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Habitat Use and Association of Native and Nonnative Fishes in the San Juan River, New Mexico and Utah

KEITH B. GIDO AND DAVID L. PROPST

Habitat use and associations of native and nonnative fish species in secondary channels of the San Juan River, New Mexico and Utah were investigated. Most species and age classes within species (larvae, juveniles, subadults, and adults) used low velocity habitats with silt substrata. Discriminant function analysis revealed broad overlap in habitat use among species, with a trend of older age classes occurring in deeper habitats with faster current velocities. Overall, discriminant function analysis was able to correctly classify species and age classes, based on habitat use, 23.4% of the time. Native juvenile fishes exhibited the greatest interspecific association with nonnative fishes, whereas adult and subadult native fishes showed the least. Depending on the availability of resources, overlap in habitat use may result in negative interactions among native and nonnative fishes.

MANY native riverine fish assemblages in the American Southwest have been adversely affected by habitat modifications that directly and indirectly resulted from stream impoundments (Miller et al., 1989; Minckley and Deacon, 1991). In addition, establishment of nonnative fish species has substantially changed community structure in southwestern rivers, and in some cases numbers of introduced species are greater than natives (Minckley, 1973; Moyle, 1976; Sublette et al., 1990). Many of these changes cannot be reversed but must be managed to reduce their negative impacts on native fish assemblages. Elton (1958) proposed that, rather than trying to eradicate nonnative species, we should "promote an even balance and damp down the explosive power of outbreaks and new invasions." Under such a strategy, management designed to conserve native fish assemblages should be focused on enhancement of the habitat requirements of native species while attempting to reduce the suitability and availability of habitats for nonnative fishes. The extent to which habitat needs overlap spatially and temporally may, however, make this task difficult.

Because many southwestern rivers are regulated by reservoir releases, manipulation of river discharge is potentially an important tool for the conservation of native fish populations (Tyus, 1992). Changes in discharge of rivers is associated with changes in habitat-use patterns of fishes (Moyle and Baltz, 1985; Aadland, 1993; Scheidegger and Bain, 1995). Variation in discharge can cause short-term changes in depth, velocity, substrata, and cover (Bain et al., 1988). Over longer periods, flushing flows may change the morphometry of the river by aggregation or degradation of sediments and banks (Waters,

1995), which may influence riparian vegetation (Gregory et al., 1991; Friedman et al., 1996). Conversely, persistent low flows can result in armored substrata, loss of seasonally ephemeral habitats, or encroachment of erosion-resistant riparian vegetation (Friedman et al., 1996).

Information for recommending reservoir release patterns to benefit native fish assemblages should include habitat-use data on native and nonnative species (Moyle and Baltz, 1985). It is also important to consider the age classes of each species to account for ontogenetic shifts in habitat use (Matthews and Hill, 1979; Moyle and Vondracek, 1985; Mullen and Burton, 1995). Moreover, an understanding of the degree of habitat-use overlap among native and nonnative species must be obtained. Consideration of these aspects of habitat use is necessary so that management strategies to create or enhance habitat for native species do not inadvertently benefit nonnative species.

Patterns of association in habitat use between two species can be difficult to interpret because several mechanisms may explain these patterns (Begon et al., 1996). A negative association between two species could mean the species competitively exclude each other, or they have different habitat requirements. Positive associations in habitat use could mean the species require similar habitats (and potentially compete for the same resources), or they are indifferent to each other. Characterizing the degree of habitat overlap among species, and age classes of each, is an important preliminary step toward assessing potential biotic interactions among species in fish assemblages. Field experiments may then be designed and used to examine and test for mechanisms and/or consequences of these patterns of association. In San Juan River

secondary channels, where numerical abundance of nonnative species exceeds that of native species (Gido et al., 1997) and hydrologic variability has been reduced by flow regulation, there is presumably a higher potential for negative interactions.

The research reported herein was part of a long-term, multidisciplinary study to evaluate the responses of native and nonnative fishes to biotic and abiotic features of the San Juan River that were, in part, controlled by reservoir releases that mimicked natural flow regimes. This paper follows Gido et al. (1997) in which we described species distributions among four secondary channels across time in the San Juan River. Secondary channels were investigated because they are abundant on the San Juan River and provide habitats that are used extensively by native and nonnative fishes. Our objectives in this study were to describe habitat use by native and nonnative fish species within these channels and to characterize the degree of overlap among the fishes that occupy them. This information was analyzed to ascertain when and where potential interactions among species may be manifested and to identify possible management options that might be implemented to reduce putative negative effects of nonnative fishes on native fishes.

MATERIALS AND METHODS

Study area.—The San Juan River is a major tributary of the Colorado River and drains 99,200 km² in Colorado, Utah, Arizona, and New Mexico (Carlson and Carlson, 1982). A detailed description of the study reach and individual sites is provided in Gido et al. (1997). Routine operation of Navajo Dam (approximately 100 km upstream from our study sites) reduces the natural variability of the river's flow regime by diminishing flows during spring runoff and elevating base flows during late summer, autumn, and winter (historic low-flow periods). Reservoir releases during snow-melt (late spring to early summer) and flow from unregulated tributaries, however, maintained a quasi-natural pattern of elevated spring-early summer flows followed by low flows from late-summer through winter during our study.

We defined secondary channels as water courses within the flood plain that contained < 25% of the total discharge of the river and that had a minimum length of 0.5 km. Study sites were located in four secondary channels, and each had a range of habitats and abiotic characteristics (e.g., depth, velocity, and substratum) that was representative of San Juan River sec-

ondary channels. Length of study sites ranged 115–300 m and were located in channels that were between 0.9 and 3.4 km in length.

