FACTORS LIMITING THE DISTRIBUTIONS OF NATIVE FISHES IN THE LITTLE COLORADO RIVER, GRAND CANYON, ARIZONA

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Abstract--Native fishes are not distributed evenly in the terminal 21 km of the Little Colorado River (Blue Spring to the mouth); speckled dace (*Rhinichthys osculus*) are present throughout the 21 km; humpback chub (*Gila cypha*), bluehead sucker (*Pantosteus discobolus*), and flannelmouth sucker (*Catostomus latipinnis*) are restricted to the 14.2 km below Chute Falls. Water chemistry (primarily carbon dioxide concentrations) and food resources have been hypothesized to limit fish distributions in the Little Colorado River. We sampled algae, invertebrates, and water chemistry in reaches above and below Chute Falls to determine if native fish distributions were limited by these parameters. Chlorophyll *a* content of algae samples collected from fine substrates was greatest above Chute Falls. Densities and biomasses of invertebrates known to be food items for native fishes were also greatest in that reach. Longitudinal water chemistry gradients were consistent across seasons; dissolved oxygen, pH, and conductivity generally increased from Blue Spring to the mouth, whereas alkalinity and carbon dioxide generally decreased. To determine if native fishes other than speckled dace could survive in the waters above Chute Falls, we captured age-0 and age-1 humpback chub, and age-1 bluehead suckers near 10.5 km, relocated subsets to 12.5, 15, 17.5, and 20 km, and held them for three days. All age-1 humpback chub and bluehead suckers survived three days of relocation at all sites. Age-0 humpback chub experienced significantly more mortality, and exhibited more stress behaviors at the 20 km relocation site than at any other site. Longitudinal food resource patterns and the results of the relocation experiment suggest that neither food resources nor water chemistry prohibit humpback chub and bluehead sucker from inhabiting the reach above Chute Falls. We believe that during base flow, Chute Falls is a physical barrier to upstream movement of fishes. If humpback chub and the two sucker species could transgress Chute Falls during high discharge, or if these species were artificially reintroduced above the falls, we believe that sufficient habitat and food resources are available to sustain populations.

Introduction

Native fishes in the Southwest have been in decline since at least the early 1900s due to such factors as damming, water diversions, groundwater pumping, overgrazing, and from the effects of introduced nonnative fishes (Minckley and Douglas 1991). The Little Colorado River (LCR), tributary to the Colorado River in Grand Canyon, is a prime example of a stream altered by such practices. Previous to 1900, the LCR was a perennial stream from headwaters in the mountains of eastern Arizona and western New Mexico to its mouth (Colton 1937, Miller 1961). Spanish explorers in the sixteenth century noted the river was almost as large as the 'Del Norte' (Colorado River) and bordered by many groves of willows and poplars (Colton 1937). A century later, Whipple (1855) described it midway through the drainage to be about 30 ft wide and flowing between alluvial banks eight to ten feet in height.

Beginning in the mid-1800s and continuing into the 1900s, land and water use increased in much of the basin. As a result, the LCR had become an intermittent stream between Holbrook, Arizona and Blue Spring (a perennial, saline spring 21 km above the mouth) by the early 1900s (Colton 1937, Hereford 1984). Due to the loss of perennial input from above, water chemistry in the lower 21 km became dependent on the chemical contributions of Blue Spring and other smaller source springs. Chemical concentrations, such as salinity and carbon dioxide, likely became more concentrated. The change in water chemistry may have negatively affected the physiology of the native fishes, thus restricting their distributions (Kaeding and Zimmerman 1983).

All eight fishes indigenous to the Colorado River in Grand Canyon were likely distributed throughout the LCR below Grand Falls (approximately 120 km above the mouth) when the river was perennial throughout its length; although fish surveys in this reach of the LCR have been sporadic. In the early 1900s, Colorado squawfish, bonytail chub, and roundtail chub were present in plunge pools immediately below Grand Falls (Miller 1963, Smith et al. 1979, Minckley 1973). Both bluehead sucker (*Pantosteus discobolus*) and flannelmouth sucker (*Catostomus latipinnis*) presently are found in East Clear Creek, a tributary of the LCR entering above Grand Falls, and in the lower 14 km of the LCR above the mouth. Humpback chub (*Gila cypha*) also occurs in the lower 14 km, and razorback sucker (*Xyrauchen texanus*) have been collected sporadically at the mouth. Speckled dace (*Rhinichthys osculus*), the only 'small-bodied' (maximum length < 150 mm) native fish, is present in perennial waters of the LCR both above and below Grand Falls.

Colorado squawfish, bonytail chub, and roundtail chub have been extirpated from the Grand Canyon region, and the razorback sucker is rare in occurrence (Minckley 1990). Within the perennial lower reach of the LCR, the four remaining native fish species are not distributed equally. All four inhabit the 14.2 km reach from the mouth to Chute Falls, but only speckled dace are present from Chute Falls to Blue Springs (Kaeding and Zimmerman 1983). Two of the five nonnative species reported in the LCR since 1983 (fathead minnow, *Pimephales promelas* and common carp, *Cyprinus carpio*), have also been recorded above Chute Falls (Kaeding and Zimmerman 1983, Mattes 1993). The main objective of this study was to determine the factors responsible for the disparate distributions of native fishes in the lower 21 km of the LCR. Four hypotheses have been advanced to explain present distributions of native fishes in this reach (Gorman 1994): (1) water chemistry is limiting above Chute Falls; (2) food resources are limiting above Chute Falls; (3) Chute Falls is a physical barrier to upstream movement; and (4) suitable physical habitat is not available above Chute Falls. We concentrated on the first two hypotheses in this study. An additional objective, for the federally endangered humpback chub, was to determine if the reach between Blue Spring and Chute Falls could be a potential site for population augmentation.

Study Site

The study area was the perennial 21 km of the Little Colorado River immediately above the mouth, in Grand Canyon, Arizona. The LCR in the Grand Canyon (Figure 1) is deeply entrenched in an often vertical-walled canyon that in places narrows to less than 50 m in width (Minckley 1990). Blue Spring (21 km above the mouth) and a downstream series of lesser unnamed springs produce a perennial mean base flow of 6.31 m^3/s (cms) at the mouth (Johnson and Sanderson 1968, Cooley et al. 1969). Waters emanating Blue Spring are 20°C, (temperatures at the mouth average 9°C warmer than the Colorado River; Kaeding and Zimmerman 1983), highly charged with free carbon dioxide and oversaturated with calcium carbonate (calcite; Cole 1975). As the waters pass downstream from Blue Spring, carbon dioxide vaporizes to the atmosphere and calcite precipitates. The calcite precipitate increases turbidity, imparting a milky blue color to the water, and covers the stream bottom with a layer of uncemented particles. The precipitate also eventually forms tufa, as evidenced by numerous tufaceous limestone dams in the lower LCR.

Most of the tufa dams occur between Chute Falls and Salt Trail Canyon (10.5 km above the mouth); several occur in close-order series that form falls and rapids in this reach. The three largest dams form a series known collectively as the 'Atomizer Falls Complex'(AFC). The complex consists of Atomizer Falls (13.6 km), Upper Atomizer Falls (13.9 km), and Chute Falls (14.2 km).

The LCR above Blue Spring vary temporally between dryness and large scale floods (U. S. Geological Survey 1954; estimated maximum ca. 3396 m^3/s, Hereford 1984). Flood flows, which affect seasonal fluctuations in water temperature in the study area (Kaeding and Zimmerman 1983, Clarkson et al. 1994), are a result of winter snowmelt and summer convection storms.

