

Spatial and temporal variation of fish communities in secondary channels of the San Juan River, New Mexico and Utah

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Synopsis

Spatial and temporal variation of fish communities in four secondary channels of the San Juan River between Shiprock, NM and Bluff, UT were investigated from July 1993 through November 1994. Fish abundance and habitat availability data were collected to determine if physical attributes of sites influenced spatial and temporal variation in their fish communities. Stability of habitat was shown to positively influence the stability of the fish community. Analysis of variance revealed greater spatial than temporal variation in the abundance of red shiner, *Cyprinella lutrensis*, fathead minnow, *Pimephales promelas*, and flannelmouth sucker *Catostomus latipinnis*, while speckled dace, *Rhinichthys osculus* showed greater temporal variation. Ordination, using detrended correspondence analysis, revealed variation in fish communities by site, date, and sample year. Spatial variation was greatest during low-flow periods when the greatest differences in habitat among the four sites occurred. Spring runoff had the greatest temporal effect on the fish communities in secondary channels and appeared to 'reset' the communities by displacing those species that were less resistant to increased current velocities. This annual event may help maintain native fish species adapted to these conditions in the San Juan River while moderating the abundance of nonnative fish species.

Introduction

Research to elucidate the dynamics of stream fish communities has generally focused on either abiotic or biotic factors. Within the abiotic approach, factors such as habitat complexity (Pearsons et al. 1992, Capone & Kushlan 1991), physical-chemical gradients (Edds 1993, Taylor et al. 1993), and flow regime (Bain et al. 1988, Schlosser 1990) have been demonstrated to have spatial and temporal effects upon stream fish community stability. The relative

influence of each varies with stream size, discharge (e.g., controlled versus natural), geomorphology, and anthropogenic activities. The longevity of particular habitats and the relative predictability of temporal disturbances such as spates, floods, or droughts also influence survivorship of individuals and displacement of resident fishes (Meffe 1984, Ross et al. 1985, Matthews 1986, Capone & Kushlan 1991). The impacts of such disturbances are highly variable. For example, at one time an increase in discharge may serve as a cue to initiate spawning while

a similar event at another time may eliminate nursery habitats or displace fish larvae downstream into unsuitable habitats. Generally, streams with frequent and intense disturbances have greater temporal variability in their fish communities than do streams with lower levels of disturbance (e.g., Ross et al. 1985, Schlosser 1990). The metrics by which the influence of given factors upon fish community structure and stability are measured are typically some aspect of individual species abundance or index of community structure (e.g., species richness or evenness).

Lotic systems of the arid American southwest are subject to dramatic and substantial changes in discharge (Minckley et al. 1986, Poff & Ward 1989). The normal or expected pattern of elevated spring flows, early-summer low flows, brief and sporadic flow spikes in association with late-summer and early-autumn convective storms, and late-autumn and winter low flows frequently does not occur. Viewed from a disturbance perspective, fish communities in southwestern streams might be expected to have comparatively high variability and demonstrate little stability. Conversely, habitat heterogeneity and presence of refugia may enhance their stability and reduce variability (Townsend 1989, Sedell et al. 1990, Yount & Niemi 1990, Pearsons et al. 1992).

The scale by which stream fish communities are investigated should be chosen to reflect biologically meaningful units (Matthews et al., 1994). The San Juan River of northwestern New Mexico and southeastern Utah is a hydrologically dynamic system with considerable and unpredictable changes in discharge. For a substantial portion (130 km) of its 350 km course, the river channel below Navajo Reservoir is braided with a majority of the flow in the primary channel and the remainder in one or more secondary channels. These secondary channels provide habitats that are uncommon and seasonally absent in the primary channel and support a fish fauna at least qualitatively different from that of the primary channel (Gido 1995, Gido & Propst unpublished data). We hypothesized that secondary channel habitats were essential to the persistence of several native and nonnative fish species in the San Juan River. An initial step in assessing the relative

importance of secondary channels to the structure and stability of the San Juan River fish community was to characterize the spatial and temporal variability and dynamics of secondary channel fish communities. Spatial variation in secondary channel fish communities may be the consequence of channel length, habitat complexity, persistence of flowing water, or temperature. Temporal variation may result from seasonal changes in discharge that affect the physical-chemical attributes of these channels.

Herein, we focused on characterizing the response of San Juan River secondary channel fish communities to temporal changes in flow and the resultant spatial changes in habitat. As such, this examination presents only one facet of the complex array of biotic and abiotic factors which influence the structure and stability of the San Juan River fish community.

Study area and methods

Study area

The San Juan River is a major tributary of the Colorado River and drains 99200 km² in Colorado, Utah, Arizona, and New Mexico (Carlson & Carlson 1982; Figure 1). Elevation of the river ranges from 3048 m in the San Juan Mountains of southwestern Colorado to 1130 m at Lake Powell in southeastern Utah. Mean gradient of the river between Shiprock, NM and Bluff, UT was 1.5 m km⁻¹. Annual discharge at Shiprock averaged 68 m³ s⁻¹ from 1978 through 1993 with an average yearly peak flow of 464 m³ s⁻¹ and an average yearly minimum flow of 3 m³ s⁻¹.¹ Water releases from Navajo Reservoir, located near the New Mexico/Colorado border, reduce the natural variability in the flow regime of the river by diminishing peak flows during spring runoff and elevating base flows during lowflow periods (early summer, late autumn, and winter). Current reservoir releases and flow from unimpounded tributaries, however, enable retention of a semi-

¹ U. S. Geological survey. 1993. U.S. Geological Survey Water-Data Report New Mexico 93-1.

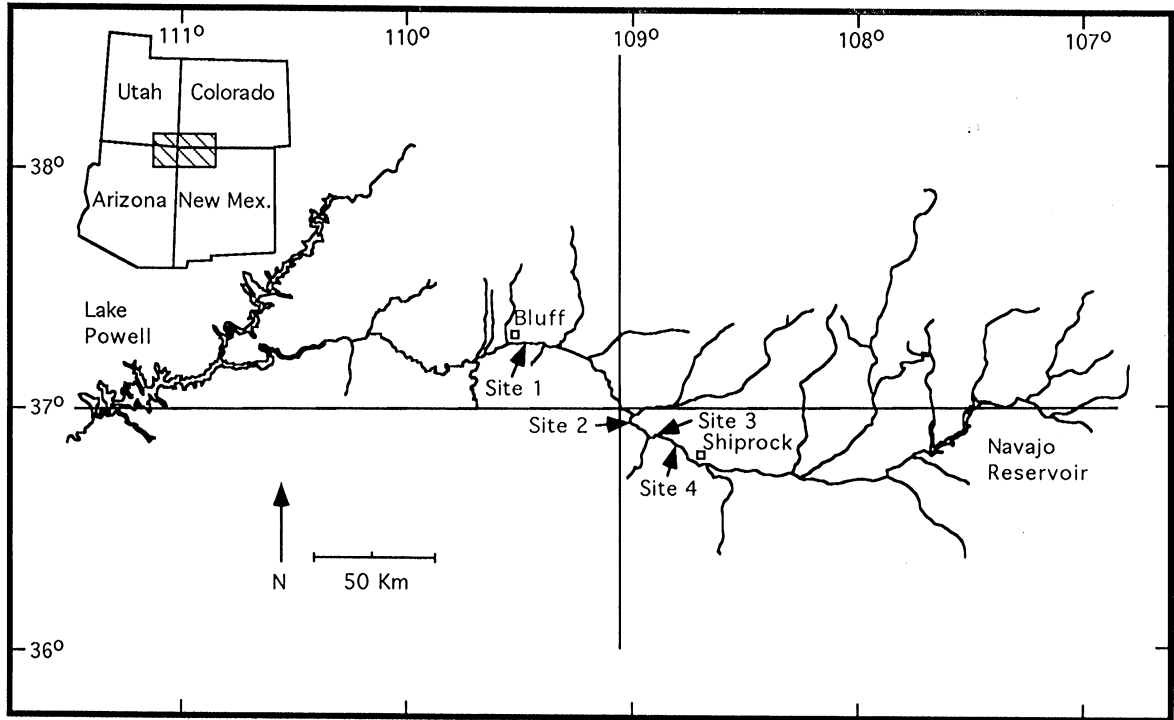


Figure 1. Location of the four secondary channels studied on the San Juan River, New Mexico and Utah.

