, Minckley & Carufel 1967, Runck & Blinn 1993). As a result, rainbow trout may compete with spinedace in addition to preying on them. Distributions of the two species overlap to some extent, but spinedace distributions extend into lower elevations and rainbow trout extend into higher elevations (Arizona Game and Fish Department, unpubl. data). However, Little Colorado spinedace may have developed tactics to coexist with salmonids, because they evolved in streams inhabited by Apache trout, *Oncorhynchus apache*.

In this study, we assessed the potential for ecological interactions (primarily competition) between rainbow trout and Little Colorado spinedace. Information on interactions between these species is necessary to effectively conserve spinedace populations while managing a trout fishery in the area. We report on microhabitat use of both species in sympatric and allopatric situations. Our objectives were to: (1) determine whether Little Colorado spinedace and rainbow trout co-occur on a small scale (within 5-m sites), (2) determine microhabitat use by and overlap between the two species, and (3) assess if spinedace shift habitat use in response to rainbow trout. Because these fishes are not the only species present in the fish assemblage, we also determined co-occurrence and microhabitat use of other fish species present in one of our study streams.

Materials and methods

Study area

We conducted the study in Rudd Creek, in the upper Little Colorado River Basin in eastern Arizona (Figure 1). Rudd Creek originates in spruce-fir forest and flows through meadows and forest for about 13 km until it empties into Nutrioso Creek 2 km below Nelson Reservoir. A fish barrier (cement dam with culvert) 4.9 km upstream from the confluence with Nutrioso Creek divides Rudd Creek into upper and lower reaches. Little Colorado spinedace, speckled dace, bluehead sucker, rainbow and brook trout make up the fish assemblage in the lower reach (Arizona Game and Fish Department, unpubl. data). Sampling on Rudd Creek was restricted to the lower reach.

Species occurrence and habitat in 5-m sites

During 1996 and 1997, we documented species occurrence and associated environmental characteristics within 5-m reaches (sites) in lower Rudd Creek; data from 1997 is not presented because only one rainbow trout was captured that year. We randomly selected 80 5-m sites, 20 within each of four randomly selected 500-m reaches. These 80 sites were sampled in late April through early May immediately following spring runoff (before the Little Colorado spinedace spawning season), during June in the dry period before summer monsoons (spawning season), and in September after the summer monsoons (post-spawning period); total sample size each year was 240 sites. We measured environmental (microhabitat) characteristics in each site along five perpendicular-to-flow transects 0.5, 1.5, 2.5, 3.5, and 4.5 m upstream from the downstream end of each site. Depth (cm), current velocity (cm s^{-1}), substrate type, and cover type were recorded along each transect at points 0.2, 0.4, 0.6, and 0.8 the width of the stream. Current velocity was measured at 60% of the water column depth using a Marsh–McBirney® Model 2000 Portable Flowmeter. Turbidity (nephelometric turbidity units; NTU) was measured using a DRT-15CE Turbidimeter (HF Scientific, Inc., Fort Myers, FL) on a sample collected in the middle of the site. Gradient (%) was measured for the entire site, and surface area (m^2) was calculated. Temperature was measured but results are not reported because they were confounded by time of day.

To capture fish, we placed block nets at the upstream and downstream end of each site, and then made three passes through each site with a Smith–Root model 15-C backpack electrofisher. All fish captured were measured for total length (TL; mm) and mass (±0.1 g). Fish were returned to the stream immediately after examination.

Because spinedace length frequency distribution was bimodal, we assigned spinedace to two size classes (29–60 mm TL or 61–128 mm TL) for use in subsequent analyses. Speckled dace and bluehead sucker were assigned to the same two size classes. For rainbow trout, we only had sufficient sample size ($n = 71$) to evaluate associated environmental characteristics of one size class (84–177 mm TL); only five fish were <84 mm TL (all <36 mm). Because species may exhibit ontogenetic shifts in resource use, we evaluated differences in microhabitat characteristics among 84–177 mm rainbow trout and 29–60 and 61–128 mm TL spinedace, speckled dace, and bluehead sucker.