Methods

Longitudinal Limnology

We divided the river into two reaches: reach 1 = 0-14.2 km above the mouth (below Chute Falls), and reach 2 = 14.2-21 km (Chute Falls to Blue Spring). Six sampling sites, at 21 (Blue Spring), 20, 15, 10, 5, and 0.6 km above the mouth, were sampled once during each season: autumn (October 18-21, 1991), winter (January 23-26, 1992), spring (June 4-7, 1993), and summer (August 3-8, 1993). We sampled water chemistry parameters at these sites; we also sampled water chemistry parameters immediately below AFC in October 1991 and January 1992. Water temperature, conductivity, pH, and dissolved oxygen were measured with a Hydrolab Surveyor 3 datalogger and H2O transmitter. We used a Hach Model AL-36 digital titrator kit to measure alkalinity (brom-cresol green-methyl red endpoint, sulfuric acid titrant) and free carbon dioxide (phenolphthalein endpoint, sodium hydroxide titrant). Nitrate-nitrite nitrogen (cadmium reduction method) and soluble reactive phosphate (ascorbic acid method) were measured using a Hach DREL 2000 spectrophotometer. We measured turbidity with a Milton Roy Spectronic Mini-20 nephelometer.

To determine if biomass of primary producers varies longitudinally, periphyton biomass samples were collected at the five lower sites during June and August 1993 from two broad substrate categories: fines (clay, silt and sand) and cobble (64-256 mm). At each site, three perpendicular-to-flow transects were established in each substrate category. Samples were collected at four transect points at the distance from shore where depths of 10, 30, 50, and 90 cm were first encountered. One (June) to three pooled (August) samples were collected from fine substrates using a mini-core sediment sampler (4.15 cm^2 cross sectional area). Equivalent epilithon samples were collected from cobble using a 4.15 cm^2 diameter neoprene rubber-gasketed template and an X-acto #17 knife blade (Angradi and Kubly 1993). The dislodged material was removed with forceps and the scraped area backflushed with a pipette of river water. Periphyton species composition at each site was determined from samples collected opportunely during fall 1991 and winter 1992.

All periphyton biomass samples were wrapped in aluminum foil, frozen on dry ice and kept frozen in the dark until laboratory chlorophyll analysis could be performed. Chlorophyll *a* content of the samples was determined by the methanol extraction technique of Tett et al. (1975). For each month and each substrate category, differences in chlorophyll *a* content between the two reaches were assessed with Kruskal-Wallis (K-W) analysis of variance.

To estimate fish food resources, benthic invertebrates were collected using a Hess Sampler (0.09 m^2) at the five lower sites. At each site, one perpendicular-to-flow transect was opportunely established in each substrate category (see periphyton sampling above). Three samples per transect were collected at 0.5, 1, and 2 m from shore. In the laboratory, invertebrates were identified, enumerated, and burned to determine ash free dry weight (AFDW). For each month and each substrate category, differences in densities and AFDW between the two reaches were assessed with the K-W test.

Relocation Experiment

To determine if the water chemistry above Chute Falls was lethal to humpback chub and bluehead sucker populations in the LCR, we captured fish from reach 1 and held them in both reach 1 (control) and reach 2. We collected 40 age-0 and 40 age-1 humpback chub, and 15 age-1 bluehead suckers, from the vicinity of 10.5 km, June 11-12, 1994. On June 13, ten randomly selected humpback chub from each age group, and three age-1 bluehead suckers were transported in aerated buckets to four study sites: 12.5 (control site), 15, 17.5, and 20 km above the mouth. Fish were tempered for 1-h prior to being placed in the river at 1230 h and held for 72 h. Age-0 fish were held in 0.6 X 0.6 X 0.3 m, 500 μm mesh holding pens; age-1 fish were held in 0.6 X 0.6 X 0.6 m, 0.003 m mesh holding pens.

Mortality and behavior were monitored continuously during tempering, and for the first 15 min after being transferred to the river. Thereafter, instantaneous behavioral observations (Altman, 1974) were recorded at increasing intervals from 15 min to 1 h until 2030 h, and thereafter at 3 h intervals from 0730-1930 h, until 1330 h on June 16. Categorical stress behaviors monitored were: flashing, hyperactivity (continuous darting movements), lethargy (little or no movement), swimming in circles, loss of equilibrium, gulping air, and laying on the bottom. Behavioral activities other than these stress behaviors, were categorized as normal. Dead fish were removed from the holding pens as soon as noticed. On June 17, 1993, surviving fish were released near their point of capture, after being tempered for 15 minutes. Differences in percent mortality among sites were analyzed with the G-test (Sokal and Rohlf 1981).

Water chemistry parameters were measured at each site using the same methods described for longitudinal limnology. At each site free carbon dioxide and alkalinity were measured at 6-12 h intervals from 1300 h on June 13 to 1300 h on June 16. Temperature, pH, dissolved oxygen, and conductivity were monitored hourly at each site, from 1200 h on June 13 through 1200 h on June 16. Turbidity was measured at 1.25 km intervals from 11.25 to 20 km on June 16. Site differences in water quality parameters were analyzed with oneway ANOVA and the Tukey-Kramer multiple comparison test.

Results

Longitudinal Limnology

Spring, summer and autumn sampling trips were completed during periods of base flow (6.31 cms). The January 1992 trip was conducted during a period of runoff (6.76-6.88 cms).

Except for phosphate, longitudinal trends in water chemistry were consistent across seasons (Figure 2). Dissolved oxygen, pH, and conductivity increased from Blue Spring to the 15 km sampling site and then leveled off through the 0.6 km sampling site. Alkalinity and free carbon dioxide decreased from Blue Spring to the 0.6 km sampling site. Turbidity increased from Blue Spring to the 10 km sampling site, and then decreased towards the mouth. Turbidity levels were greater than the nephelometer could record (>100 NTU's; nephelometer turbidity units) during the entire January 1992 sampling period, due to the sediment load of the runoff. Nitrate levels increased from Blue Spring to the 20 km sampling site, and then generally decreased towards the mouth. No trend was evident in phosphate levels.

Longitudinal patterns of periphyton chlorophyll *a* are presented in Figure 3. Chlorophyll *a* biomass did not vary significantly between the two sample periods ($H=1.89$, $p=0.17$), or between the two substrate types ($H=1.15$, $p=0.28$). Chlorophyll *a* content was significantly greater in reach 2 than in reach 1 ($H=39.71$, $p<0.001$).

One hundred and thirteen algal taxa (Appendix) were identified from samples collected during October 1991 (Sommerfeld and Bartholomew 1994); ninety-three were collected at the six sampling sites. Some species, such as *Achnanthes affinis* and *Navicula cryptocephala*, were abundant and ubiquitous throughout the river, whereas others, such as *Cladophora glomerata* and *Spirogyra* sp. dominated only at certain sites.

More invertebrate families (taxonomic) were found in reach 2 than in reach 1 (Tables 1 and 2) in both June (11 and 7, respectively) and August (14 and 8, respectively). Eight of the taxa (Ephydridae, Simulidae, Corydalidae, Hydrophiidae, Saldidae, Veliidae, Copepoda, and Nematoda) were found only in reach 2. Ostracods, trichopterans, ephemeropterans, and larval/pupal stages of dipteran families Chironomidae, Ceratopogonidae, and Empididae were abundant enough in each reach to statistically examine differences in distribution. Densities of these selected invertebrate taxa were either significantly greater in reach 2 than reach 1, or did not differ between reaches (Table 3).