Data collection.—We began sampling study sites 1 through 3 in July 1993 and site 4 in August 1993. Each site was sampled at three-week intervals from peak spring runoff (late June to early July) through November and then every sixth week until the next year's spring runoff. Our study lasted almost two years, ending in May 1995.

The high turbidity of the San Juan River precluded direct observations of fish. As an alternative, we sampled fish by seining or electrofishing specific habitats. These habitats represented distinct areas of the channel (e.g., pools, riffles, and eddies) with homogeneous characteristics such as depth, velocity, and substrata. The majority of the habitats (97%) were sampled using a 1.6 mm mesh drag seine (2.5 m × 1.2 m). In habitats where seining was ineffective (shallow, low velocity, and large substrata), we electrofished (battery-powered back pack electrofisher with pulsed DC current) over agitated substrata and captured stunned fish with an aquarium net or drag seine anchored at the downstream edge of the sampled habitat. Although the different sampling techniques may have varied in efficiency, the use of only a seine in these habitats would have grossly underestimated the abundance of fishes. Mean width and length were determined for each sampled habitat to calculate fish density (number of individuals m⁻²). Fish >100 mm TL were identified in the field and released; the remainder were preserved in 10% formalin and returned to the laboratory for identification and enumeration. All retained specimens were accessioned into the New Mexico Department of Game and Fish Collection of Fishes.

Depth, water velocity, dominant substrata, and cover were determined at three points along three evenly spaced transects within each habitat sampled (nine measurements per sampled habitat). Velocity was measured with a Marsh-McBirney Model 2000 digital flow meter at 60% depth. At each point within a sampled habitat, dominant substrata were estimated visually and by touch using a modified Wentworth scale (Cummins, 1962). Substrata categories included silt (< 0.12 mm), sand (0.12–1 mm), gravel (1–64 mm), cobble (64–128 mm), rubble (128–256 mm), and boulder (> 256). Cover was recorded as presence or absence of woody debris within a habitat. The nine measurements were averaged to give mean depth and velocity for each habitat. Percent coverage of each sub-

TABLE 1. SIZE RANGES (mm) OF THREE ONTOGENETIC STAGES OF FISHES TAKEN FROM THE SAN JUAN RIVER. Species codes are used to designate species in other tables and figures. Native species = N and introduced species = I.

Species	Common name	Status	Code	Larvae	Juvenile	Adult/Subadult
<i>Cyprinella lutrensis</i>	Red shiner	I	(CYPLUT)	0–10	10–30	>30
<i>Pimephales promelas</i>	Fathead minnow	I	(PIMPRO)	0–10	10–30	>30
<i>Rhinichthys osculus</i>	Speckled dace	N	(RHIOSC)	0–15	15–40	>40
<i>Catostomus latipinnis</i>	Flannelmouth sucker	N	(CATLAT)	0–17	17–60	60–140
<i>Catostomus discobolus</i>	Bluehead sucker	N	(CATDIS)	0–17	17–60	60–140
<i>Ameiurus melas</i>	Black bullhead	I	(AMEMEL)		18–70	
<i>Ictalurus punctatus</i>	Channel catfish	I	(ICTPUN)		18–70	
<i>Fundulus zebrinus</i>	Plains killifish	I	(FUNZEB)		10–35	
<i>Gambusia affinis</i>	Western mosquitofish	I	(GAMAFF)		10–35	

stratum for a habitat was calculated as the proportion of the nine measurements in which a particular size class of substratum was dominant.

To quantify habitat availability at our study sites, measurements were made at 100 points per site, independent of fish collections, for each sample date. Measurements were taken along 10 equally spaced transects at the wider sites (3 and 4) and 20 equally spaced transects at the narrower sites (1 and 2). Depth, velocity, and dominant substrata were determined at equidistant points along each transect.

Data analysis.—To evaluate how representative our sampling was of available habitats, mean values for habitats available (transects) and those we sampled (seined and electrofished) were calculated for each sample site and date. Wilcoxon sign ranks tests were then used to test for differences in these values across sample dates for each site. Bonferonni corrections were used to account for multiple comparisons across sites (Rice, 1990).

For analysis of habitat use, species were categorized into three age classes (larvae, juvenile, or subadult/adult) to account for ontogenetic shifts in habitat use (Table 1). Because larvae and adults for some species occurred in low abundance, only juveniles of those species were considered in our analyses. The separation between larvae and juveniles was made at the approximate size at which a species acquired its full complement of fin rays. The upper size for juveniles was determined using length-frequency histograms and was approximately the maximum size the species attained through the first winter of life (31 December). For small-bodied species (*Cyprinella lutrensis*, *Pimephales promelas*, and *Rhinichthys osculus*), any specimen larger than a juvenile was considered an adult. For

large-bodied fish (*Catostomus discobolus* and *Catostomus latipinnis*), adults were excluded from our analysis due to low sample sizes. For these species, we classified specimens larger than juveniles but < 140 mm as subadults.

For each species/age class, a weighted mean, based on the number of individuals, for each habitat characteristic was calculated across all habitats occupied by that species/age class. To assess patterns of habitat use, frequency histograms were generated representing the mean abundance (number of individuals m^{-2}) of individuals for categories of velocity, depth, and substrata.

Discriminant function analysis was used to classify species (and age classes) by habitat variables. Discriminant analysis has been used to classify fish species based on characteristics of microhabitats (Baker and Ross, 1981; Ross et al. 1987), stream reaches (Grady et al., 1983; Taylor and Lienesch, 1996), and reservoirs (Dolman, 1990). This analysis is an objective method for determining those variables that are most useful in discriminating habitat use among species. In our case, environmental variables included mean depth, mean velocity, and percent coverage by each substratum. Depth and velocity were square-root transformed, and percent coverage of substrata was arcsine-square-root transformed, prior to the analysis. Based on calculations of skewness and examination of frequency histograms, these transformations were shown to better approximate normality than log transformations. To account for the large variation in species abundances among habitats, each habitat was weighted by the number of individuals in that habitat.