We assessed co-occurrence between all pairs of species at 5-m sites using chi-square analysis and the phi_2 (ϕ_2) coefficient (Zar 1984). A significant chi-square indicates that the occurrence of one species is associated with the other. The ϕ_2 coefficient provides additional information, indicating whether the association is due to co-occurrence (positive coefficient) or to disjunct occurrence (negative coefficient), and ranges from -1 (species never occur together) to $+1$ (species always occur together). We also assessed whether the density of native fish (each species and size class) was correlated (Spearman's r_s) with the density of rainbow trout. In addition, we assessed whether lengths of native fishes differed between trout present and trout absent sites using two-way analysis of variance (ANOVA), with sampling season as the second factor.

Means (depth, current velocity, area, turbidity, and gradient) and percents (primary cover type and primary substrate type) of environmental characteristics measured at each site during each period were calculated. These were used to assess differences in species habitat use with two-way MANOVA. We compared site characteristics where each species was found, among species-size classes and seasons. Although the same sites were measured in all seasons, we considered measurements in each season to be independent, because environmental characteristics and occupation of sites by species changed as a result of changes in stream discharge and season. Univariate comparisons were evaluated if the MANOVA (Wilk's Λ) had a $p < 0.05$. We were not interested in temporal changes in and of themselves (habitat did change due to climatic factors) and do not present results of season main effects. We considered nonsignificant results to indicate extensive overlap between species in habitat use.

Habitat use experiments with rainbow trout and Little Colorado spinedace

We experimentally evaluated the effects of density of rainbow trout on space and cover use by three size classes of Little Colorado spinedace. We conducted experiments in two 530-L ($213 \times 61 \times 56\,cm^3$) living streams (LSW-700 Living Stream, Frigid Units Inc., Toledo, OH). Gravel was placed on the bottom for substrate. Each stream was filled with water and held at 17–19°C. Lines were drawn on the side observation glass of each tank to create six cells (upper, middle, and lower depth zones for both upstream and downstream ends); each cell was 74 cm long × 61 cm wide × 9 cm high. Cover (simulated undercut bank) was created with a translucent dark gray plexiglass plate ($43 \times 30\,cm^2$), set with one end on the gravel at the downstream end of the tank and the other end propped up by two 15 cm long PVC pipes. Lighting in the laboratory provided by a combination of fluorescent and incandescent lights and was held at a photoperiod of 14:10 h (light:dark) to simulate outside conditions.

Fish were captured in Rudd Creek (rainbow trout from above the barrier and Little Colorado spinedace from below the barrier) using a backpack electrofisher. Fish were held in aquaria for 24 h prior to experimentation, and were fed flake food and trout pellets twice a day *ad libitum*, both prior to and during experiments.

We conducted six experiments; three for each of two densities of rainbow trout. For each experiment, 10 spinedace were placed into each stream at 1700 h. Observations (behind a blind) began the next day at 0700 h and were conducted every 20 min thereafter through 1640 h (30 pre-treatment observation periods). At 0630 h on the following day, rainbow trout were added to each tank (two into one tank and five into the second tank). Observations began at 0700 h and were conducted every 20 min thereafter through 1640 h (30 post-treatment observation periods). New fish were used in each experiment. In the first set of experiments, we added rainbow trout (115–182 mm TL, mean = 154 mm) in with 50–80 mm TL spinedace (mean = 61 mm). In the second set of experiments, we added rainbow trout (124–230, mean = 184) in with slightly larger spinedace (68–112 mm TL, mean 86 mm), and in the third set we added 135–172 mm TL (mean = 148 mm) rainbow trout in with large adult spinedace (93–124 mm TL, mean = 103 mm).

Each observation was a 'snapshot' of the locations of fish in the stream. For each species and observation period, we recorded the number of fish in each cell and the number of fish under cover.

We evaluated if spinedace changed their depth zone and cover use from pre- (trout absent) to post-treatment (trout present) periods using contingency table analysis. Because the total number of fish across the depth zones or cover use was fixed, the design was a model II test of independence, and the G (likelihood ratio) statistic was used to assess significance (Sokal & Rohlf 1981). The G statistic is based on the multinomial distribution, which has assumptions that total sample size is fixed and the cell counts are not statistically independent. We used similar G tests to compare depth zone and cover use between species in the post-treatment period. We also assessed species co-occurrence in cells (six cells and 30 observations resulted in an $n = 180$) and under cover with Spearman's correlation analyses.