AFDW biomass was determined for 14 invertebrate taxa, however data were lumped into 6 general taxonomic categories to increase sample size. Longitudinal trends in invertebrate biomass were similar to those of periphyton chlorophyll *a* (Figure 3). Invertebrate AFDW was either significantly greater in reach 2 than reach 1, or did not differ between reaches (Table 4).

Relocation Experiment

Mortality of age-0 humpback chub was dependent on site ($G=13.70$, $p<0.01$); 70%, 0%, 30%, and 20% at the 20.0, 17.5, 15, and 12.5 km sites respectively, were dead at the end of the experiment. None of the age-0 humpback chub at the 17.5 km site exhibited stress behaviors during of the experiment. At the 15 km site, two age-0 fish began laying on the bottom after 2.5 h; both died soon after. After 37 h, another dead age-0 fish was discovered. At the 12.5 km site, the two age-0 humpback chub that died were lethargic and laid on the bottom prior to death. One of these fish exhibited stressful behaviors at the beginning of the experiment and died soon after. The second fish was lethargic and laying on the bottom after 46 h.

At the 20 km site, all 10 age-0 humpback chub were lethargic and gulping for air by the end of the tempering process. One fish died 2 h after being placed in the river, and two more were dead after 5 h. The final stage of stress before death was loss of equilibrium. By 19 h one fish was acting normal, however another fish was dead at 25 h. Two other fish were dead 46 h after the initiation of the experiment. By the end of the experiment (70 h at the 20 km site) two of the three surviving fish were still lethargic and gulping for air, the third was behaving normal.

All of the age-1 humpback chub and bluehead suckers at each of the sites survived the 72 h experiment. All of the age-1 fish at the 12.5, 15, and 17.5 km sites behaved normally during the entire experiment. At the 20 km site all of the age-1 humpback chub became hyperactive at the start of the tempering process. After 30 min of tempering, all 10 fish became lethargic and were gulping for air. The fish were still behaving this way when first placed into the river, but one fish also lost equilibrium. After 24 h and 48 h, three fish were acting normally. By the last observation, 70 h after being placed in the river, six fish were behaving normally.

The bluehead suckers at the 20 km site became lethargic and were gulping for air 45 minutes into the tempering process; however, after 1 h of tempering, all were behaving normal. Two of the bluehead suckers were exhibiting lethargy and gulping for air 10 min after being placed in the river. All of the suckers were lethargic and loosing equilibrium after 4 h. All three were still lethargic and laying on the bottom after 31 h. After 37 h only one bluehead was exhibiting lethargy; the other two were behaving normally. All three bluehead suckers were behaving normally 49 h after being placed in the river, and they continued to do so for the rest of the experiment.

Longitudinal patterns of water chemistry parameters during the relocation experiment (Figure 4) were similar to the results obtained from longitudinal limnology sampling (Figure 2). Oneway ANOVAs and post hoc Tukey-Kramer tests revealed significant differences among sites for most water chemistry parameters measured (Table 5). For instance, conductivity and pH differed for all pairwise comparisons among sites. For alkalinity and carbon dioxide, both the 12.5 and 20 km sites differed from all other sites, but the 15 and 17.5 km sites did not differ from each other. For dissolved oxygen, the 15 and 17 km sites differed from all other sites, but the 12.5 and 17.5 km sites were similar to each other (Table 5). Hourly patterns in dissolved oxygen concentrations tracked water temperature (Figure 5). Water temperature, however, did not differ significantly among the four sites (Table 5). Turbidity remained below 3.5 NTUs above Chute Falls, peaked at 16.9 NTUs immediately below Upper Atomizer Falls and then decreased to 7.62 NTUs at 11.25 km. Turbidity was not analyzed statistically due to the lack of replicates in data collection.

Discussion

Pronounced water chemistry gradients are evident in the lower LCR; reach 1 differs from reach 2. Carbon dioxide, conductivity, and dissolved oxygen changed sharply in magnitude from Blue Spring to 20 km, results similar to those of Mattes (1993). These initial changes in magnitude are likely due to shifts in chemical equilibria upon the water's contact with the atmosphere. Carbon dioxide concentration decreased from Blue Spring downstream, however the rate of decrease was greatest in the first kilometer below Blue Spring. In the reach from 20 km to 15 km the carbon dioxide levels became relatively stable. The mechanical action of the AFC, and other rapids and falls in the two kilometers immediately downstream may cause large amounts of carbon dioxide to be lost to the atmosphere, resulting in large amounts of calcium carbonate precipitate (Johnson and Sanderson 1968). Turbidity patterns indicate that calcite precipitation peaked within the 13.6-12.5 km reach, below the major falls, and thereafter decreased to the mouth. Turbidity was greater overall during October 1991 than the two 1993 sampling periods (base discharge conditions during all three trips), possibly due to lingering effects of September, 1991 floods. In addition, the low turbidity levels during the 1993 sampling periods may have been a result of dilution from increased groundwater water input as a result of the large amount of precipitation (rain and snow) during the winter of 1992-93.

The deposition of calcium carbonate probably also results in the observed drop in alkalinity immediately below AFC. The decrease in alkalinity and the increase in conductivity from Blue Spring to the AFC is a counterintuitive result. However, the increase in conductivity below Blue Spring is a result of saline spring input; concentrations of dissolved ions, such as Na^+, SO_4^-, and Cl^- are nearly twice as great in several downstream springs than in the waters of Blue Spring (Cooley 1976).

Native fishes are likely sensitive to chemical gradients (Hoglund 1961). Water quality in the reach above the AFC differs from the reach below, and yet, all of the age-1 humpback chub and bluehead suckers that we relocated above the falls survived. In addition, most of the age-0 humpback chub survived at the 15 km site and all survived at the 17.5 km site. However, most of the age-0 humpback chub held at the 20 km site died, and both age-0 and age-1 fish exhibited stressful behaviors at this site. Further, other species inhabit reach 2; speckled dace are common below 20 km and both fathead minnow and common carp have recently been reported in this reach (Kaeding and Zimmerman 1983, Mattes 1993). Therefore, we do not believe that water chemistry alone prohibits humpback chub and bluehead suckers from inhabiting reach 2. Even though humpback chub and bluehead sucker can survive above Atomizer Falls, fish may avoid this area due to non-preferable water chemistry. Carbon dioxide levels during periods of base flow may inhibit humpback chub from entering the reach above Atomizer Falls (Mattes 1993). Carbon dioxide tolerance limits for humpback chub and the other native fish species found in the Little Colorado River are as yet unknown. Lethal concentrations of CO_2 vary with species and environmental conditions such as temperature and oxygen concentrations (Powers 1937, Black et al. 1954, Alabaster 1957, Takeda and Itazawa 1983). Carbon dioxide concentrations at the 15 km (179 mg/l) and 17.5 km (190 mg/l) sites are well below the lethal limits reported by Black et al. (1954) for fathead minnows (293 mg/l CO_2 at 20.4 °C for 50 g fish) and common white suckers (*Catostomus commersoni*; 260 mg/l CO_2 at 17.1 °C for 265 g fish). Our studies indicate that age-0 and age-1 humpback chub, and age-1 bluehead sucker, can acclimate to the carbon dioxide concentrations of the 2.5 km immediately above Chute Falls. It is likely that carbon dioxide concentrations at the 20 km site (348 mg/l) were very near the lethal limit for age-0 humpback chub, since the mortality rate was high for these fish and all behaved stressfully. The carbon dioxide concentrations were also likely near the lethal limit of age-1 humpback chub and bluehead suckers, since all of these fish exhibited stressful behaviors.