A stepwise discriminate analysis was used to determine those variables that accounted for the greatest amount of variation among species and age classes. Only variables that were signif-

icant ($P < 0.05$) were included in the analysis. Fifty percent of habitats occupied by each species/age class were randomly chosen to create the discriminate function. The other half was used to test how well species/age classes were classified from the derived function. Prior probability of classifying a particular species/age class was weighted by the frequency of occurrence of that species. An additional discriminant function analysis was performed to classify the three age classes of native and nonnatives, with species combined ($n = 6$ groups). All statistics were calculated using Statistical Package for the Social Sciences (SPSS Inc., vers. 7.0 for Windows, Chicago, IL, 1996, unpubl.).

Hurlbert's (1969) coefficient of interspecific association (C_7), including the modification of Ratliff (1982), was used to determine patterns of overlap in habitat use among species and age classes (Appendix 1). This method provides a measure of association that is unbiased by species frequencies (Hurlbert, 1969). Calculations only consider presence/absence of species pairs, and values range between -1 (negative association) and $+1$ (positive association) with a value near zero indicating a random pattern of coexistence. A contingency chi-square analysis was used to test whether a pair of species/age-classes coexisted greater or less than expected by random (Cox, 1996). To account for the large number of pairwise comparisons, a Bonferroni adjusted alpha level was used (Rice, 1990). Because Bonferroni adjustments tend to be conservative when a large number of comparisons are involved (Sokal and Rohlf, 1995), it is possible weak associations were not detected with this analysis.

Spearman's rank correlations were calculated to determine whether the abundance of species pairs was positively or negatively correlated across habitats (Ludwig and Reynolds, 1988). Because a large number of habitats had only one species/age class present, we only considered those habitats where both were present. Thus, for many of the less-common species there were low sample sizes (< 5 comparisons); these were omitted from the analysis.

RESULTS

Each sample site, except site 4, was visited 17 times during the two-year study; site 4 was sampled 15 times. A total of 1132 habitats was sampled, of which 929 were occupied by fish. We collected 55,590 specimens of 13 species in these habitats (Appendix 2). Three nonnative species, *C. lutrensis*, *P. promelas*, and *Gambusia affinis* were the first, second, and fourth most

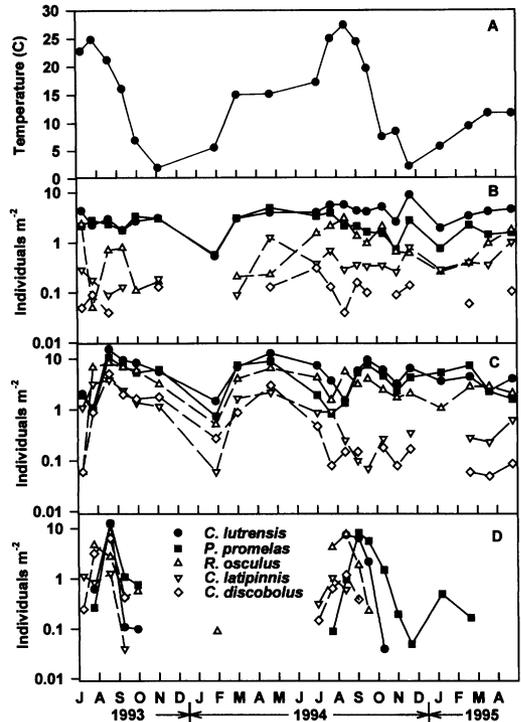


Fig. 1. Variation in temperature (A) and fish density (B–C) in San Juan River secondary channels. Number of individuals m^{-2} is given for B—adults, C—juveniles, and D—larvae of two nonnative and three native species. Solid symbols represent nonnative species and open symbols represent native species.

abundant taxa, accounting for 77.0% of the total catch. Native *R. osculus*, *C. latipinnis*, and *C. discobolus* were the third, fifth, and sixth most abundant (respectively) and accounted for 17.8% of the catch. Peaks in abundance of each age class of each common species usually occurred in late summer (Fig. 1). Juvenile and adult *C. latipinnis* and *C. discobolus* density, however, did not peak in late summer in both years. Juvenile *C. latipinnis* and *C. discobolus* densities peaked in late summer 1993 but were comparatively depressed in late summer 1994. Adult *C. discobolus* and *C. latipinnis* density remained fairly constant during the study. Juveniles of all common species had a spike in their densities during spring 1994. In general, native fish larvae appeared and reached peak abundance earlier in the summer than did nonnative larvae. In particular, larval *C. latipinnis* and *C. discobolus* were present when water temperature was < 18 C, but larval *C. lutrensis* and *P. promelas* did not appear until water temperature exceeded 21 C (Fig. 1).

Significant differences between habitats sampled and those available were found in two of

TABLE 2. MEANS AND STANDARD DEVIATIONS FOR HABITATS VARIABLES SAMPLED (S) AND THOSE AVAILABLE (A) IN SAMPLING LOCATIONS. Asterisks indicated a significant difference ($P < 0.05$) determined by Wilcoxon-Signed Ranks test with Bonferroni adjustments for comparisons across multiple sites.