Results

Site-level species occurrence and microhabitat

Little Colorado spinedace were numerically the least abundant of three native fish species captured in Rudd Creek, but were more abundant than rainbow trout and also were captured in more 5-m sites (Table 1). Of six tests comparing presence–absence between species pairs, co-occurrence between rainbow trout and Little Colorado spinedace and between rainbow trout and speckled dace were not significant (Table 2). The other four species-pairs had positive associations (tended to co-occur at sites); brook trout were not included in these or any following analyses due to small sample size. Similarly, densities of rainbow trout were not significantly correlated with densities of Little Colorado spinedace (Spearman's $r_s = 0.10$, $p = 0.11$) or speckled dace (Spearman's $r_s = -0.03$, $p = 0.66$), but were positively correlated with densities of bluehead sucker (Spearman's $r_s = 0.23$, $p < 0.001$). In addition, pairwise correlations between densities of native fishes were all positive ($r_s = 0.44$, $p < 0.001$ for spinedace *versus* speckled dace, $r_s = 0.43$, $p < 0.001$ for spinedace *versus* bluehead sucker, $r_s = 0.21$, $p = 0.001$ for speckled dace *versus* bluehead sucker).

Mean total length of each native fish species was significantly ($p < 0.001$) less at allopatric sites than at sites where they were sympatric with rainbow trout (Figure 2). Spinedace had mean lengths of 56.1 ± 2.1

Table 1. Catch of fish, by species, in Rudd Creek during 1996, including number of 5-m sites with fish of each species, number of fish captured each period, yearly mean densities in sites with a given species, and yearly range in lengths (mm TL).

Species	No. of sites. period			No. of fish. period			Mean (±SE) density (No./m^2)	Range in length (mm TL)
	1	2	3	1	2	3		
Little Colorado spinedace	24	18	13	57	44	21	0.39 (0.06)	29–128
Speckled dace	48	39	29	453	261	141	1.15 (0.11)	21–96
Bluehead sucker	15	9	6	80	54	19	0.40 (0.08)	39–143
Rainbow trout	20	10	6	42	22	7	0.29 (0.03)	25–177
Brook trout	6	4	1	6	4	1	0.26 (0.03)	47–166

Periods are: 1 = April–May, 2 = June, and 3 = September.

Table 2. Occurrence (presence or absence) of species pairs at 5-m sites in Rudd Creek during 1996. Dependence in occurrence between species or lack thereof was tested (df = 1 for all tests) with χ^2 (corrected for continuity; not shown) and the ϕ_2 coefficient (Zar 1984). The ϕ_2 coefficient ranges from −1 (species never occur together) to +1 (species always occur together).

Species		Frequency of sites with				ϕ_2	P
A	B	A and B absent	Only A	Only B	A and B present		
RBT	LCS	162	23	42	13	0.13	0.07
RBT	SPD	109	15	95	21	0.08	0.26
RBT	BHS	185	25	19	11	0.23	0.001
LCS	SPD	119	5	66	50	0.47	<0.001
LCS	BHS	177	33	8	22	0.43	<0.001
SPD	BHS	119	91	5	25	0.27	<0.001

Species codes are: RBT = rainbow trout, LCS = Little Colorado spinedace, SPD = speckled dace, and BHS = bluehead sucker.

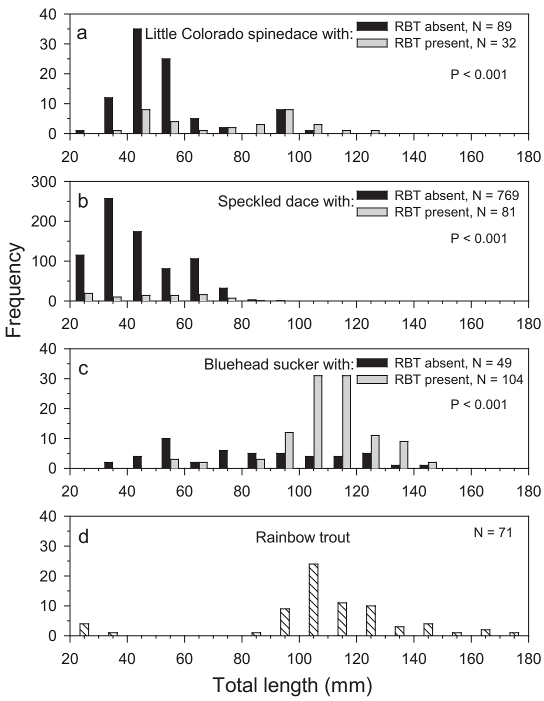

Figure 2. Length frequencies (5-mm classes) of (a) Little Colorado spinedace, (b) speckled dace, and (c) bluehead sucker at sites with or without rainbow trout, and (d) of rainbow trout in Rudd Creek, 1996. P-values indicate significance levels of ANOVAs comparing total lengths of native fishes between allopatric sites and sites sympatric with rainbow trout. N is the number of fish measured.