natural pattern of elevated spring flows followed by low summer through winter flows.¹ Riparian vegetation is primarily saltcedar *Tamarix chinensis*, Russian olive *Eleagnus angustifolia*, willow *Salix* sp., and cottonwood *Populus fremontii*. River substrate is mainly bedrock, boulder, and silt-sand with interspersed cobble bars.

Channel braiding of the San Juan River is most extensive between Shiprock, NM and Bluff, UT. In this reach (130 km), the floodplain broadens and lateral movement of the channel creates a relatively high diversity of habitat types (e.g., secondary channels, backwaters, and riffles). Above this reach, the river flows through several municipalities and is largely constrained by bank reinforcements. Downstream of Bluff, the river is generally confined to a canyon and braiding is minimal.

We selected study channels that were of sufficient length to have different physical-chemical properties (e.g., temperature and conductivity) from the main channel, less than one-fourth the discharge of the main channel, and representative of the array of

secondary channels in the river. Study sites, which ranged from 115 to 300 m in length, were in the middle or lower portion of the secondary channel and encompassed all primary habitats (riffle, pool, and run). The four secondary channels chosen were between Shiprock and Bluff (Figure 1) at river kilometers 140.6, 207.4, 216.6, and 226.7 (sites 1 through 4, respectively; Piute Farms Marina, UT = river kilometer 0.0). Lengths of these channels were 2.90, 0.88, 3.38, 2.17 km, respectively.

Fish sampling

Sampling began in July 1993 for sites 1 through 3 and in August 1993 for site 4. We sampled each site every three weeks from peak spring flow (May or June) through November and every sixth week thereafter. Several collection techniques were used to maximize sampling efficiency and to ensure that all species present were collected in proportion to their true abundance. A 1.8 x 2.4 m drag seine with

2.6 mm mesh was the primary and most efficient sampling gear in most habitats. A pulsed DC 12 v battery-powered backpack electrofisher was used where substrate or debris inhibited seining. The backpack electrofisher and seine were used in combination to sample riffles. Surface area of each habitat sampled was measured and used to compute catch per unit area (number of individuals m^{-2}). At least 10 and up to 30 habitats were sampled at each site, the number depended upon wetted area.

Care was taken to sample all fish habitats within the study area in proportion to their availability. One exception was during spring runoff when only shoreline habitats were sampled because mid-channel habitats were either too deep (> 1.5 m) or current too swift (> 2 m^3 s^{-1}) to allow effective sampling. Exclusion of mid-channel habitats during spring runoff probably did not bias results as such areas have fewer individuals (Ross & Baker 1983).

Most larger specimens (> 100 mm total length) were identified, counted, and released near point of capture. Smaller individuals were preserved in 10% buffered formalin and returned to the laboratory for identification and enumeration.

Habitat characterization

Habitat measurements were taken concurrent with fish sampling, beginning in August 1993. We quantified available habitat by measuring depth, velocity, and substrate at 100 points within each site. At the two widest sites (3 and 4), 10 measurements were taken across 10 equally spaced transects within the study reach. At the narrower sites (1 and 2), five measurements were taken across 20 equally spaced transects. Velocity was determined at 60% depth. Dominant substrate type at each point was estimated visually and by touch as silt (< 0.12 mm), sand (0.12-1.0 mm), gravel (1.0-64 mm), or cobble (> 64 mm). Percent coverage of each substrate type was then calculated as the proportion of points where that substrate was dominant. Discharge of each secondary channel was determined at the transect that yielded the most accurate measurement (smooth bottom and laminar flow). To reduce bias, all habitat measurements were made by the same

individual. Temperature and conductivity were measured with each collection with the exception of a few sample dates when the meters malfunctioned.

Data analysis

Mean, standard deviation, and coefficient of variation ($cv = \text{standard deviation}/\text{mean}$) were calculated for discharge, channel width, depth, velocity, and percent coverage by substrate type. Coefficient of variation was used as a means to determine the heterogeneity of each habitat variable by site. Those sites with homogeneous conditions had relatively low cv compared to higher cv for more heterogeneous sites. Repeated measures analysis of variance (ANOVA) was used to assess differences among sites for each habitat variable. If differences were found, Bonferroni adjustments were made for multiple comparisons. To approximate normality, Log_{10} transformations were performed on discharge, depth, and velocity prior to this analysis. Principal components analysis (PCA) was used to characterize the variation in habitat measurements across space and time. Analysis of variance was used to determine significant differences between sample sites and sample dates based on axes scores.

Similarities of fish assemblages among study sites and sample dates were estimated using Morisita's index (Morisita 1959). To estimate stability of the fish community within each of the four sites, we calculated the mean similarity of the fish community across time. Differences in mean similarity between sites were tested using ANOVA with a Bonferroni adjustment for multiple comparisons. To examine temporal variation in the fish communities among secondary channels, we calculated the mean similarity of all pair-wise comparisons of the four sites for each sample period. To examine temporal changes in the fish community within a secondary channel, we calculated the similarity of the fish community with the previous sample period for each channel.

Although Morisita's index does not account for sampling variance (Smith & Zaret 1982) it is independent of diversity (Wolda 1981) and provides a simple comparative measure independent of other

methods used in this paper. Morisita's index ranges from zero (no similarity) to slightly greater than one (high similarity). Means and standard deviations were calculated for all pair-wise comparisons of sample dates by site and for all pair-wise comparisons of sample sites by date.

We analyzed the variation in species abundances using detrended correspondence analysis (DCA). DCA is a multivariate technique derived from reciprocal averaging that maximizes the correlation between species scores and sample scores along an assumed gradient (Hill & Gauch 1980). Thus, sample scores are constrained by the species scores, and species scores are constrained by the sample scores. Species abundance was calculated as the number of individuals m^{-2} seined at each site for a given date. These values were then square root transformed to

reduce the influence of extreme values. Rare species (< 0.1% of total catch) were excluded from the analysis. Eigenvalues, eigenvectors, and axes scores were calculated using CANOCO².

Analysis of variance was used to determine if significant differences existed between sample sites and sample dates based on axes scores. If significant differences were found, Bonferroni multiple comparisons test was used to determine where the differences occurred. Differences in community structure between sample years were also tested using Student's *t*-test. Because this study began in July 1993 and ended in November 1994, only the July-November period was compared between years.

Repeated measures ANOVA without replication (Sokal & Rohlf 1995) was used to determine spatial and temporal variation in individual species abundances. We estimated abundance as the number of individuals captured/unit surface area sampled. This number was $\text{Log}_{10}(x + 1)$ transformed to approximate normality. Because of the normality assumptions of this model, only four species that occurred consistently (spatially and temporally)

² ter Braak, C. J. F. 1987. CANOCO = a FORTRAN program for canonical community ordination by [partial][detrended][canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Agricultural Mathematics Group, Wageningen. 95 pp.