Presence of Colorado squawfish, bonytail and roundtail chub in the pools below Grand Falls in the early 1900s (Miller 1963, Smith et al. 1979, Minckley 1973) indicates that the native large-bodied fishes were able to transgress the AFC in the past. However, the extent to which they occupied the reach above AFC is unknown. The additional perennial discharge from above Blue Spring may have been sufficient to allow fish to transgress the falls complex, and the travertine dams may have been smaller in the past. The loss of perennial input from above Blue Spring concentrated chemicals in the waters and may have increased the rate of travertine deposition; as a result present dams may be taller than in the beginning of the century.

Furthermore, high stage flooding events may dilute chemical concentrations (i.e., CO_2) and eliminate the vertical barrier of the falls. Four consecutive days of mean flows 283-464 cms were recorded at Cameron during a flood in January 1993, and none of the native large-bodied fishes have been observed above Chute Falls since this flood; however, fish sampling above AFC has been sporadic. Upstream movement transgressing the falls would be most likely during an extended high stage flood that occurred during the spawning season, when humpback chub are hypothesized to migrate upstream.

It is possible that during base flow, water quality in conjunction with the physical obstacle of AFC limits the distribution of the three large-bodied native fishes to below Chute Falls. Dahlberg et al. (1968) reported that high concentrations of free carbon dioxide had a more pronounced effect on the swimming speed of coho salmon at dissolved oxygen concentrations near or above the air-saturation value than at oxygen concentrations far below air-saturation. In our study, the dissolved oxygen concentrations were near saturation immediately below (12.5 km site) and above AFC (15 km site), and the carbon dioxide concentrations increased from 179 mg/l at the 12.5 km site to 192 mg/l at 15 km. These changes in oxygen and carbon dioxide concentrations may negatively effect the swimming abilities of humpback chub and the native suckers. Fish are capable of detecting slight changes in 'free' carbon dioxide gradients and will avoid both low and high levels (Hoglund 1961). In addition, it may require great physical effort for fish to transgress the AFC. Therefore, the physical aspect of the falls in conjunction with increasing carbon dioxide levels at near-saturation oxygen levels may limit the upstream movements of humpback chub, and bluehead and flannelmouth suckers.

Our results indicate that food resources do not limit the distributions of native fishes in the lower 21 km of the LCR; invertebrate biomass was either greater in reach 2 than reach 1 or did not differ between the reaches. Although phosphate concentrations did not exhibit a longitudinal trend in the LCR, nitrate concentrations may have effected the generally greater algal biomass in reach 2 compared to reach 1. In addition, carbon dioxide as well as low turbidity, may have promoted greater algal biomass in reach 2 than reach 1; carbon dioxide levels are known to influence primary productivity in periphytic algae (Minckley and Tindall 1963, McIntire and Phinney 1965, Wiegert and Fraleigh 1972). Further, the generally greater algal biomass in reach 2, compared to reach 1, likely allowed the greater invertebrate biomass observed in this reach. A second piece of evidence indicating that food resources are not limiting is the presence of speckled dace in both reaches. Although we have not quantified speckled dace abundances in the two reaches, we have observed great numbers of dace in reach

2. Therefore, we believe that sufficient food resources are available in reach 2 to support fish species diversity and abundances comparable to reach 1.

Adult humpback chub have been reported to occupy deep, fast current waters near ledges or boulders (Kaeding and Zimmerman 1983, Kaeding et al. 1990, Valdez et al. 1990). Adult bluehead and flannelmouth suckers also have been reported to occupy swift waters (Minckley 1973). Data from Mattes (1993) indicates that habitat (depth, current velocity, and substrate) above Chute Falls is similar to that immediately below, where humpback chub are present. Mattes only statistically compared habitat between his reaches for one sampling period, June 1993, and his results were inconclusive. Mattes (1993) habitat data for areas above Chute Falls fit the habitat suitability index curves developed by Valdez et al. (1990). In addition, we have observed deep pools (>4 m) in the reach above Chute Falls, below small rapids and on outside bends. Therefore, we believe that suitable habitat is available to humpback chub in the Chute Falls-Blue Springs reach.

We believe that humpback chub and the two sucker species could be successfully reintroduced to the LCR to the reach above Chute Falls. Physical alteration of Chute Falls, to decrease the vertical drop, would be a means to enable fishes to move into the reach upstream, and circumvent the costs of artificial stocking.

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TABLE 1. Mean densities (numbers/m^2) of invertebrates by site (km) from fine substrates, Little Colorado River, 1993. Sites 0.6, 5, and 10 are in reach 1; sites 15 and 20 are in reach 2.

	Kilometer Above the Mouth				
	0.6	5	10	15	20
June					
Diptera					
Chironomidae	185.19	244.44	700.00	11051.85	1985.19
Ceratopogonidae	0	0	3.70	0	0
Empididae	0	0	3.70	18.52	3.70
Ephydridae	0	0	0	11.11	0
Ephemeroptera					
Baetidae	3.70	0	0	325.93	0
Trichoptera					
Hydropsychidae	0	3.70	11.11	44.44	0
Megaloptera					
Corydalidae	0	0	0	3.70	0
Ostracoda	0	0	37.04	3.70	7.41
Oligochaeta	0	0	3.70	0	0
Total	188.88	248.14	759.25	11459.26	1996.30
August					
Diptera					
Chironomidae	7.41	229.63	1207.41	3692.59	5225.93
Ceratopogonidae	0	11.11	33.33	455.56	40.74
Empididae	0	14.81	0	22.22	0
Ephemeroptera					
Baetidae	0	0	0	151.85	444.44

TABLE 1. continued...

	Kilometer Above the Mouth				
	0.6	5	10	15	20
Trichoptera					
Hydropsychidae	0	0	0	55.56	0
Coleoptera					
Hydrophilidae	0	0	0	3.70	0
Dytiscidae	0	3.70	0	259.26	0
Ostracoda	37.04	1077.78	874.07	1220666.67	11.11
Copepoda	0	0	0	18.52	0
Oligochaeta	0	11.11	3.70	5955.56	0
Nematoda	0	0	0	14.81	0
Nemertina	25.93	151.85	7.41	455.56	0
Total	70.37	1500.00	2125.93	131803.70	5722.22

TABLE 2. Mean densities (numbers/m^2) of invertebrates by site (km) from cobble substrates, Little Colorado River, 1993. Sites 0.6, 5, and 10 are in reach 1; sites 15 and 20 are in reach 2.

	Kilometer Above the Mouth				
	0.6	5	10	15	20
June					
Diptera					
Chironomidae	166.67	37.04	92.59	2214.81	911.11
Ceratopogonidae	3.70	3.70	0	0	0
Empididae	3.70	0	3.70	14.81	0
Simulidae	0	0	0	3.70	0
Ephemeroptera					
Baetidae	3.70	0	0	3.70	251.85
Hemiptera					
Saldidae	0	0	0	3.70	0
Trichoptera					
Hydropsychidae	0	0	0	229.63	4514.81
Hydroptillidae	0	0	0	0	33.33
Megaloptera					
Corydalidae	0	0	0	0	7.41
Ostracoda	3.70	3.70	0	0	11.11
Nematoda	0	0	0	3.70	0
Total	181.48	44.44	96.30	2474.07	5729.63
August					
Diptera					
Chironomidae	0	11.11	144.44	855.56	114.81
Ceratopogonidae	0	3.70	37.03	211.11	3.70

TABLE 2. continued...