and 78.0 ± 5.0 mm TL, speckled dace had mean lengths of 45.6 ± 0.6 and 54.1 ± 2.2 mm TL, and bluehead sucker had mean lengths of 89.8 ± 3.8 and 113.8 ± 2.2 mm TL at allopatric and rainbow trout-sympatric sites, respectively.

Microhabitat characteristics of sites where fish were found differed among species-size classes (Table 3; Wilk's $\Lambda = 0.74$, $F = 1.8$, $df = 48, 1376$, $p = 0.001$). Five of eight variables examined in subsequent univariate tests were significantly different among species-size classes, but significant (Bonferonni-corrected) pairwise multiple comparisons among species were only detected for three of these variables: area, depth, and percent cover. Microhabitat characteristics at sites with 80–177 mm TL rainbow trout did not differ from that where other species-size classes were found. However, microhabitat characteristics differed between species-size class pairs for the native species. Little Colorado spinedace ≤60 mm TL used shallower sites (mean 17.0 ± 1.4 cm) than >60 mm TL spinedace (mean 25.2 ± 2.1 cm). Spinedace and bluehead sucker >60 mm TL were found in larger and deeper sites than either size class of speckled dace. Bluehead sucker >60 mm TL were found in larger and deeper sites than ≤60 mm TL spinedace. Both size classes of speckled dace were found at sites with more cover than those where >60 mm TL spinedace were present.

Laboratory experiments with rainbow trout and Little Colorado spinedace

We observed rainbow trout predation on Little Colorado spinedace twice, both during the experiment when two trout were added in with medium-sized (68–112 mm TL) spinedace. The larger (224 mm

Table 3. Microhabitat characteristics at 5-m sites with each of the species present in Rudd Creek, May–September 1996. Means (SE in parentheses), probabilities of MANOVA univariate comparisons (6, 286 df) among species-size-classes, and results of Bonferonni-corrected multiple comparisons (lower-case letters indicate significant, $p < 0.05$, pairwise comparisons) are presented.

Habitat variable	LCS		SPD		BHS		RBT	P
	≤60 mm (N = 42)	>60 mm (N = 18)	≤60 mm (N = 89)	>60 mm (N = 74)	≤60 mm (N = 10)	>60 mm (N = 27)	80–177 mm (N = 33)	
Gradient (%)	0.7 (0.21)	0.7 (0.32)	1.0 (0.15)	1.3 (0.16)	0.1 (0.43)	0.6 (0.26)	1.0 (0.24)	0.040
Turbidity (NTU)	31.8 (3.64)	40.9 (5.57)	32.2 (2.50)	35.5 (2.75)	24.9 (7.47)	38.0 (4.55)	42.3 (4.11)	0.201
Area (m^2)	7.6e (0.92)	12.0ab (1.41)	7.2ac (0.63)	6.7bd (0.70)	11.5 (1.89)	12.5cde (1.15)	8.2 (1.04)	<0.001
Depth (cm)	17.0ab (1.40)	25.2acd (2.15)	15.5ce (0.96)	15.2df (1.06)	23.4 (2.88)	25.4bef (1.75)	18.6 (1.58)	<0.001
Current velocity ($cm\,s^{-1}$)	2.5 (0.52)	1.8 (0.79)	3.6 (0.36)	3.8 (0.39)	1.1 (1.06)	1.7 (0.65)	2.8 (0.59)	0.009
Substrate size (ranked)	2.3 (0.11)	2.1 (0.17)	2.4 (0.08)	2.6 (0.08)	2.3 (0.23)	2.4 (0.14)	2.3 (0.13)	0.246
Cover (arcsine proportion)	0.5 (0.07)	0.2ab (0.10)	0.5a (0.05)	0.5b (0.05)	0.5 (0.14)	0.3 (0.08)	0.4 (0.08)	0.002
Undercut bank	0.03 (0.01)	0.03 (0.02)	0.01 (0.01)	0.03 (0.01)	<0.01 (0.02)	0.02 (0.01)	0.06 (0.01)	0.053

Species codes are the same as in Table 2, size categories are for mm TL, and N = number of sites.