Table 1. Number of each species caught and average number of individuals caught m^{-2} (in parentheses) in the four San Juan River secondary channels sampled. The last column represents the percent of the overall catch by species (rows) and site (columns). Species codes are used in the detrended correspondence analysis.

Species	Species code	Site				Total number (number m^{-2})	Percent
		1	2	3	4		
<i>C. lutrensis</i> ^d	RED SHIN	7120 (7.801)	5001 (1.539)	12464 (3.537)	2578 (1.060)	27163 (3.493)	46.3
<i>C. carpio</i> ^d	COMMCARP	90 (0.060)	137 (0.037)	83 (0.022)	30 (0.005)	340 (0.031)	0.6
<i>Gila robusta</i>		5 (0.006)	2 (<0.001)	5 (0.001)	0	12 (0.002)	< 0.1
<i>P. promelas</i>	FATHMINN	3773 (4.938)	5480 (3.692)	8371 (2.549)	1103 (0.310)	18727 (2.919)	31.9
<i>R. osculus</i>	SPECDACE	731 (0.469)	1117 (0.358)	2509 (0.641)	1523 (0.612)	5880 (0.512)	10.0
<i>C. discobolus</i>	BLUESUCK	104 (0.126)	225 (0.056)	783 (0.195)	320 (0.079)	1432 (0.115)	2.4
<i>C. latipinnis</i>	FLANSUCK	731 (0.480)	315 (0.059)	361 (0.089)	125 (0.044)	1532 (0.167)	2.6
<i>A. melas</i> ^d	BLACBULL	1 (< 0.001)	1 (< 0.001)	95 (0.027)	0	97 (0.007)	0.2
<i>I. punctatus</i> ^d	CHANCATF	325 (0.165)	1 (< 0.001)	76 (0.020)	317 (0.109)	719 (0.071)	1.2
<i>F. zebrinus</i> ^d	PLAIKILL	11 (0.012)	1029 (0.495)	12 (0.003)	1 (< 0.001)	1053 (0.133)	1.8
<i>G. affinis</i> ^d	WESTMOSQ	94 (0.066)	1326 (0.733)	231 (0.080)	77 (0.012)	1728 (0.233)	2.9
<i>Lepomis cyanellus</i> ^d		1 (< 0.001)	4 (0.001)	2 (0.001)	0	7 (0.001)	< 0.1
<i>L. macrochirus</i> ^d		1 (< 0.001)	0	1 (< 0.001)	0	2 (< 0.001)	< 0.1
<i>Micropterus salmoides</i> ^d		1 (< 0.001)	6 (0.002)	2 (< 0.001)	1 (< 0.001)	10 (0.001)	< 0.1
Total (number m^{-2})		12 988 (5.850)	14 644 (4.019)	24 995 (5.922)	6075 (1.856)	58 702 (4.396)	100.0
Percent		22	25	43	10	100	

¹ Introduced into the San Juan River

throughout the study period were used in this analysis. Proportion of total variation accounted for by site and time were calculated by the proportion of the total sum of squares accounted for by each effect. Three types of variation could be detected using this analysis; spatial, temporal, and error. Spatial variation occurred when the variance of abundance of a species was affected by site specific characters. Temporal variation occurred when abundance of a species changed across sample dates regardless of spatial differences. In this analysis there were no replicate samples at any site on a given date, thus the error sum of squares included any interaction between space and time (Sokal & Rohlf 1995). The ratio of spatial to temporal variation was calculated to determine the relative magnitudes of spatial and temporal variance.

Results

Fish sampling

During the study, 58 702 specimens of 14 fish species were collected (Table 1). Six species comprised 96% of the total catch. Nonnative red shiner *Cyprinella lutrensis*, fathead minnow *Pimephales promelas*, and western mosquitofish *Gambusia affinis* were the first (46.3%), second (31.9%), and fourth (2.9%) most common species. Native speckled dace *Rhinichthys osculus*, flannelmouth sucker *Catostomus latipinnis*, and bluehead sucker *C. discobolus*

were the third (10.0%), fifth (2.6%), and sixth (2.4%) most common species. The largest proportion of the total catch and highest CPUE was at site 3 and the lowest at site 4.

Habitat stability

Site 4 was the most physically stable channel as evidenced by the comparatively low cv for all significant habitat variables, except coverage of silt (Table 2). This site had significantly greater width, depth, velocity, and coverage of cobble than the other sites and had the least coverage of silt ($p < 0.05$). Similar to the primary channel, this site had continuous flow and a lower proportion of low velocity habitats compared to other sites. Site 2 was the most hydrologically variable and had the highest cv in discharge, depth, and velocity. This site had a less confining bank and the greatest difference in discharge between low flow and spring runoff. During low flow, the site remained permanently watered and connected to the main channel only by subsurface flow. Periodic increases in conductivity, greater than in the adjacent main channel, apparently resulted from this hyporheic flow. Sites 1 and 3 had intermediate cv values for most habitat variables. Site 1 was a relatively narrow, confined channel which formed isolated pool that were disconnected from the main channel during low-flow periods. Site 3 was the most physically complex site with

Table 2. Mean, standard deviation, and coefficient of variation for the eight habitat variables measured in each San Juan River secondary channel across time. Asterisk indicates a significant difference among sites ($p < 0.05$). Higher coefficient of variation indicate a less stable conditions.

Habitat variable	Site 1			Site 2			Site 3			Site 4		
	mean	SD	cv	mean	SD	cv	mean	SD	cv	mean	SD	cv
Disc. ($\text{m}^3 \text{s}^{-1}$)	0.39	0.87	2.24	1.75	6.18	3.52	2.53	6.89	2.73	5.49	6.97	1.27
Width(m)*	2.93	1.63	0.56	6.26	3.37	0.54	17.92	3.94	0.22	24.91	1.87	0.08
Depth(m)*	0.16	0.11	0.65	0.09	0.10	1.04	0.21	0.06	0.30	0.38	0.10	0.27
Velocity (m s^{-1})*	0.08	0.15	1.78	0.04	0.15	3.41	0.10	0.13	1.37	0.47	0.12	0.27
% silt*	47.8	17.5	0.37	41.6	17.9	0.43	14.1	18.3	0.45	16.1	8.35	0.52
% sand	10.1	15.3	1.51	4.1	6.0	1.46	4.7	7.0	1.50	13.8	7.3	0.53
% gravel	15.2	9.5	0.62	11.1	5.0	0.45	19.1	8.2	0.43	10.7	6.8	0.64
% rubble*	26.9	8.0	0.30	43.3	12.0	0.28	35.1	8.6	0.25	59.5	8.2	0.14