Habitat variable		Site 1	Site 2	Site 3	Site 4
Velocity (cm sec ⁻¹)	S	15.0 (14.3)	8.6 (12.9)	15.4 (10.9)	27.4 (3.6)*
	A	11.1 (14.4)	10.0 (21.8)	15.6 (19.2)	52.1 (17.5)*
Depth (cm)	S	24.3 (10.5)	16.5 (9.6)	31.0 (4.9)*	29.2 (7.6)*
	A	20.0 (10.5)	14.2 (18.3)	23.5 (9.5)*	40.9 (12.8)*
Percent silt	S	42.1 (18.8)	37.5 (15.0)	35.2 (12.9)	29.1 (16.6)*
	A	36.5 (24.7)	32.8 (23.2)	31.9 (23.5)	13.2 (10.3)*
Percent sand	S	8.2 (13.1)	7.7 (12.8)	9.9 (13.2)	17.9 (16.8)
	A	9.1 (13.3)	5.2 (7.1)	4.6 (6.6)	14.2 (9.3)
Percent gravel	S	17.9 (14.6)	10.9 (9.1)	16.4 (12.1)	17.5 (13.9)
	A	15.7 (9.4)	10.5 (5.5)	17.2 (8.2)	8.3 (6.7)
Percent cobble	S	23.6 (14.7)	20.8 (13.9)	25.2 (15.3)	18.0 (11.4)*
	A	37.7 (22.8)	29.3 (16.8)	33.8 (12.2)	34.8 (6.0)*
Percent rubble	S	8.1 (14.2)	20.3 (11.5)	11.8 (10.8)	15.2 (8.3)*
	A	0.9 (1.4)	21.7 (16.5)	12.4 (12.8)	29.3 (11.7)*
Percent boulder	S	0.1 (0.4)	2.8 (4.9)	1.5 (3.6)	2.3 (5.4)
	A	0 (0)	0.5 (0.9)	1.0 (0.2)	0.2 (0.5)

the four sites (Table 2). The greatest deviation was at site 4, where sampled habitats were shallower, had slower velocities, and greater percent coverage of silt than available habitats. Of the habitats sampled, mean density of fishes (individuals m⁻²) was greatest in low velocity (< 20 cm sec⁻¹) silt bottomed habitats (Fig. 2). Mean density of fishes was variable among depths with a slight trend for lower density in deeper habitats (> 60 cm). Several species/age-classes occupied notably different habitats than others (Appendix 2). Adult *R. osculus* occupied habitats with the highest mean velocity (48.9 cm sec⁻¹). Adult and subadult *C. discobolus* also occupied habitats with higher mean current velocities than other species. Adult *C. lutrensis*, juvenile *Ictalurus punctatus*, and subadult *C. discobolus* and *C. latipinnis* commonly occupied habitats with depths > 35 cm.

Stepwise discriminant function analysis indicated that all variables significantly contributed toward discriminating habitat use among the 20 species and age classes (Table 3). The first two axes accounted for 77% of the variation in habitat use among the species/age classes. The first axis contrasted low velocity, shallow, silt bottomed habitats with high velocity, deep habitats. The second axis contrasted shallow, cobble-bottomed habitats with deep habitats. Species centroids plotted on the first two axes indicated that adults of both native and common nonnative species used habitats with higher current velocities than larvae or juveniles (Fig. 3). On the second axis, juvenile and adult *C. lutrensis* and *P. promelas* also appeared to use slightly

deeper habitats than the respective age class of native species. Although the overall model was significant, it only classified groups correctly 23.4% of the time. Of those, groups of native species were classified correctly 10.9% of the time, whereas nonnatives were classified correctly 26.8% of the time. Of the native species, the model was most accurate for *R. osculus*, correctly predicting its presence 54.1% of the time. Combining native and nonnative species into age classes improved the classification percentage to 50.4%. Again, nonnative age classes were classified correctly more than native age classes (50.8% vs 14.3%). In most cases, native larvae and juveniles were erroneously classified as nonnative juveniles.

Nonnative fishes in San Juan River secondary channels showed high levels of habitat overlap with different age classes of native species using presence/absence criteria (Figs. 4–6). Of the 99 possible comparisons of interspecific associations among nonnative and native fish species and age classes, 42 (42%) were found to be significantly greater than random coexistence. The greatest number of significant positive associations were among juvenile and larval native and nonnative species and the least among adult native and nonnative species. Overall, there were only seven significant negative associations between native and nonnative species, six of which involved *R. osculus*.

Interspecific association among native species showed similar patterns to those among native and nonnative fishes. Of the 36 possible comparisons among native species/age classes, 18

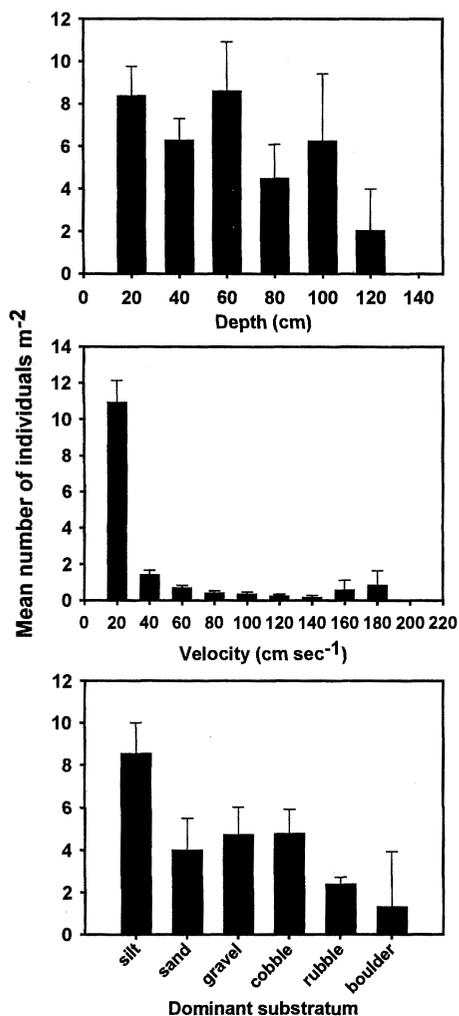


Fig. 2. Frequency histograms of mean abundance of fishes (number of individuals m^{-2}) in habitats sampled in San Juan River secondary channels for depth, velocity, and dominant substratum. Vertical bars represent one standard deviation.