TL) rainbow trout ate both spinedace and was exceptionally aggressive; we did not observe any overt aggressive interactions between species in the other five experiments.

Spinedace spatial use changed when rainbow trout were added to the artificial streams (Figures 3 and 4). After rainbow trout were added, spinedace decreased use of the upper depth zone in all experiments and increased use of the lower depth zone in all experiments except the one with small spinedace and high density of rainbow trout. The lower depth zone was typically the zone also used most by rainbow trout. When both species were present, species differed significantly in depth zone use in four of the six experiments (Figure 3a,b,d, and f). In three experiments (Figure 3a,b, and f), spinedace tended to use the lower depth zone more than rainbow trout, but in one experiment (high trout density with medium-sized spinedace), spinedace used the lower depth zone less than and the middle depth zone more than rainbow trout. In addition, when both species were present in the tanks, the two species tended to co-occur in cells in all experiments ($r_s = 0.20$, 0.53, 0.36, 0.51, and 0.24, for experiments 1, and 3–6, respectively; all $n = 180$ cells and all $P < 0.005$) except the one with small spinedace and high density of rainbow trout, when numbers of individuals of each species in cells were not significantly correlated ($n = 180$, $r_s = -0.06$, $p = 0.36$).

Spinedace use of cover (Figure 4) appeared dependent upon the density of rainbow trout added. After two rainbow trout were added, spinedace cover use did not change in two of the experiments, and in the third experiment (Figure 4c, medium-size spinedace) spinedace increased their use of cover. After five rainbow trout were added, cover use by the smallest (Figure 4a) and largest (Figure 4f) spinedace decreased, whereas cover use by medium-size (Figure 4d) spinedace did not change. Cover use by medium-size spinedace was very infrequent (<3%) both before and after trout were added.

When both species were present, rainbow trout used cover more than spinedace in all experiments except the one with the largest spinedace, when cover use did not differ between species. In addition, when both species were present in the tanks, there was no significant correlation between the number of spinedace and the number of trout under cover for five of six experiments

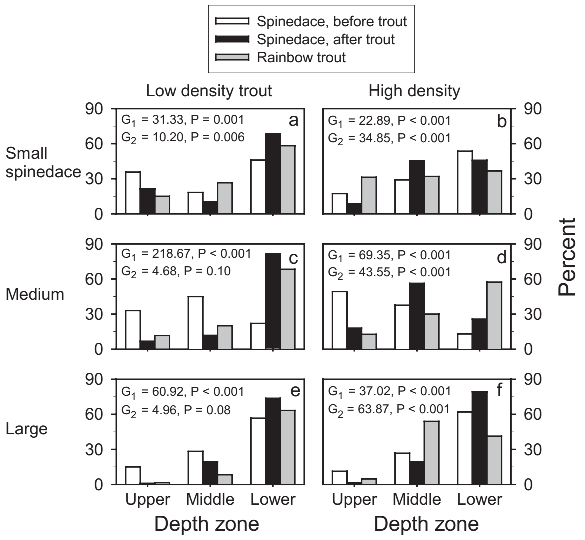

Figure 3. Use of depth zones in artificial streams by three size classes of Little Colorado spinedace before and after addition of a low (2) or high (5) density of rainbow trout, and by rainbow trout during six (a–f) experiments. Ten spinedace were used in each experiment and were small (50–80 mm TL), medium (68–112 mm TL), or large (93–124 mm TL). Sixty observations of rainbow trout were recorded for low-density experiments and 150 for high-density experiments; all trout were (115–230 mm TL). For spinedace, 300 observations were recorded before and after trout were added, except in a (N = 299 before), b (N = 292 after), and c (N = 279 after). G-values with subscript 1 indicate comparisons of spinedace zone use before with after rainbow trout added, whereas those with subscript 2 indicate comparisons between species (when sympatric).