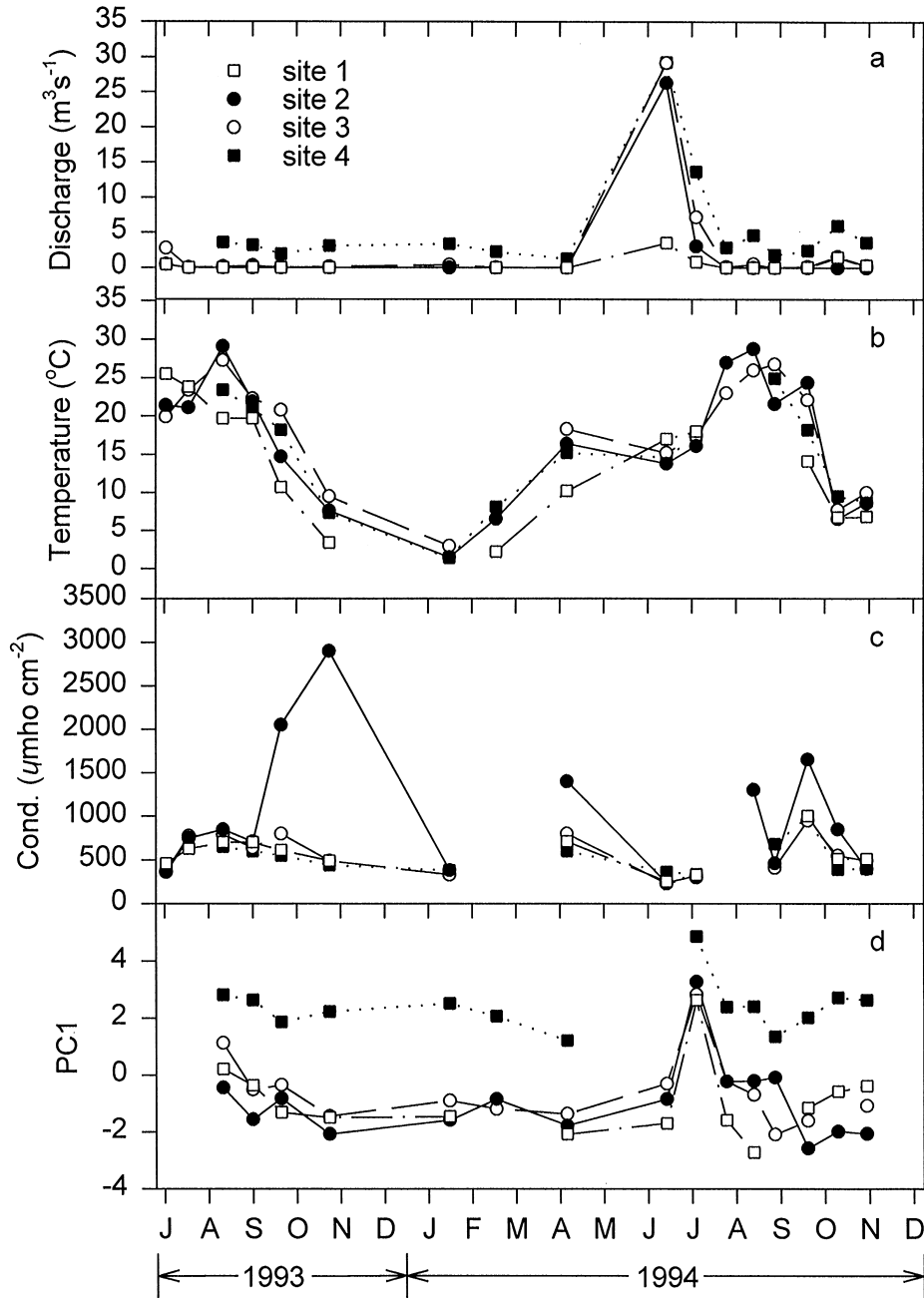


Figure 2. Temporal changes in physical and chemical properties in four San Juan River secondary channels: a-discharge, b-temperature, c-conductivity, and d-the first principal component axis from an analysis of seven habitat variables (positive loadings indicate greater depth, velocity, and percent coverage of rubble; negative loadings indicate greater coverage of silt).

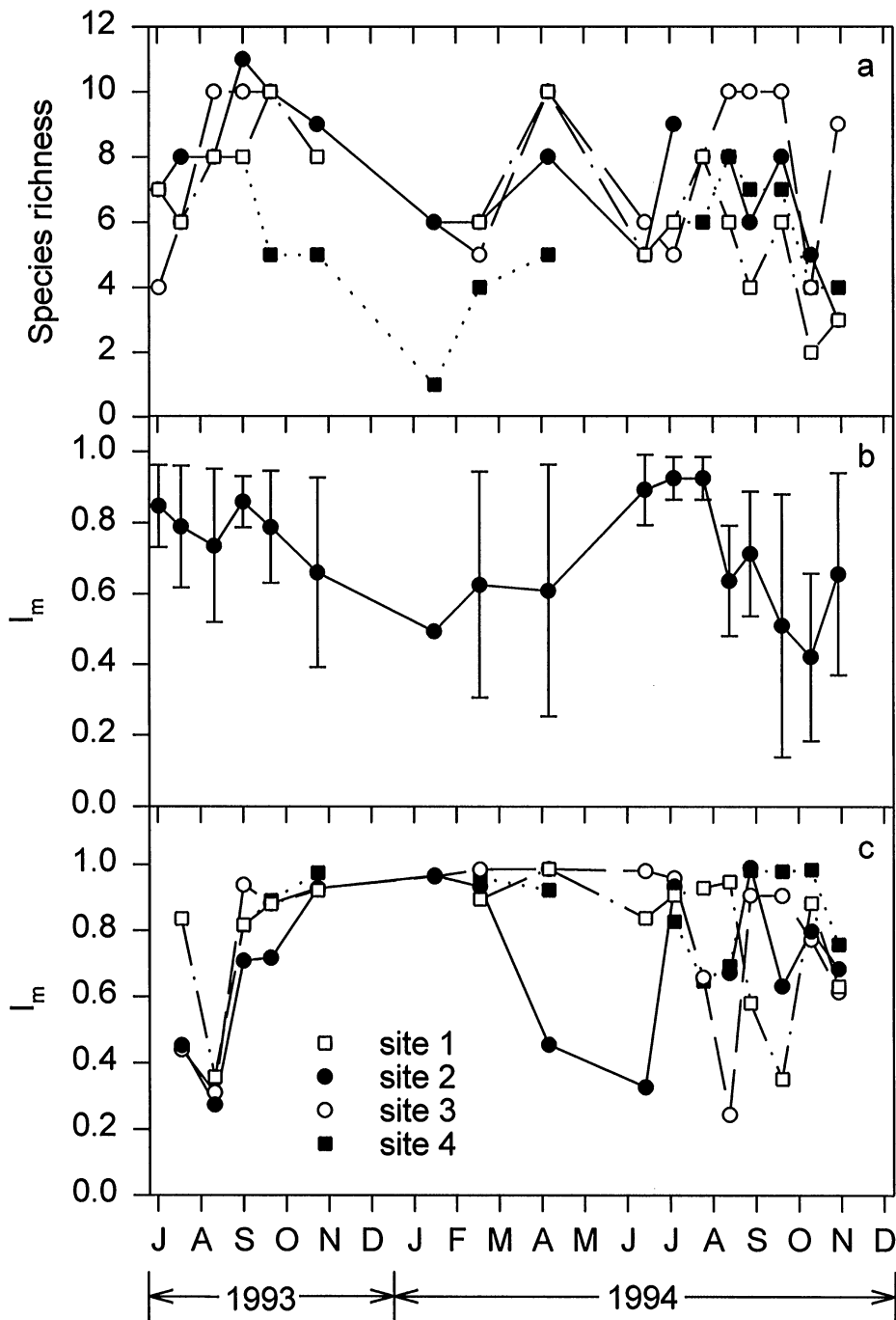


Figure 3. Temporal changes in fish community in four San Juan River secondary channels: a-species richness (number of species captured), b-mean and standard deviation of Morisita's index values calculated for all pair-wise comparisons of the fish community among the four study channels, c-Morisita's index values calculated for the similarity of the fish community with the community in the previous sample period at that site.

a series of riffles, pools, and backwater areas present during all flows.