(50%) were significantly positive. The only significant negative association was between adult *R. osculus* and juvenile *C. discobolus*. Again, the greatest overlap was among juveniles and larvae.

Larval and juvenile *P. promelas* and *C. lutrensis* showed high overlap with larval native species (Fig. 4). There was also a significant association among native fish larvae and juvenile *Gambusia affinis* (except *C. latipinnis*) and *Cyprinus carpio*. *Catostomus discobolus* larvae had a greater number of significant associations in habitat use with nonnatives than did other native fishes. Similar patterns of overlap with native fish larvae were seen among juvenile and larvae of other native

TABLE 3. EIGENVALUES, PERCENT VARIANCE EXPLAINED, AND DISCRIMINANT FUNCTION COEFFICIENTS FOR HABITAT VARIABLES SELECTED FROM A STEPWISE DISCRIMINANT ANALYSIS USED TO SEPARATE HABITAT USE BY THE 20 SPECIES AND AGE CLASSES OF FISH IN SAN JUAN RIVER SECONDARY CHANNELS.

Axis	I	II	III	IV
Eigenvalue	0.520	0.182	0.111	0.095
% of Variance	57.4	20.1	10.6	9.1

Habitat variables	I	II	III	IV
Velocity	-0.886	0.210	0.403	0.222
Depth	-0.500	-0.688	-0.401	-0.436
Debris	-0.022	-0.207	0.373	0.388
Boulder	0.072	0.024	0.042	0.246
Gravel	0.160	-0.174	-0.411	1.693
Rubble	0.174	0.263	0.238	0.594
Sand	0.190	0.180	-0.220	2.135
Cobble	0.477	0.510	0.579	1.786
Silt	0.615	0.010	0.374	3.362

fishes, where all but one association was significantly positive.

Native juvenile fishes showed significant positive associations with all nonnative fishes except adult *C. lutrensis* and juvenile *Ictalurus punctatus*, *Ameiurus melas*, and *Fundulus zebrinus* (Fig. 5). The magnitude of these associations was greatest for the two native catostomids. Significant

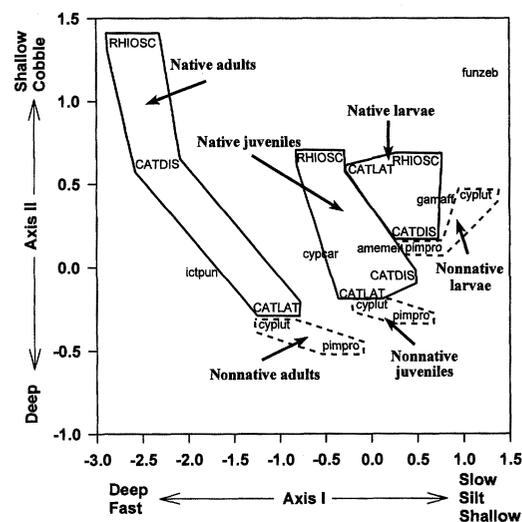


Fig. 3. Plot of species/age-class centroids on the first two axes derived from a discriminant function analysis to classify species by habitat associations (species codes are listed on Table 1). Species codes for native species are in capital letters and nonnative species are in lower case. Solid-line polygons represent age classes of native species, and dashed-line polygons represent age classes of common nonnative species, *Cyprinella lutrensis* and *Pimephales promelas*.

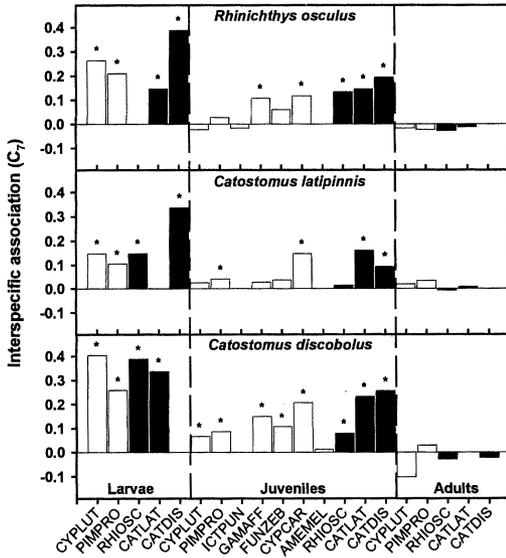


Fig. 4. Index of interspecific association (C_7) among larvae of three native fishes with other species/age-class in San Juan River secondary channels. Asterisks indicate significant deviation from random coexistence. Open bars represent native versus non-native comparisons and closed bars represent native versus native comparisons.

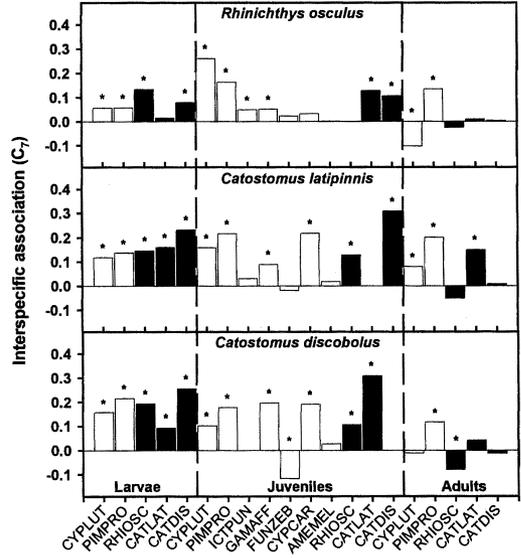


Fig. 5. Index of interspecific association (C_7) among juveniles of three native fishes with other species/age class in San Juan River secondary channels. Asterisks indicate significant deviation from random coexistence. Open bars represent native versus non-native comparisons, and closed bars represent native versus native comparisons.

negative associations occurred between juvenile *R. osculus* and adult *C. lutrensis*, and juvenile *C. discobolus* and *F. zebrinus*. Juvenile native fishes also showed high overlap with other native juveniles but little overlap with native adults.