	Kilometer Above the Mouth				
	0.6	5	10	15	20
Empididae	14.81	11.11	3.70	3.70	0
Ephemeroptera					
Baetidae	0	0	0	22.22	3259.26
Hemiptera					
Veliidae	0	0	0	3.70	0
Trichoptera					
Hydropsychidae	0	0	0	0	4374.07
Hydroptillidae	11.11	0	0	0	0
Coleoptera					
Hydrophilidae	0	0	0	77.78	0
Dytiscidae	0	0	7.41	0	0
Megaloptera					
Corydalidae	0	0	0	0	3.70
Ostracoda	203.70	3.70	74.07	6766.67	0
Oligochaeta	0	0	7.71	1666.67	0
Nemertina	96.30	3.70	0	0	0
Total	325.93	33.33	2125.93	9666.67	7755.56

TABLE 3. Results of Kruskal-Wallis tests comparing mean ranks of invertebrate densities, from fine and cobble substrates, among reaches, Little Colorado River, 1993. For each month and substrate type, 9 samples were collected from reach 1, and 6 from reach 2; * = $p<0.05$.

	June			August		
	Reach 1	Reach 2	F	Reach 1	Reach 2	F
Chironomidae						
Fine	5.22	12.17	8.70*	5.11	12.33	9.41*
Cobble	5.00	12.50	10.16*	5.39	11.92	7.98*
Ceratopogonidae						
Fine	8.33	7.50	0.67	5.89	11.17	5.37*
Cobble	8.67	7.00	1.44	6.61	10.08	2.56
Empididae						
Fine	7.28	9.08	1.20	7.56	8.67	0.37
Cobble	7.56	8.67	0.37	9.61	5.58	3.59
Trichoptera						
Fine	7.06	9.42	1.28	7.00	9.50	3.21
Cobble	5.00	12.50	12.89*	6.83	9.75	2.17
Ephemeroptera						
Fine	6.72	9.92	3.03	5.00	12.50	12.89*
Cobble	6.17	10.75	5.37*	5.50	11.75	9.97*
Ostracoda						
Fine	7.89	8.17	0.02	7.89	8.17	0.01
Cobble	7.56	8.67	0.37	8.56	7.17	0.37

TABLE 4. Results of Kruskal-Wallis tests comparing mean ranks of invertebrate biomass (AFDW), from fine and cobble substrates, among reaches, Little Colorado River, 1993. For each month and substrate type, 9 samples were collected from reach 1, and 6 from reach 2; * = $p<0.05$.

	June			August		
	Reach 1	Reach 2	F	Reach 1	Reach 2	F
Chironomidae						
Fine	5.22	12.17	9.26*	6.11	10.83	4.05*
Cobble	5.17	12.25	10.07*	5.00	12.50	12.89*
Other Diptera						
Fine	7.00	9.50	3.21	6.33	10.50	3.98*
Cobble	7.50	8.75	1.50	6.22	10.67	5.04*
Trichoptera						
Fine	7.00	9.50	3.21	7.50	8.75	1.50
Cobble	5.00	12.50	12.89*	6.50	10.25	5.17*
Ephemeroptera						
Fine	7.00	9.50	3.21	5.50	11.75	9.97*
Cobble	6.50	10.25	5.17*	6.00	11.00	7.41*
Ostracoda						
Fine	7.83	8.25	0.08	7.11	9.33	0.95
Cobble	8.00	8.00	0.00	7.00	9.50	3.21
Other Taxa						
Fine	9.50	5.75	2.71	5.11	10.17	2.41
Cobble	8.39	7.42	0.18	6.94	9.58	1.30
Total						
Fine	5.33	12.00	8.00*	5.11	12.33	9.39*
Cobble	5.00	12.50	10.22*	5.00	12.50	10.14*

TABLE 5. Oneway ANOVA comparisons of water parameters (means) among sites during the humpback chub relocation experiment. Pairwise comparisons among sites were tested with the Tukey-Kramer Multiple Range Test; * indicates significant ($p<0.05$) differences among all possible pairwise comparisons of the site with other sites.

Parameter	12.5 km	15.0 km	17.5 km	20.0 km	F	p
Water temperature (°C)	20.99	20.97	20.94	20.66	1.46	0.22
pH	7.17*	7.45*	7.24*	6.53*	4715.34	<0.001
Alkalinity (mg/L $CaCO_3$)	596.65*	672.30	671.53	740.48*	335.00	<0.001
Carbon dioxide (mg/L)	171.33*	178.67	190.00	320.00*	585.55	<0.001
Dissolved Oxygen (mg/L)	7.48	8.34*	7.57	6.62*	106.62	<0.001
Conductivity (μS/cm)	4762.57*	4545.74*	4493.70*	4468.71*	505.26	<0.001

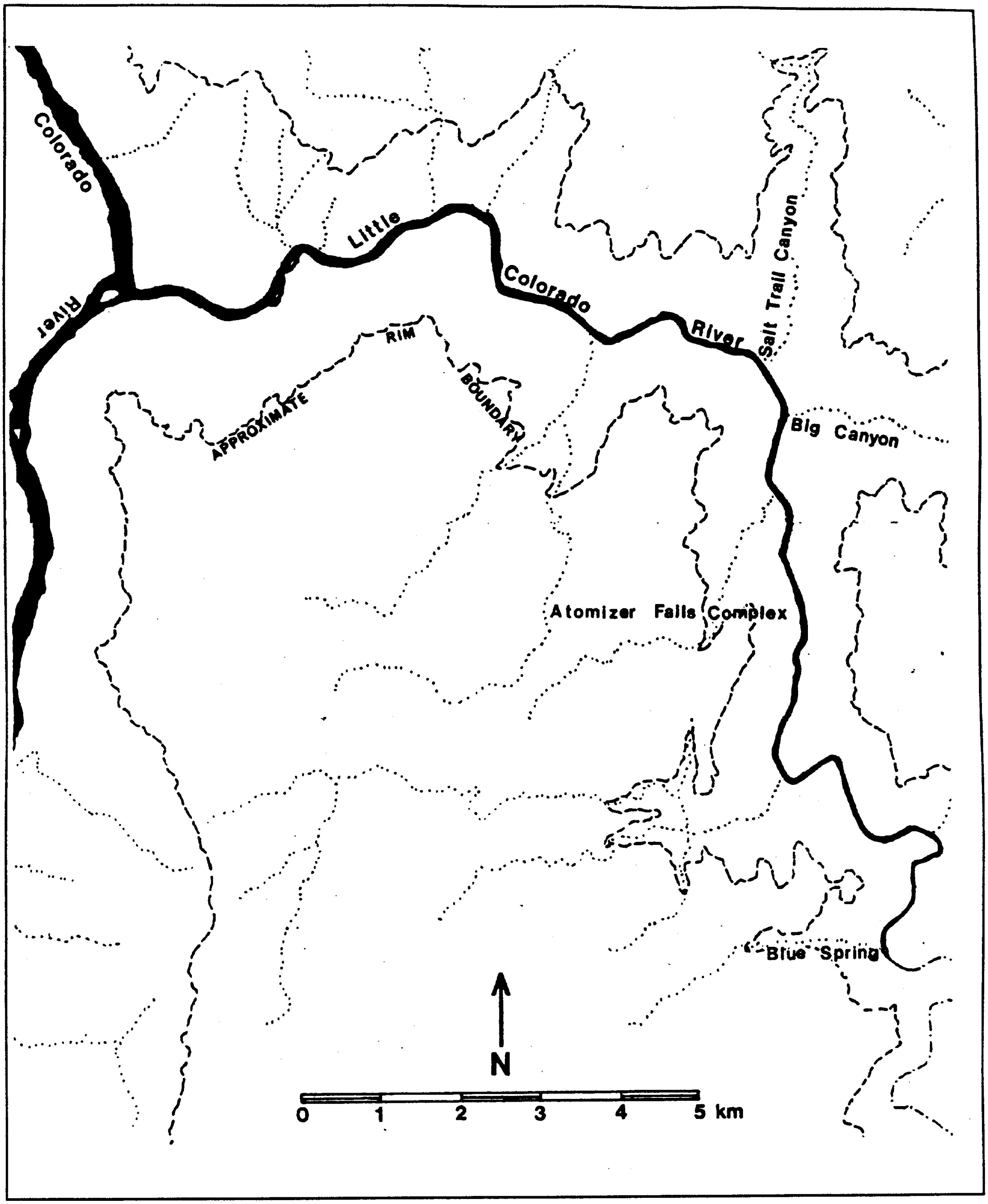

FIGURE 1. Map of the study area showing the Colorado River and the lower 21 km of the Little Colorado River.