Discharge within the four study sites ranged from as high as $30 \text{ m}^3 \text{ s}^{-1}$ in June 1994 to $0.0 \text{ m}^3 \text{ s}^{-1}$, primarily in the autumn and winter (Figure 2a). Mean water temperature in the study channels ranged from 29.1°C in August 1993 and 1994 to 1.4°C in January 1994. Temperature generally increased in the spring before runoff, attenuated as cooler waters from snowmelt passed through the system, and then increased to late summer maxima (Figure 2b). Conductivity was similar at all sites, typically between 300 and $1000 \mu\text{mhos cm}^{-2}$, except site 2 which had erratic increases up to $2900 \mu\text{mhos cm}^{-2}$ during low flows (Figure 2c).

The first principal component axis derived from an analysis of habitat variables provided a reasonable index for variation in habitat characteristics across space and time, and accounted for over 58 percent of the variation in the model (Figure 2d). Depth, velocity, and cobble had high positive loadings (> 0.40) while silt had a high negative loading (< -0.40). Site 4 had significantly higher axis scores than the other sites ($F = 78.70$, $p = < 0.001$). This reflected greater depth, velocity, and cobble coverage of this channel throughout the year. We also found a significant difference by sample date ($F = 9.54$, $p = < 0.001$). Most of this variation was because of the July 1994 sample where there was increased discharge from snowmelt.

Patterns of variation in fish species

Average number of species captured at the four sites varied with mean discharge and temperature (Figure 3a, compare with Figures 2a,b). Species richness was highest during late summer-early autumn when discharge was low and temperature was declining and in April before spring runoff. Generally, species richness was lower after an increase in discharge or when temperature was low.

In both years, similarity of the fish communities among sites was typically highest during or just after spring runoff (June and July) and generally declined as the year progressed (Figure 3b). The variance about the mean also increased after runoff, in-

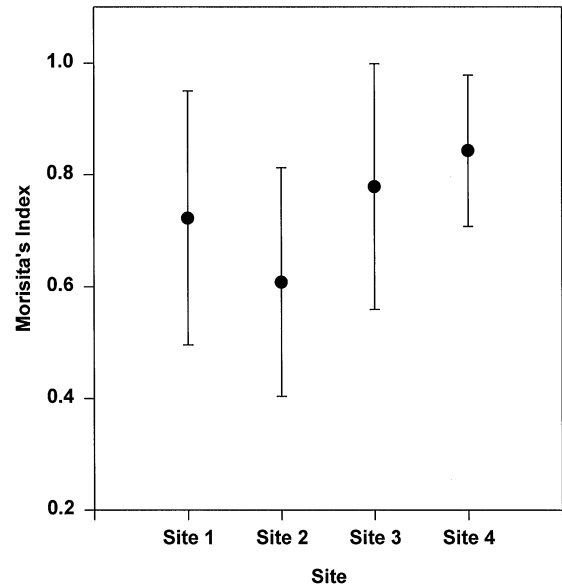


Figure 4. Mean and standard deviation of Morisita's index values calculated for all pair-wise comparisons of the fish community across sample dates for each of the four San Juan River secondary channels studied. Higher mean with less variation indicates a more stable fish community within a site.

dicating a general post-runoff divergence of the four communities. Comparisons of the fish community within each site to the previous sample showed that from September 1993 through March 1994 the fish community was relatively stable (Figure 3c). After March, however, site 2 showed a decline in the similarity of the community to the preceding sample and after July, the other sites showed a similar divergence in similarity. Mean similarity of the fish community across sample dates was significantly different between sites (Figure 4; $F = 21.38$, $p < 0.001$). Multiple comparisons between sites showed that site 4 had higher mean similarity than sites 1 and 2 but not site 3. Site 1 and 3 had higher similarity than site 2 but there was no statistical difference between them. Overall mean similarity was relatively high (> 0.6) at all sites.

The first three DCA axes summarized most of the variation in the fish communities within the four study channels. Eigenvalues for the first, second, and third axes were 0.231, 0.071, 0.039, respectively. Subsequent axes had much lower eigenvalues and did not appear to have any biological significance.

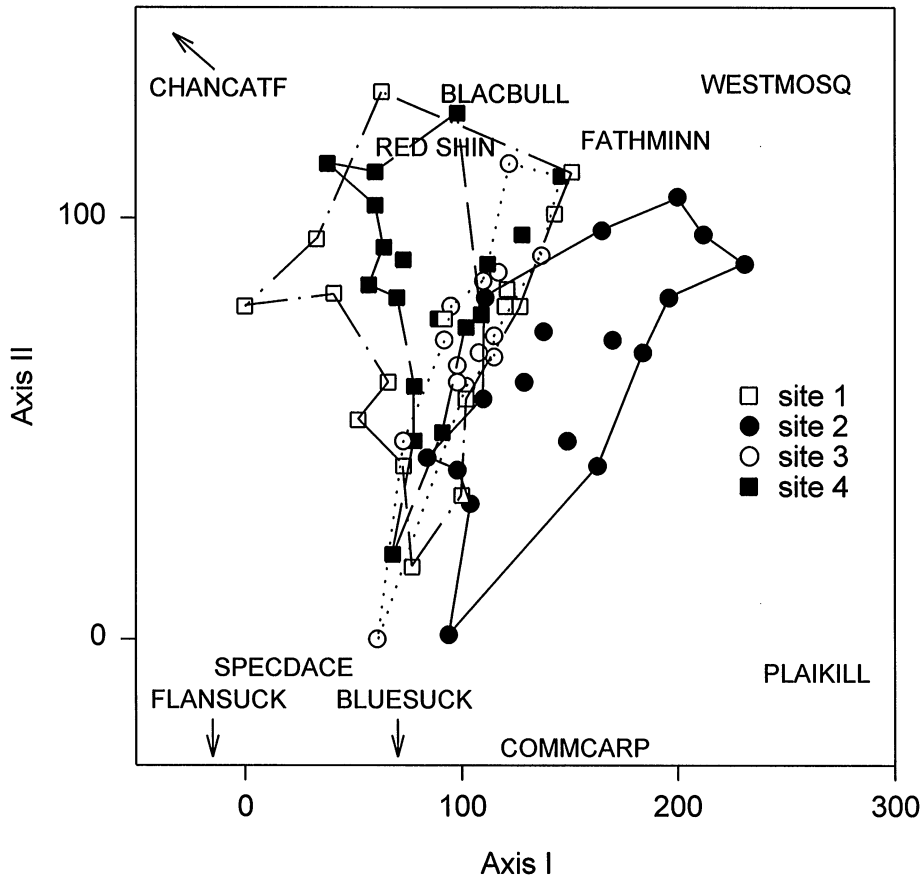


Figure 5. Plot of the first and second axis scores for species and sites from a detrended correspondence analysis (DCA) of San Juan River secondary channel fish communities. Polygons are drawn around each site for reference. Refer to Table 1 for species codes.

Scores for the first two DCA axes show a separation of samples by site, however there was still much overlap (Figure 5). Site 2 generally had the highest scores separating it from the other sites. High scores coincided with greater abundance of western mosquitofish, plains killifish, and fathead minnow while low scores indicated greater abundance of channel catfish, speckled dace, and flannelmouth sucker. DCA axis II appeared to reflect temporal variation in the fish community (see below) and high scores indicated greater abundance of nonnative fish such as red shiner, fathead minnow, and western mosquitofish. Low values indicated greater abundance of the native flannelmouth sucker, bluehead sucker, and speckled dace. A plot of DCA axis I and III showed moderate separation of site 1 from the other sites (Figure 6). High values on axis III reflected

higher abundance of speckled dace, black bullhead, and channel catfish.