Adult/subadult native species showed the lowest degree of habitat overlap with nonnative species (Fig. 6). Among these, subadult *C. latipinnis* had the greatest number of significant positive associations with nonnative fishes. Adult *R. osculus* had significant positive associations with adult *C. lutrensis* and *C. latipinnis*, whereas it had significant negative associations with juvenile *P. promelas*, *F. zebrinus*, *G. affinis*, and larval *C. lutrensis* and *P. promelas*. Of the three possible comparisons among adult native species, two showed significant positive associations.

When sample size was sufficiently large, we also assessed correlations in rank abundance among native and nonnative fishes. Significant positive correlations of larval native fishes and nonnative fishes only occurred between larval *C. discobolus* and juvenile *C. lutrensis* ($r = 0.30$, $P < 0.01$) and *C. carpio* ($r = 0.47$, $P < 0.01$). Abundance of larval *C. latipinnis* showed a significant negative correlation with juvenile *P. promelas* ($r = -0.54$, $P < 0.01$) and larval *C. lutrensis* ($r = -0.48$, $P = 0.05$). Thus, even though there was a significant positive association

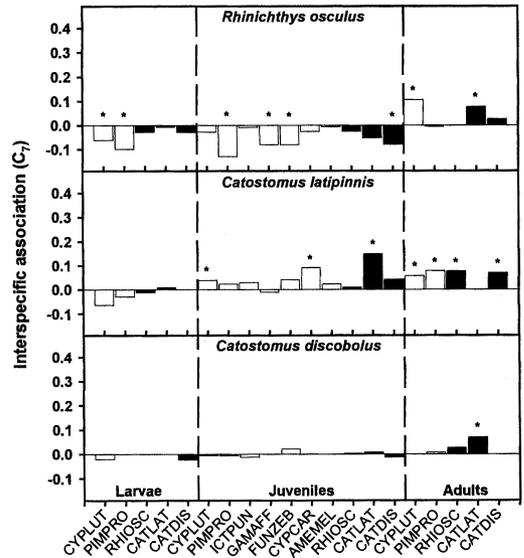


Fig. 6. Index of interspecific association (C_7) among adult of three native fishes with other species/age class in San Juan River secondary channels. Asterisks indicate significant deviation from random coexistence. Open bars represent native versus non-native comparisons, and closed bars represent native versus native comparisons.

among these species (using presence/absence), abundance was negatively correlated. Among native species, larval *R. osculus* was significantly correlated with larval *C. latipinnis* ($r = 0.42$, $P = 0.04$) and juvenile *R. osculus* ($r = 0.34$, $P < 0.01$).

Abundance of the two catostomid juveniles were positively correlated with juvenile and adult *P. promelas* and adult *C. lutrensis* ($r = 0.21$, $P < 0.05$). Juvenile *C. latipinnis* abundance was negatively correlated with *F. zebrinus* ($r = -0.54$, $P = 0.02$) as was the abundance of juvenile *R. osculus* with *G. affinis* ($r = -0.26$, $P = 0.01$) and larval *C. lutrensis* ($r = -0.28$, $P = 0.02$). There was no significant positive correlation among native juveniles. The only significant correlation of an adult/subadult native species with either native or nonnative fishes was between *C. latipinnis* and juvenile *C. lutrensis* ($r = 0.30$, $P = 0.01$).

DISCUSSION

Secondary channels in the San Juan River provide habitats commonly used by native and nonnative fishes (Gido et al., 1997). Within these channels, we examined habitat use and associations among native and nonnative fishes at the pool/riffle scale (sensu Frissel et al., 1986). Thus, our sampling methods did not enable us to characterize microhabitat partitioning (e.g., vertical position in water column). Overlap in habitat use at the scale we examined was seasonally quite high, especially among larval and juvenile fishes.

The degree of overlap in habitat use by stream fishes appears to be quite variable and dependent upon the scale of analysis and/or age classes of species considered. In our study, classification success among species/size classes using discriminant function analysis was poor (23.4%), indicating high overlap in habitat use. Similarly, in a study on habitat partitioning in Black Creek, Mississippi, Ross et al. (1987) were only able to predict the occurrence of 24 fish species based on microhabitat variables 18% of the time. In contrast, Baker and Ross (1981), also on Black Creek, were able to predict the occurrence of eight cyprinid species 62.4% of the time using microhabitat data that included vertical position in the water column. Moreover, Rinne (1992) showed significant differences in habitat use among adults of seven native fish species in a southwestern stream using analysis of variance.

Much of the overlap in habitat use in our study occurred among species within age classes. When the analysis was performed with spe-

cies combined into age classes, the classification success improved (50.4%). This indicated a greater ability to predict habitat use by age class than by species. The low classification success of native juvenile and larval fishes relative to nonnative fishes was because they used similar habitats to those occupied by the numerically dominant nonnative fishes. These included low velocity, silt bottomed habitats. Given the similarities in habitat use, especially that of native and nonnative larvae and juveniles, there is potential for negative interspecific interactions.

Habitat partitioning between subadult/adult native and nonnative fishes probably limited the potential for negative interactions at this life stage. Adult *R. osculus* had the least overlap with nonnative fishes because it occupied riffle habitats with high current velocity. Currently, no riffle-dwelling nonnative has become established in the San Juan River. Subadults of the two native catostomid species tended to occupy deep habitats (> 0.3 m) that were only seasonally abundant in secondary channels. For much of the year, catostomid subadults occupied the deeper primary channel where they coexisted with other large-bodied nonnative fishes (*C. carpio* and *I. punctatus*; unpubl. data).