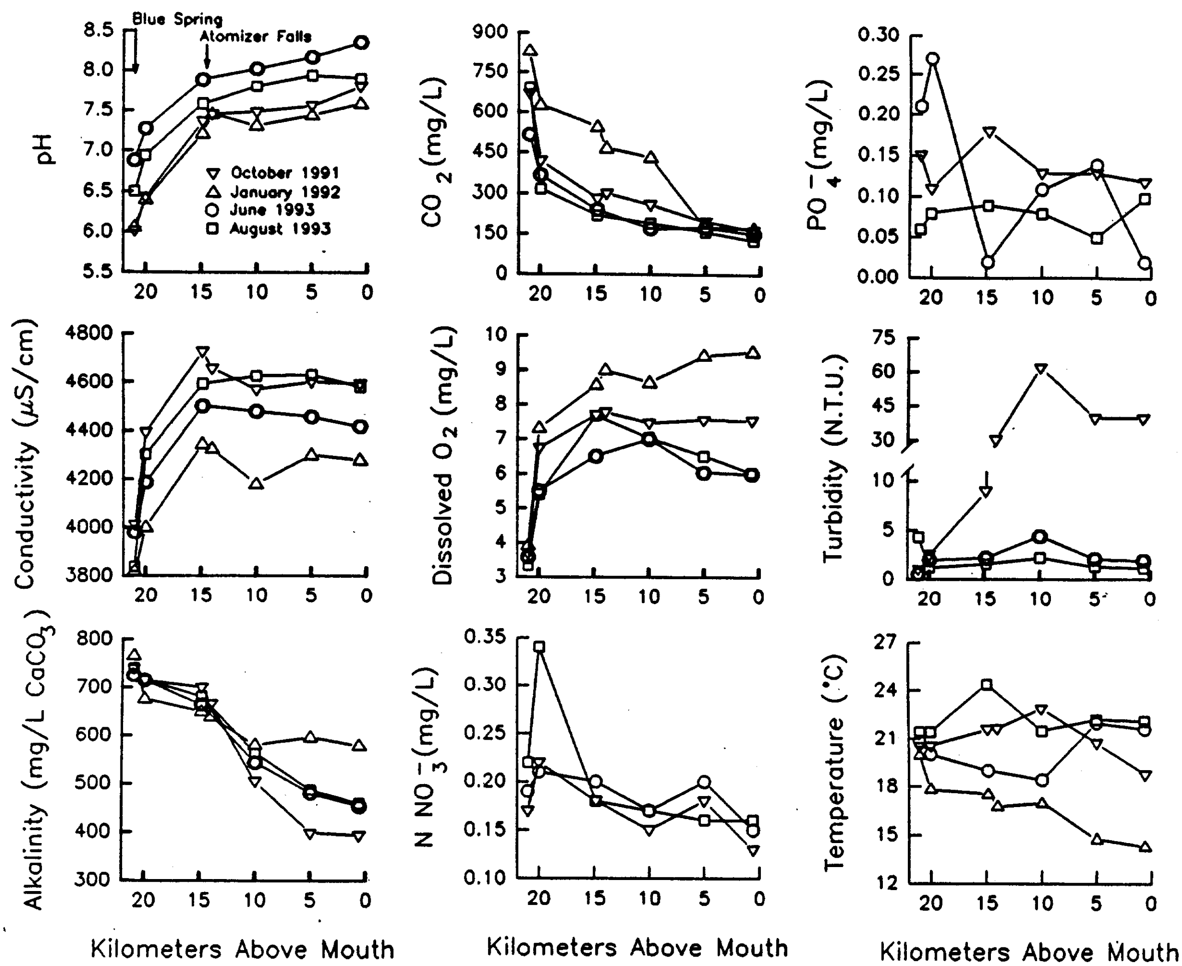

FIGURE 2. Longitudinal patterns of selected water quality parameters from the Little Colorado River, October 1991 through August 1993.