DCA axes scores plotted across time for each site characterized much of the temporal variation in species abundance (Figure 7). Sample scores from DCA axis I generally showed a temporal pattern of greatest similarity during or just after snow melt (July or August) and greatest divergence in axis scores among sites from September until the next runoff event. There also appeared to be much greater variation in the fish community between sites in the fall and winter of 1994 than in 1993.

DCA axis II did not appear to show any consistent variation by site, however, there was considerable temporal variation in the fish community. All sites, except site 4, showed a decline in axes scores during late July 1994 sampling just after spring run-

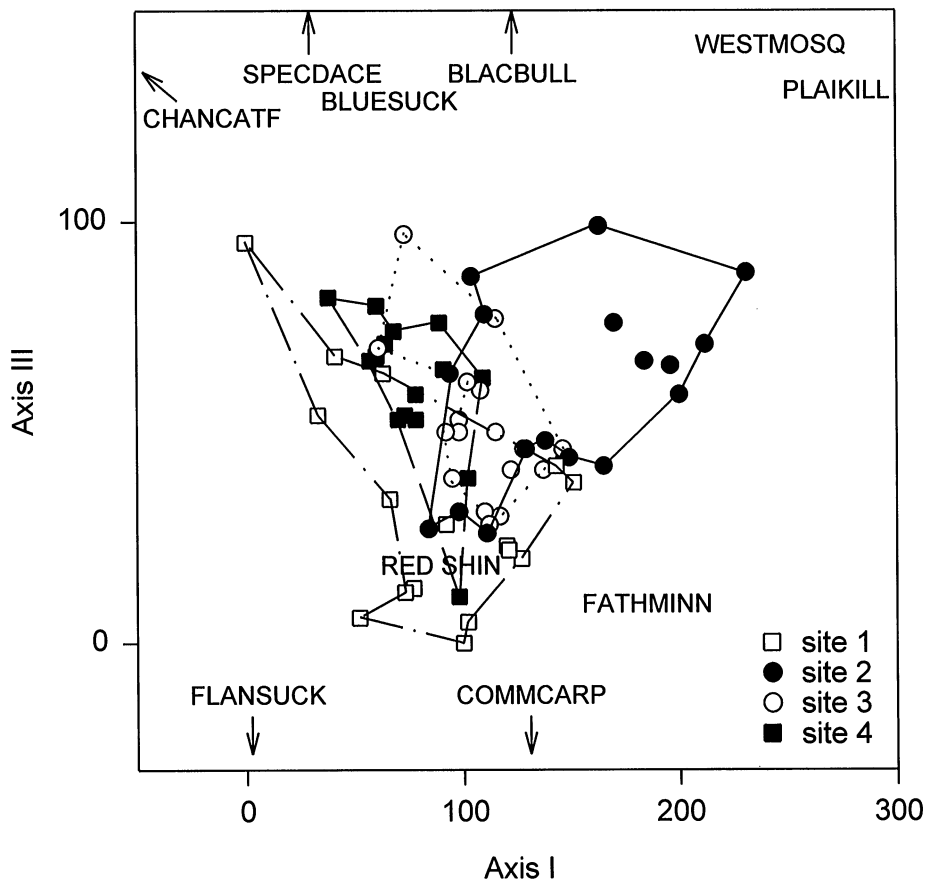


Figure 6. Plot of the first and third axis scores for species and sites from a detrended correspondence analysis (DCA) of San Juan River secondary channel fish communities. Polygons are drawn around each site for reference. Refer to Table 1 for species codes.

off. This appeared to be correlated with greater numbers of the two native sucker species during this time. In addition, all samples showed higher scores between September and November 1994 than in 1993. This was related to greater abundance of channel catfish and western mosquitofish.

Variation in the fish community as indicated by DCA axis III scores appeared to reflect both variation by site and year. Site 1 had consistently lower scores than the other sites through the spring of 1994. This appeared to be attributed to higher abundance of channel catfish, flannemouth sucker and speckled dace. However, in the late summer and autumn of 1994 there was little separation of sites and all sites had relatively high scores.

Analysis of variance on axes scores revealed sig-

nificant differences between sample sites and dates (Table 3). No differences were found between sample dates on axis I but there were significant differences between sites. Site 2 had higher scores than other sites indicating greater abundance of western mosquitofish, plains killifish, and fathead minnow. DCA axis II showed significant differences by sample date, but not by site. Of the sample dates, 28 July 1993 was significantly different from all others except 7 July, 17 August, and 8 September 1993, and 27 July 1994. These differences reflected a higher abundance of flannemouth sucker, bluehead sucker and common carp. DCA axis III indicated that site 1, was significantly different from sites 2 and 4. This appeared to be caused by greater abundance of flannemouth sucker and channel catfish.