Larvae of both native and nonnative fishes occurred in similar habitats, but the abundance of native larvae usually peaked before that of nonnatives. The temporal separation of abundance peaks was because reproduction of most native fishes in southwestern streams is closely linked to spring runoff when water temperature is comparatively cool (Baltz and Moyle, 1993). Most nonnative species in the San Juan River spawned later when water temperatures were warmer. The negative correlation between abundance of larval *C. latipinnis* and *C. lutrensis* best illustrates this point. Larval *C. latipinnis* were in very low abundance by the time larval *C. lutrensis* were common (late July and early August). Only *C. carpio* spawned early enough in the year to show high overlap of its juveniles with native larval fishes. Because of similar resource requirements of larval fishes, differences in spawning chronology may reduce resource sharing (Floyd et al., 1984). Thus, the temporal segregation of spawning by native and nonnative species in the San Juan River may reduce overlap in habitat use among larvae.

The greatest degree of overlap in habitat use was among native and nonnative juveniles. In the San Juan River, during the late summer-autumn when flows are typically low, fish densities exceeded 50 individuals m^{-2} in many secondary channel low-velocity habitats, and most of these individuals were juveniles. Competition for re-

sources would presumably be most likely when habitats are limited and species abundances are high (Schlosser, 1982; Yant et al., 1984; Bart, 1989). Nonnative *C. lutrensis*, which accounted for the large majority of these individuals, has also been shown to be more aggressive (Karp and Tyus, 1990) and able to displace (Douglas et al., 1994) native fishes. Thus, during periods of low flows, when habitat dimensions are reduced and densities of all species are at or near their annual peak, competitive bottlenecks may exist within San Juan River secondary channel habitats.

Several abiotic attributes of the San Juan River may, however, diminish the potential for competition among species that use similar habitats. Because mortality and displacement by disturbance can moderate abundance of fish species, resource availability is not believed to be a limiting factor in streams that are hydrologically variable (Grossman et al., 1985; Moyle and Baltz, 1985; Baltz and Moyle, 1993). Thus, the high overlap in habitat use we detected may have been the result of juveniles aggregating in areas with abundant resources. The timing and magnitude of disturbance events (e.g., floods) appears to influence the importance of biotic interactions in southwestern streams (Minckley and Meffe, 1987).

Avoidance of predators may influence the fish assemblage of secondary channels. Juvenile and larval native and nonnative fishes may remain in secondary channel habitats to avoid predation by piscivores that are common in primary channel habitats (e.g., *I. punctatus*; J. Brooks, pers. comm.). This may concentrate these individuals into refugia habitat and increase the potential for biotic interaction (e.g., Persson and Greenberg, 1990). In particular, predation of native larval by adult nonnative fishes (e.g., *C. lutrensis*; Ruppert et al., 1993) in secondary channel habitats may also reduce survival of native fishes.

Although determining whether negative interactions occur among native and nonnative fishes and thence identifying the specific modes of interaction is problematic, control of nonnative fish abundance is probably critical to conservation of native fishes in southwestern river systems (e.g., Miller, 1961). Several native San Juan River fishes (e.g., *Gila robusta* and *Ptychocheilus lucius*) have experienced substantial declines in abundance that coincided with the impoundment of the river and establishment of nonnative fish species (Platania et al., 1991). Regardless of the mechanisms influencing the fish assemblages in San Juan River secondary channels (including random associations), several

nonnative fish species are numerically dominant for much of the year. At least one (*C. lutrensis*) has been implicated in the decline of native fishes elsewhere in the American Southwest (e.g., Minckley and Deacon, 1968; Douglas et al., 1994). Until the issues of competition and predation among native and nonnative fish species in the San Juan River is more accurately defined, prudent resource management should incorporate measures to suppress nonnative fish abundance.

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APPENDIX 1. EQUATIONS USED TO DETERMINE ASSOCIATIONS BASED ON PRESENCE AND ABSENCES OF SPECIES/AGE-CLASS PAIRS IN THE SAN JUAN RIVER (RATLIFF 1982).

Given the following:

Species A	Present Absent	Species B	
		Present a c	Absent b d
When $ad \geq bc$ and $c < b$		$C_7 = \frac{ad - bc}{(a + b)(b + d)}$	
When $ad \geq bc$ and $c \leq b$		$C_7 = \frac{ad - bc}{(a + c)(c + d)}$	
When $ad < bc$ and $a \leq d$		$C_7 = \frac{ad - bc}{(a + b)(a + c)}$	
When $ad < bc$ and $a > d$		$C_7 = \frac{ad - bc}{(b + d)(c + d)}$	

APPENDIX 2. SPECIES OF FISH COMMONLY COLLECTED IN SAN JUAN RIVER SECONDARY CHANNEL HABITATS AND THE WEIGHTED MEAN (STANDARD DEVIATION) OF HABITAT ATTRIBUTES OCCUPIED BY EACH AGE CLASS OF EACH SPECIES. Larvae = L, juvenile = J, subadult = SA, and adult = A.