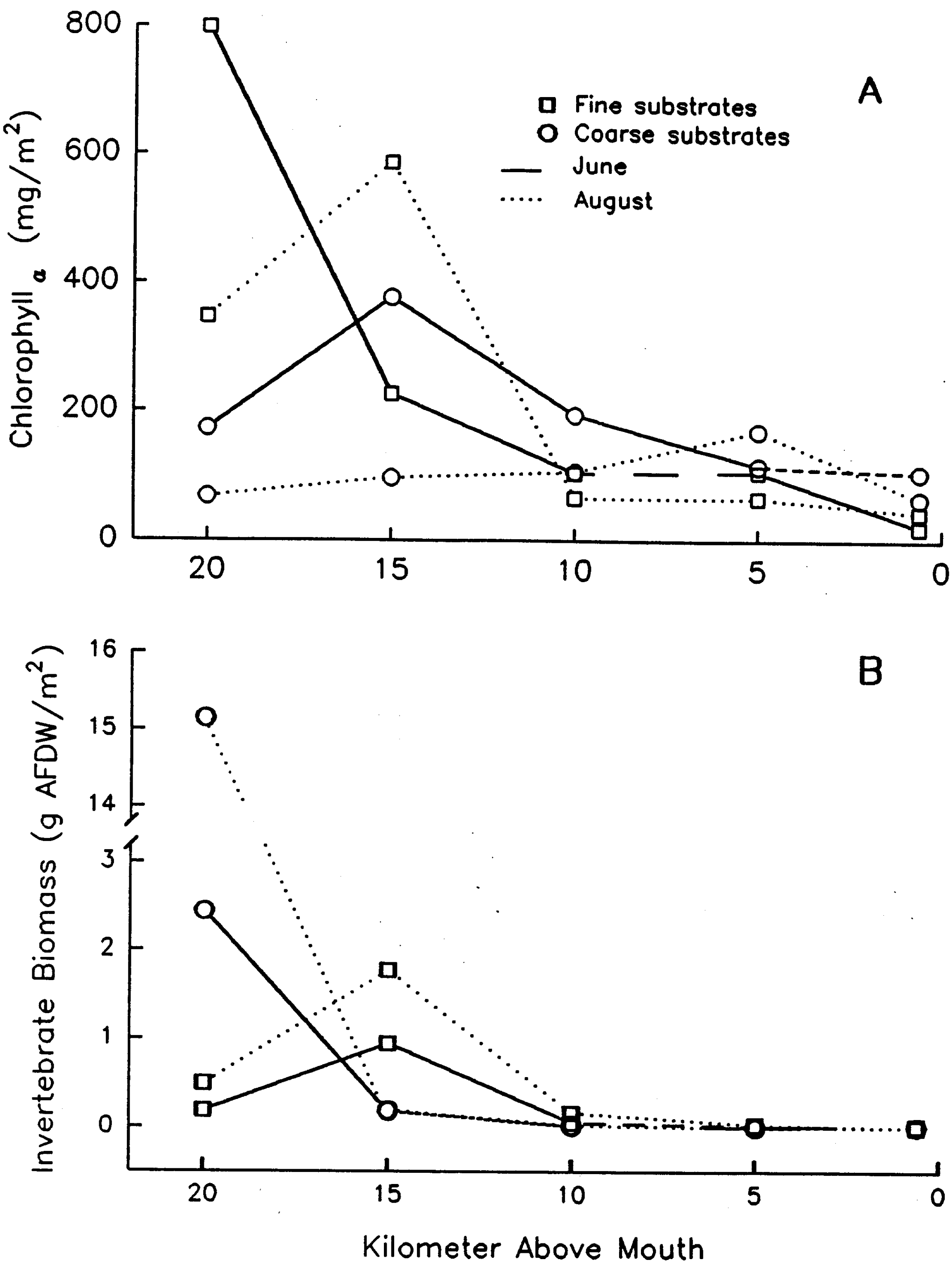

FIGURE 3. Means of chlorophyll *a* concentrations (A) extracted from algal samples, and (B) invertebrate biomass, collected at six sites from coarse and fine substrates, Little Colorado River, 1993.

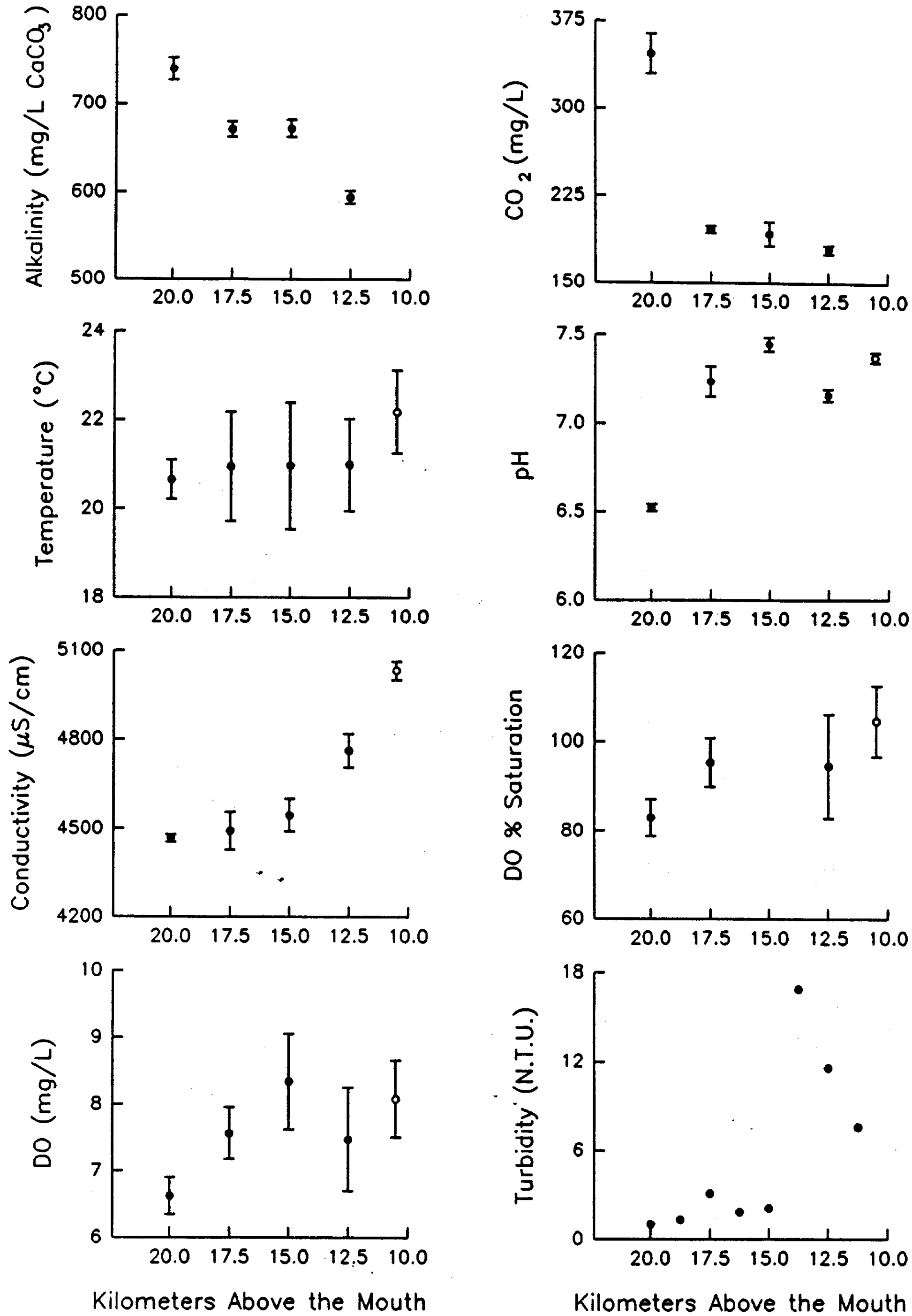

FIGURE 4. Means and standard deviations of water chemistry parameters measured at each site during the humpback chub relocation experiment, Little Colorado River, June 1993. Turbidity, measurements, at 1.25 km intervals, were not replicated.