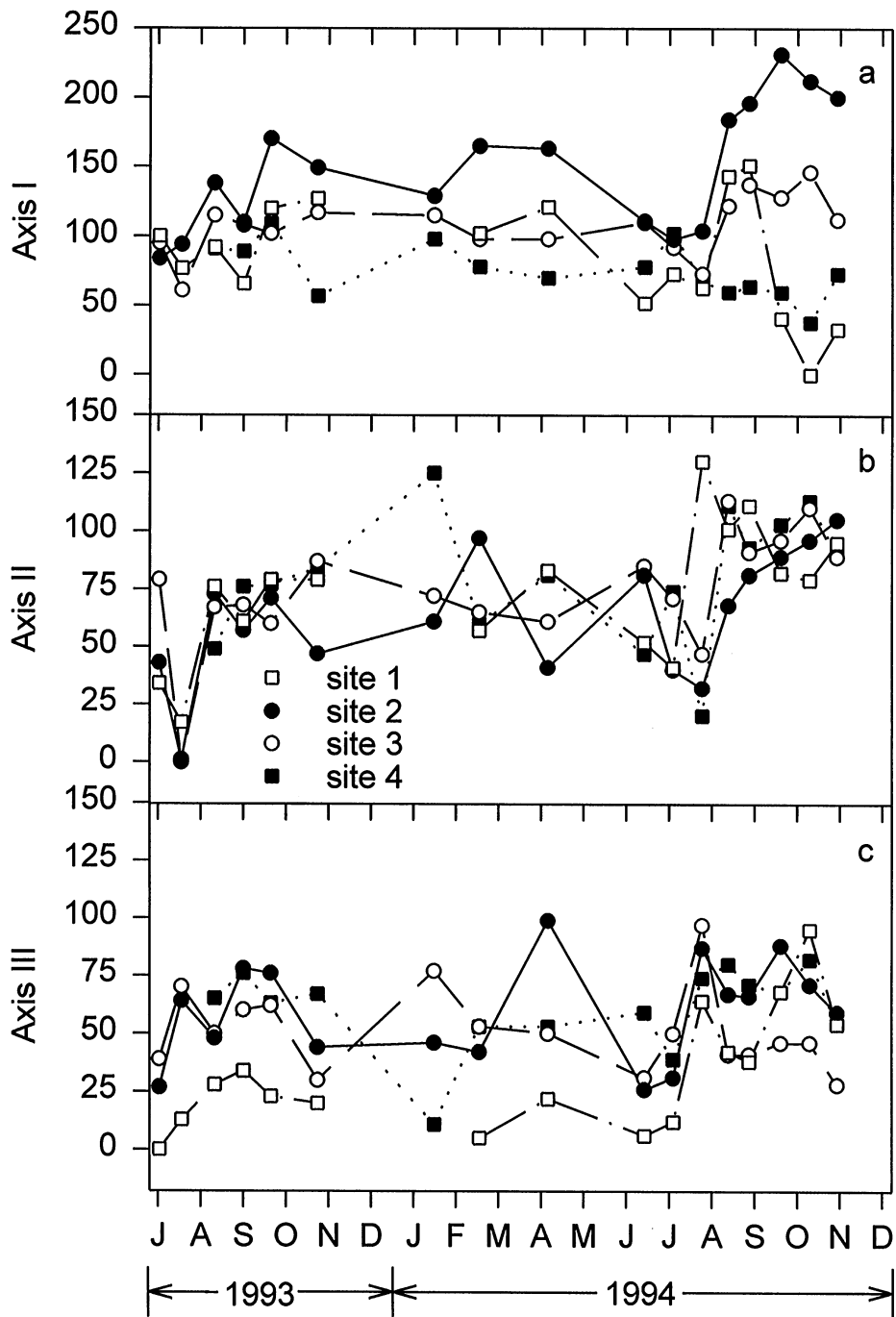


Figure 7. Temporal variation in detrended correspondence analysis (DCA) axis scores derived from the fish community sampling of the San Juan River secondary channel fish communities.

We only found significant differences between sample years on DCA axis II, although axis III was marginally significant (Figure 8). Relatively low scores in 1993 on axis II reflected higher abundance of bluehead sucker, flannelmouth sucker, and common carp relative to channel catfish, western mosquitofish and black bullhead. DCA axis III also indicated a greater abundance of speckled dace in 1994.

Significant differences in catch per unit effort

Table 3. Results of a ANOVA on DCA axis scores derived from fish community samples of San Juan River secondary channels by sample site and date. Sites and sample dates with the same letter indicate no significant difference using Bonferroni adjusted multiple comparisons.

Site	Axis		
	I	II	III
F-ratio	16.27	0.33	4.88
p-value	< 0.01	0.81	< 0.01
Site 1	A		B
Site 2	B	ns	A, B
Site 3	A		A
Site 4	A		A

Date	Axis		
	I	II	III
F-ratio	0.71	4.15	2.27
p-value	0.72	< 0.01	0.01
7.7.1993		A,B	
28.7.1993		A	
17.8.1993		A,B	
8.9.1993		A,B	
28.9.1993		B	
2.11.1993		B	
12.1.1994		B	
25.2.1994		B	
2.4.1994		B	
15.6.1994	ns	B	ns
6.7.1994		B	
27.7.1994		A,B	
16.8.1994		B	
1.9.1994		B	
24.9.1994		B	
15.10.1994		B	
5.11.1994		B	

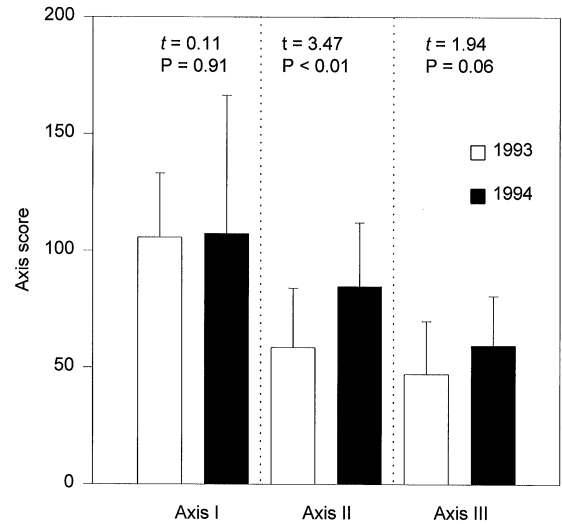


Figure 8. Mean and standard deviation for the first three axes scores derived from a detrended correspondence analysis (DCA) of the fish community in the four San Juan River secondary channels, separated by sample year. Test statistic and p values are derived from a two sample t-test between years for each axis.

were found among sites for three of the four commonly collected species (Table 4). Red shiner, fathead minnow, and flannelmouth sucker exhibited significant spatial ($p < 0.05$), but nonsignificant temporal variation. Conversely, speckled dace showed nonsignificant spatial and marginally significant temporal variation ($0.05 < p < 0.06$). Red shiner and fathead minnow had spatial to temporal variation ratios of about 3:1 while the ratio for flannelmouth sucker was near 10:1, indicating a large spatial effect. Less than 40% of the total variation was accounted for by spatial and temporal effects.

Discussion

Habitat diversity in San Juan River secondary channels was greatest during low flow periods when there was a mixture of riffle, pool, and run habitats. During high flow periods, habitat diversity was low and consisted predominantly of run habitat. This pattern, produced by variation in flow, also appeared to affect the spatial and temporal variation in the secondary channel fish communities. Greatest similarity and least variance in the fish commu-

nity among sites occurred during the spring followed by a decline in similarity and increase in variance as the year progressed (Figures 3, 7). A similar annual pattern was reported by Closs & Lake (1994) for an intermittent stream in Australia. They showed, however, that low flow periods created a 'filter' that was responsible for structuring the overall stream community. In San Juan River secondary channels, the fish community appeared to be reset by high spring flows.

Spatial variation in fish communities has been reported to be influenced by variation in velocity, stream size (depth and width), and covariates of these factors such as cover and substrate (Meffe & Sheldon 1988). Similarly, the spatial variation of fish communities observed in this study appeared to be related to differences in habitat availability and flow regimes among the four study channels. Site 4, which had the most stable habitat, also had the most stable fish community. This was illustrated by consistently high values and low variability of Morisita's index and the relatively low variation in DCA axis scores. Correspondingly, site 2, which showed the least stable habitat, had an unstable fish community as indicated by low values and high variability of Morisita's index values and large variation in DCA axis scores. These results are consistent with those of Ross et al. (1985) who showed that in-

creased habitat stability resulted in an increase in stability of the fish community.

The number of study channels ($n=4$) precluded statistical analysis of correlations between channel characteristics (size, habitat available) and community structure. However, there were several aspects of site 2 that may have contributed to differences in its fish community. For example, an area of hydraulic upwelling provided conditions found only at this site (e.g., clear water and high conductivity during low flows) and may have been responsible for the fairly consistent high abundances of fathead minnow, western mosquitofish, and plains killifish. These waters, passing through the hyporheic zone, may have cause an increase in productivity (Stanford & Ward 1988, Valett et al. 1994) and therefore the high abundances of these species. Subsurface flow also provided a permanent water source that allowed these species to persist in a channel that might have otherwise been dry during low flow periods. Most likely, a combination of stable habitat and the chemical nature of the water contributed to the assemblage structure at this site.

Red shiner, fathead minnow, and flannelmouth sucker showed significant variation among sample sites. Spatial differences in the abundance of these species may be attributed to physical characteristics, such as flow regime, of each secondary channel. If these species used habitat discriminately, persist-

Table 4. Results from a repeated measures ANOVA to determine spatial and temporal variation in the abundance of four commonly collected species in San Juan River secondary channels. Ratio of $MS_{site} : MS_{date}$ is used to show the relative magnitude of these effects. Note that error SS accounts for > 60% of the total SS in all four species; indicating potentially large interaction between spatial and temporal effects.