Species/age class	Total number of indiv.	Number of sampled habitats present	Velocity (cm sec ⁻¹)	Depth (cm)	Percent silt	Percent sand	Percent gravel	Percent cobble	Percent rubble	Percent boulder	Percent debris
<i>C. lutrensis</i> —L	3021	89	0.3 (6.3)	14.5 (18.4)	70.6 (39.3)	3.2 (14.7)	7.9 (16.2)	15.8 (24.9)	2.1 (11.4)	0.4 (4.0)	10.4 (39.3)
<i>C. lutrensis</i> —J	13185	479	2.7 (17.3)	28.3 (19.1)	53.7 (39.5)	14.2 (26.4)	12.0 (17.5)	15.2 (23.9)	2.8 (10.8)	0.2 (2.8)	25.0 (46.6)
<i>C. lutrensis</i> —A	6688	455	11.2 (25.8)	38.2 (20.4)	52.9 (38.7)	16.4 (27.7)	8.1 (18.0)	18.6 (25.9)	3.7 (13.3)	0.3 (4.3)	28.7 (46.2)
<i>P. promelas</i> —L	3732	133	11.4 (5.3)	24.8 (19.7)	63.2 (36.9)	3.0 (13.3)	5.1 (14.5)	24.5 (23.5)	3.6 (13.0)	0.4 (3.6)	16.9 (39.1)
<i>P. promelas</i> —J	12257	377	1.1 (13.8)	26.8 (17.6)	66.5 (39.0)	3.8 (25.6)	9.1 (16.7)	15.2 (21.7)	4.1 (11.6)	0.1 (2.7)	37.6 (45.3)
<i>P. promelas</i> —A	3099	347	4.5 (21.5)	31.3 (18.6)	47.8 (39.8)	20.7 (28.7)	16.6 (18.2)	10.6 (23.3)	2.8 (10.9)	0.2 (4.2)	20.8 (47.2)
<i>R. osculus</i> —L	1243	131	2.4 (12.2)	20.2 (16.1)	43.5 (38.3)	11.6 (22.4)	11.0 (18.9)	29.1 (25.7)	4.7 (10.9)	0.1 (3.1)	20.8 (41.0)
<i>R. osculus</i> —J	4631	497	10.3 (21.2)	22.4 (16.9)	28.6 (37.6)	18.9 (25.1)	18.4 (20.1)	28.6 (27.1)	4.7 (13.8)	0.5 (2.3)	33.5 (43.7)
<i>R. osculus</i> —A	942	228	48.9 (45.9)	25.3 (17.0)	14.4 (29.4)	20.3 (28.9)	13.8 (20.2)	35.2 (30.9)	16.0 (21.3)	0.1 (4.1)	18.7 (38.8)
<i>C. latipinnis</i> —L	318	58	8.6 (10.9)	19.1 (12.8)	46.7 (35.4)	19.9 (24.8)	13.1 (17.0)	12.8 (16.3)	5.7 (8.6)	0.17 (4.9)	19.8 (36.2)
<i>C. latipinnis</i> —J	1086	197	4.1 (18.6)	24.8 (16.6)	51.9 (38.4)	19.6 (28.1)	16.0 (19.4)	10.2 (20.7)	1.7 (8.1)	0.2 (2.7)	27.1 (44.9)
<i>C. latipinnis</i> —SA	235	99	12.1 (24.0)	40.0 (18.4)	54.4 (39.7)	14.1 (24.8)	8.0 (17.2)	19.5 (29.2)	3.8 (10.1)	0.3 (4.7)	38.7 (46.8)
<i>C. discobolus</i> —L	664	100	2.0 (15.4)	21.5 (14.8)	52.5 (37.9)	16.3 (23.5)	13.7 (17.6)	14.7 (21.1)	2.9 (12.5)	0.0 (0.3)	27.1 (37.6)
<i>C. discobolus</i> —J	762	143	2.4 (15.2)	27.3 (17.0)	42.8 (38.2)	9.2 (22.0)	21.5 (20.9)	22.5 (20.3)	3.9 (12.9)	0.1 (4.0)	12.6 (43.0)
<i>C. discobolus</i> —SA	38	25	29.5 (28.7)	36.5 (19.0)	15.9 (33.3)	29.7 (29.5)	14.6 (19.6)	26.5 (28.5)	12.3 (25.7)	0.9 (6.9)	18.4 (40.0)
<i>I. punctatus</i> —J	450	92	15.0 (16.8)	40.6 (23.1)	53.3 (35.8)	11.0 (25.6)	8.7 (14.5)	15.9 (24.7)	11.1 (17.3)	0.0 (1.3)	45.3 (47.6)
<i>G. affinis</i> —J	1660	116	3.0 (7.9)	20.0 (15.0)	65.3 (38.6)	1.7 (15.5)	2.4 (14.5)	23.9 (25.9)	6.6 (13.3)	0.1 (3.2)	16.3 (44.3)
<i>F. zebrius</i> —J	1130	102	3.0 (7.2)	12.5 (9.9)	51.9 (36.7)	8.8 (7.8)	2.2 (14.7)	23.5 (24.3)	12.9 (16.1)	0.0 (0.3)	8.7 (29.9)
<i>C. carpio</i> —J	324	105	5.2 (32.7)	26.0 (17.1)	39.6 (37.8)	30.1 (25.9)	11.2 (18.9)	15.3 (20.5)	3.1 (10.5)	0.4 (4.2)	18.2 (44.2)
<i>A. melas</i> —J	99	32	1.6 (7.6)	30.6 (18.7)	57.3 (39.6)	3.2 (14.2)	2.5 (11.9)	34.6 (31.3)	1.4 (7.2)	0.0 (0.0)	67.7 (49.6)
Species mean			7.3 (11.1)	27.3 (7.7)	49.4 (14.5)	13.4 (8.5)	10.7 (4.9)	19.6 (8.0)	5.3 (3.9)	0.5 (0.9)	29.2 (16.0)
Sampled mean			21.9 (25.0)	24.4 (16.5)	36.1 (16.6)	10.8 (14.6)	15.6 (12.9)	21.9 (14.2)	13.9 (12.2)	1.7 (4.2)	3.4 (42.3)

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