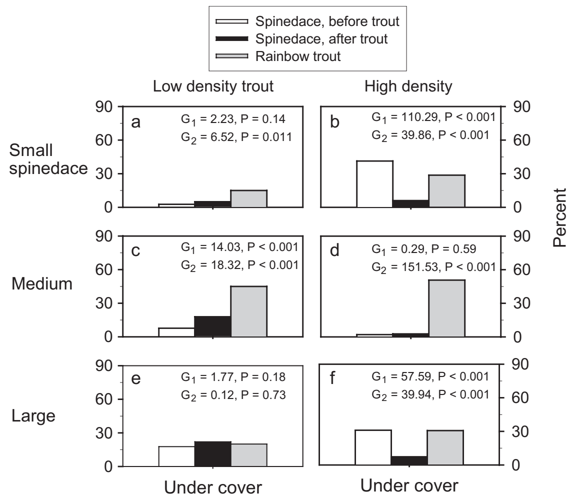

Figure 4. Use of cover in artificial streams by three size classes of Little Colorado spinedace before and after addition of a low (2) or high (5) density of rainbow trout, and by rainbow trout during six (a–f) experiments. Ten spinedace were used in each experiment and were small (50–80 mm TL), medium (68–112 mm TL), or large (93–124 mm TL). Sixty observations of rainbow trout were recorded for low-density experiments and 150 for high-density experiments; all trout were (115–230 mm TL). For spinedace, 300 observations were recorded before and after trout were added, except in a (N = 299 before), b (N = 292 after), and c (N = 279 after). G-values with subscript 1 indicate comparisons of spinedace cover use before with after rainbow trout added, whereas those with subscript 2 indicate comparisons between species (when sympatric).

($r_s = -0.01$–0.34; all n = 30 and all p > 0.07). During the experiment with the largest spinedace and two rainbow trout (Figure 4a), the numbers of spinedace and trout under cover were negatively correlated (n = 30, $r_s = -0.51$, p = 0.004).

Discussion

Introduced fishes are one of the most serious threats to persistence of native fish populations (Moyle 1976, Meffe 1985, Fausch 1988, Minckley & Deacon 1991, Ross 1991, Moyle & Light 1996). However, neither every introduced species successfully establishes itself (Moyle 1986, Baltz & Moyle 1993, Moyle & Light 1996), nor does every introduced species have detrimental effects on all native species present. Introduced fishes will primarily impact those native fishes that use similar spatial habitats. If they use different habitats, they will have little chance of interacting (through competition or predation). Interactions are also dependent on densities of the species and abundance of habitat; two species can use similar habitat and yet not co-occur in stream reaches if densities of the species are low and habitat is abundant. Because fishes can exhibit ontogenic changes in habitat use (Werner & Gilliam 1984, Byström et al. 1998, Childs et al. 1998), we are limited in what we can conclude about rainbow trout and Little Colorado spinedace interactions to the size classes we examined.

Agonistic interactions between rainbow trout and Little Colorado spinedace did not appear strong or consistent. During our artificial stream experiments, we observed very little agonistic behavior by rainbow trout toward Little Colorado spinedace. The most consistent shift in spinedace habitat use after addition of rainbow trout was an increase in the use of the lower depth zone. Interestingly, this probably does not indicate a negative interaction because this was also the depth zone most used by rainbow trout. In addition, the two species tended to co-occur in zones and used cover independently of each other, regardless of spinedace size or trout density. Our field data also indicated neutral associations between species. Bryan et al. (2002) reported that spinedace showed few behavioral responses to rainbow trout in artificial stream experiments, even though rainbow trout sometimes chased spinedace. It is possible that spinedace do not recognize rainbow trout as predators, and thus do not exhibit predator-avoidance behavior. Because predation risk is dependent on both prey and predator size (Werner et al. 1983, Lundvall et al. 1999), it is possible that the rainbow trout in Rudd Creek did not pose a great threat to spinedace, since they tended to be less than two times larger than co-occurring spinedace. The two predation events observed during artificial stream experiments involved a relatively large rainbow trout. Spinedace may experience greater predation risk and more agonistic interactions, and therefore be more likely to shift their habitat use, in response to larger rainbow trout than we tested.