Species	Source	df	MS	SS	F	P	$MS_{site} : MS_{date}$
<i>C. lutrensis</i>	Site	3	0.544	1.632	4.98	0.005	3.22
	Date	16	0.169	2.704	1.55	0.127	
	Error	44	0.109	4.796			
<i>P. promelas</i>	Site	3	0.524	1.572	3.97	0.014	3.05
	Date	16	0.172	2.752	1.30	0.239	
	Error	44	0.132	5.808			
<i>R. osculus</i>	Site	3	0.016	0.048	1.02	0.391	0.55
	Date	16	0.029	0.464	1.84	0.056	
	Error	44	0.016	0.704			
<i>C. latipinnis</i>	Site	3	0.057	0.003	10.54	< 0.001	9.50
	Date	16	0.006	0.096	1.14	0.352	
	Error	44	0.006	0.264			

ence of a particular habitat at a site should result in consistently greater abundance of species that use that habitat. For example, persistence of pools may allow some fish species to endure harsh conditions (e.g., high temperature and low dissolved oxygen) that other species cannot (e.g., Matthews 1986, Gelwick 1990). Channels that provide refugia from flood related habitat changes may also allow less flood-tolerant species, such as fathead minnow, to persist. A scenario such as this may have contributed to the greater numbers and higher species richness at site 3, where habitat complexity and presumably availability of refugia was greatest.

Several factors may have contributed to the temporal variation in the abundance of speckled dace. Adult speckled dace are habitat specialists preferring riffles with comparatively large substrata (cobble) and moderate to rapid current velocity (Rinne 1992). Because this species generally occupied similar habitats at all sites, abundance changed temporally with changes in flow and therefore habitat availability. This temporal variation was similar to that reported by Gelwick (1990), who showed that riffle communities exhibited greater temporal variation than pool communities. Duration of the spawning period may also have affected the time specific abundance of speckled dace. In the San Juan River, speckled dace spawn for about three weeks during spring runoff recession (Gido & Propst unpublished data). This abbreviated spawning period results in a single pulse of young-of-year fish, and total numbers gradually decline through the remainder of the year because of mortality and emigration. In contrast, fractional spawners, such as red shiner and fathead minnow, may continuously 'supplement' their populations (Gale 1986, Gale & Buynak 1982).

Overall, less than one-half of the variation in individual species abundances in secondary channels was accounted for by spatial and temporal effects. Other researchers have attributed this to an ephemeral or patchy distribution of a species (Lewis 1978, Matthews 1990, Meador & Matthews 1992). Unexplained variation in this study appeared to be caused by temporal changes in flow that affected the abundance of fish species differentially at each site. During low flow periods, the relative differ-

ence in habitat among sites largely explained the observed spatial differences in species present and their abundances. During high flows the different fish species had similar abundances at all sites.

Detrended correspondence analysis revealed spatial and temporal variation in the fish communities of secondary channels. A large proportion of the variation by sample date was because of high numbers of flannelmouth and bluehead sucker captured during spring runoff recession. This was seen by low scores on axis II for late July samples in 1993 and to a lesser extent in 1994. These species should show high variation in temporal abundance, as did speckled dace, because they have a restricted spawning period in late spring (McAda & Wydoski 1985, Gido & Propst unpublished data). The higher sucker abundance in the spring was caused by a brief surge of larvae and their dispersal into secondary channels during high flows. Their relative abundance in secondary channels then declined during late summer, autumn, and winter through mortality and emigration and as the abundance of nonnative fish increased.

The seasonal patterns of variation we found in secondary channel fish communities appeared to be related to water temperature and discharge. Sampling efficiency may have also accounted for some of this variation, however, estimating the relative effect of reduced efficiency vis-a-vis actual changes in individual species abundances is problematic. The fish community during spring runoff consisted mainly of species resistant to displacement by elevated flows (e.g., speckled dace and flannelmouth sucker) and those which had high abundances before runoff (e.g., red shiner and fathead minnow). Although high flow and greater current velocity reduced our sampling efficiency, rapid changes in habitat and lower resistance to displacement almost certainly reduced abundance of some species. Regardless of the relative importance of efficiency or abundance, it is unlikely that the species we found common during low flow periods were present in mid-channel habitats during high flows. Thus, our sampling of shoreline habitats during spring runoff should accurately reflect the incidence and abundance of fishes at that time.

After runoff, as flow decreased and water tem-

perature increased, species uncommon or absent during runoff were present and often common in shallow, low velocity habitats. Further changes in community structure were induced by increased spawning and recruitment by several nonnative fish species in the warmer waters. In the winter, as water temperature dropped, species richness declined. Again, our sampling efficiency may have decreased because fish had patchy distributions within each secondary channel. The fact that species were not lost to the system was illustrated by an increase in mean species richness in early spring 1994, as temperatures increased but flow was still near base levels. As cool spring runoff waters passed through the system in 1994 and current velocity increased, species richness declined once again.

Annual and seasonal variation in secondary channel fish communities was, in part, a consequence of differential reproductive success and duration of spawning season in the primary as well as secondary channels. Most reproductive activity of longer-lived species (common carp, flannelmouth sucker, and bluehead sucker) probably occurred in the primary channel, while secondary channels were mostly used by juveniles and sub-adults of these species. Thus, the fish community in secondary channels was influenced by faunal exchanges with the primary channel. The extent of this exchange was mediated by contemporaneous factors such as flow regime and habitat availability, and antecedent factors such as prior years reproductive success and survivorship.

Historically, native fish probably used secondary channels as foraging areas or refugia during high flows and as rearing areas for larvae and juveniles during low flows. Several nonnative species now seasonally dominate secondary channel fish communities and the use of these habitats by native fishes may be restricted. Nonnative fish have been shown to alter the structure of native fish communities through competitive displacement (Douglas et al. 1994) and predation (Meffe 1985, Scoppettone 1993). Although we did not examine the possibility of negative associations between native and nonnative species, the numerical dominance of nonnatives suggests a high probability of negative interactions between these species.

Spring runoff in San Juan River secondary channels appears to 'reset' the fish communities and thus preclude continuous numerical dominance by nonnative fishes. These elevated spring flows may be essential to the maintenance of native fish populations in this system. Two considerations tend to support this hypothesis. First, although several nonnative species (e.g., red shiner, fathead minnow) exploit low-flow periods by extended spawning, which increases their numerical dominance during low flows, most age 1 nonnatives are relatively small during runoff. Native species, conversely, by spawning only during spring runoff have an abbreviated spawning period but a longer growing season than later-spawned nonnative fishes. Thus, individuals in the native cohort by virtue of their greater relative size may be less susceptible to displacement during elevated spring flows. Secondly, the greater adult size of most native fishes (e.g., flannelmouth and bluehead suckers) coupled with fusiform bodies (e.g., speckled dace) presumably means they are physiologically and morphologically better prepared to resist displacement by high flows.

Accurate characterization of the influence that secondary channels exercised in the structure and dynamics of native fish communities of the San Juan River prior to establishment of nonnative fishes and human mediated flow regimes is not possible. Elsewhere in the upper Colorado River basin, low velocity habitats such as backwaters and embayments are critical nursery areas for imperiled and common native fishes (Tyus & Haines 1991). During low flow periods, San Juan River secondary channels have an abundance of low velocity habitats that superficially appear suitable as nursery and rearing areas for native fishes. Yet few native fishes are found in these habitats. From a native fish conservation perspective, high spring flows are essential to moderate the abundance of nonnative fishes. Further investigations should focus on interactions between native and introduced species and how these may vary with seasonal changes in discharge and habitat. In particular, how does variation in discharge during late summer and autumn (via irrigation releases and returns) affect these assemblages?

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