Although rainbow trout have been documented to prey on Little Colorado spinedace in stream enclosures (Blinn et al. 1993), predation pressure by rainbow trout in the wild may be low. Sweetser et al. (2002) detected no spinedace in 54 rainbow trout stomachs collected from three Little Colorado River Basin streams where spinedace were present. Predation pressure on Little Colorado spinedace was probably decreased because there were many other fish to prey on; e.g. fathead minnow, speckled dace, and bluehead sucker (Sweetser et al. 2002). However, it is likely that large rainbow trout occasionally consume Little Colorado spinedace, particularly smaller size classes. Meffe (1985) and Minckley (1991) suggested that nonnative fishes might exert their greatest impact on native fishes by preying on early life stages.

In Rudd Creek, we found that smaller size classes of all three native fishes were more prevalent at sites devoid of rainbow trout than at sites sympatric with rainbow trout, which suggests preferential predation on smaller size classes. However, another possible explanation is that smaller native fish are simply using different habitat than larger native fish and 84–177 mm TL rainbow trout. We believe this is less likely for two reasons. For one, we only detected an ontogenetic change in habitat use for one of the native species, and for only one variable; Little Colorado spinedace used deeper water as they got bigger. Second, rainbow trout habitat use was similar to and did not statistically differ from either size class of any of the native fishes. Similar habitat use between 84–177 mm TL rainbow trout and native fish <60 mm TL, and co-occurrence increases the probability for predation or competition.

There have been relatively few studies of shifts in resource use by native species in response to the presence of introduced fishes, and only a fraction of these have detected a shift (Ross 1991). Although we detected shifts in spinedace habitat use in response to presence of rainbow trout in experimental settings, only those after a high density of rainbow trout were added appeared to be negative interactions. When a high density of rainbow trout was added to the artificial stream, spinedace use of cover decreased during two experiments and remained the same during one. Similarly, Blinn et al. (1993) reported that spinedace used open water more and undercut banks less after a high density of rainbow trout were added to stream enclosures (low-density trials were not investigated). These results suggest a displacement rather than a predator-avoidance response. Therefore, as in other predator–prey and competitive relationships (Tonn et al. 1989, 1992, Post et al. 1999), negative effects of rainbow trout on Little Colorado spinedace are likely dependent upon densities of both species where they co-occur. As rainbow trout densities increase, spinedace may be displaced or avoid optimal habitats then occupied by rainbow trout and use more sub-optimal habitat (less undercut banks; Blinn et al. 1993).

Rainbow trout may interact with speckled dace and bluehead sucker, the other two native species in our study streams. Rainbow trout and bluehead sucker tended to co-occur, whereas rainbow trout occurrence was not associated with that of speckled dace. Nevertheless, our data indicate that habitat used by 84–177 mm TL rainbow trout was very similar to that of these two native fish species. High overlap in habitat use between species indicates a high potential for interaction (Zaret & Rand 1971) when species do co-occur. In addition, smaller size classes of these two native fishes were also more prevalent at sites devoid of rainbow trout than at sites sympatric with rainbow trout in Rudd Creek indicating possible preferential predation on smaller size classes.

Even though little agonistic interactions were detected, rainbow trout and the native fishes overlap spatially and in habitat use. Therefore, the chance that rainbow trout will prey on or compete with Little

Colorado spinedace or the other native fishes is greater than it would be if they did not overlap. If rainbow trout densities remain low, the species may be able to coexist, and no management actions may be necessary. However, if rainbow trout densities increase, the potential for negative interaction will also likely increase, because we and Blinn et al. (1993) did detect some predation during experiments and did find that spinedace are displaced from cover when rainbow trout are at high densities. As such, we recommend management actions that minimize rainbow trout densities in streams and thus lessen potential negative interactions with native species.

Acknowledgements

This work was funded by a grant from Federal Aid in Sport Fish Restoration Program (Dingell-Johnson/Wallop-Breaux) and a matching state grant from the Arizona Game and Fish Department Heritage IIPAM Fund. We thank Lorraine Avenetti of Arizona Game and Fish Department for assistance in the field and input of ideas. We also thank Jim Novy, Jim Burton, and Kirk Young of Arizona Game and Fish Department, and Dean Blinn of Northern Arizona University for their contributions to the study design. We thank Mark Brouder, Steve Germaine, Mike Childs, and Ted McKinney of Arizona Game and Fish Department and Anthony Mazeroll of Soka University at Aliso Viejo California for their review of this manuscript and for their suggestions of improvement.

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