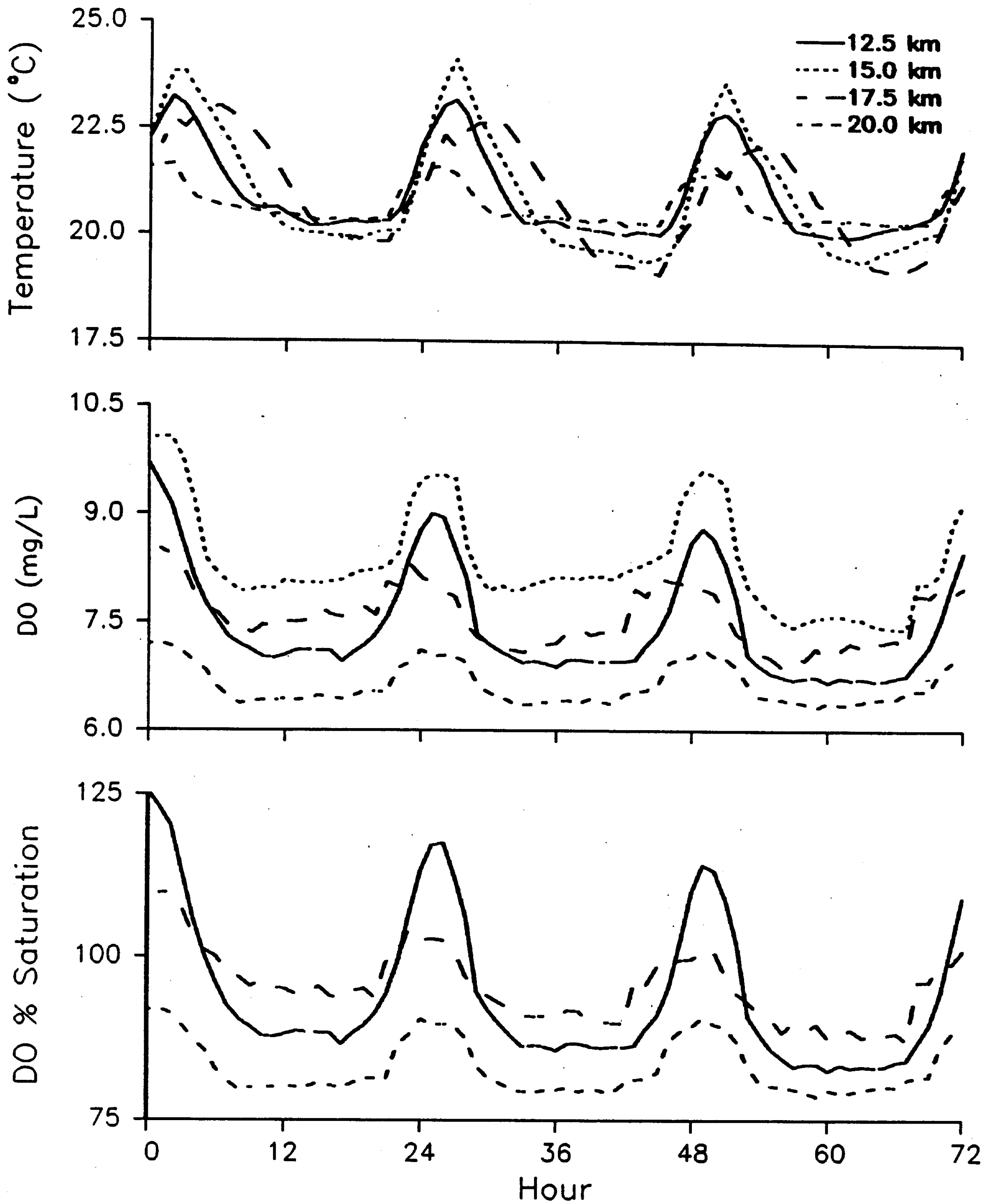

FIGURE 5. Hourly levels of temperature and oxygen at each of the relocation sites, Little Colorado River, 1993. Hour 0 = 1200 h June 13, 1993.

APPENDIX

TABLE A1. Presence of algae taxa collected from six sampling sites, Little Colorado River, October, 1991. D = dominant (>50%), C = common (10-49%), I = infrequent (1-9%), R = rare (<1%), A = absent, n = number of samples.

Species	21 km (n=5)	20 km (n=8)	15 km (n=6)	10 km (n=6)	5 km (n=6)	0.6 km (n=6)
CHLOROPHYTA						
Cladophora						
glomerata	A	A	A	A,I,D	A,D	A,R,D
Microspora sp.	A	A,R,I,D	A,R	A	A	A,R
Oedogonium sp.	A,R	A	A,R	A	A	A,R
Rhizoclonium sp.	A,I	A	A,R	A,R	A	A,R
Spirogyra sp	A,R,I	A,R	A,I,D	A,D	A	A,R,D
Ulothrix sp.	A,I,C,D	A,C	A,R,I	A,I	A	A,R,I
CHRYSOPHYTA						
XANTHOPHYCEAE						
Tribonema sp.	A,D	A,I	A	A	A	A,R
Vaucheria sp.	A	A,I	A,D	A,C	A	A
BACILLARIOPHYCEAE						
Achnanthes						
affinis	A,R,I,C	R,I,C	R,C	A,R,I,C	R,I,C	A,R,I,C
deflexa	A	A	A	A	A,R	A,R
lanceolata	R,I	I,C	R,I,C	A,R,I	A,R	A,R
lanceolata v omissa	A,I	A	A,I	A	A	A,R
linearis	A	A,R	A,R	A,R	A,I	A,R
minutissima	A	A	A,R	A	A	A
Amphora						
coffieformis	A,R	A,R	A,R,I	A,R,I	A,R,I	A,R
ovalis	A,R	A	A,R,I	A,I	A,R	A,R
veneta	A	A	A,R	A	A	A

TABLE A1. continued...

Species	21 km (n=5)	20 km (n=8)	15 km (n=6)	10 km (n=6)	5 km (n=6)	0.6 km (n=6)
Anomoeoneis						
vitrea	A	A	A	A,R	A,R,I	A,R
Bacillaria						
paradoxa	A,R	A,R	R,I	A,R	A,R	A,R
Biddulphia						
laevis	A,R	A,R,I	A,R	A,R	A	A
Caloneis						
amphisbaena	A,R	A,R	A	A,R	A	A
bacillaris v thermalis	A	A	A	A,R	A	A
bacillum	A,R	A,R	A,R	A	A	A,R
clevei	A	A	A	A	A,R	A,R
ventricosa v truncatula	A	A,R	A	A	A	A
Cocconeis						
diminuta	A	A	A	A	A	A,R
placentula	A	A,R	A,R	A,R	A,R	A,R
Cyclotella						
meneghiniana	A,R	A,R	R,I	A,R	A,R	A,R,I
Cymbella						
minuta	A	A,R	A,I	A,R,I	A,R	A,R,I
Denticula						
elegans	A,R	A,R	A,R	A	A,R,I	A,R,I,C
Diatoma						
hiemale v mesodon	A	A,R	A	A	A	A
Diploneis						
elliptica	A,R	A	A,R	A	A	A
oblongella	A,R	A,R	A,R	A,R	A,R,I	A,R

TABLE A1. continued...

Species	21 km (n=5)	20 km (n=8)	15 km (n=6)	10 km (n=6)	5 km (n=6)	0.6 km (n=6)
Entomoneis						
alata	A,R,I	A,R,I	A,R	A,R	A	A,R
paludosa	R,I	A,R,I	R,I	A,R,I,C	R,I,C	R,I,C
Fragilaria						
brevistriata v inflata	A,R	A	A	A	A	A,R
crotonensis	A	A	A	A	A,R	A,I
vaucheriae	A	A,R	A,R	A,R	A,R	A,R
Frustulia						
vulgaris	A	A	A	A,R	A,R	A,R
Gomphonema						
affine	A,R	A,R	A	A	A	A
angustatum	A,R	A,R	A,R,I	A	A,R	A,R,I
olivaceum	A	A	A,R	A,R	A,R	A,I
parvulum	A,R,I	A,R,I	A,R,I	A,R	A,R	A,R
sp.	A	A	A	A,R	A	A
Gyrosigma						
spencerii	A,R	A	A,R	A,R	A,R	A,R
Mastogloia						
elliptica v danseii	A,R	A	A	A,R,I	A,I	A
Melosira sp.	A,R	A	A	A	A	A
Navicula						
cryptocephala	A,C	A,C,D	A,I,C	R,I,C,D	A,C	A,R,I,C
cryptocephala v *veneta*	A,R,C,D	A,I,C	A,R,I,C	A,I,C	A,R,I,C	A,R,I
cuspidata	A,R	A	A	A	A	A
gregaria	A,R	A,R	A,R	A	A,R	A,R
seminulum v *hustedtii*	A	A	A,R	A,I	A,R,I	A,R,I

TABLE A1. continued...

Species	21 km (n=5)	20 km (n=8)	15 km (n=6)	10 km (n=6)	5 km (n=6)	0.6 km (n=6)
tripunctata	A,R	A,R,I,C	A,R,I,C	A,I,C	R,I,C	R,I,C
Nitzschia						
acicularis	A	A	A,R	A	A	A
apiculata	A,R	A	A,R	A,R	A	A
dissipata	A	A	A,R	A	A	A
filiformis	A	A	A,R	A	A	A
fonticola	A,R	A,R	A	A,R	A	A
frustulum	A	A	A,R	A	A	A
frustulum v *perpusilla*	A,R	A,R,I	A,R	A,R	A	A,R
gracilis	A	A,R	A	A	A	A
hungarica	A,R	A	A,R,I	A,R	A,R	A
longissima v *closterium*	R,I	R,I	A,R,I	A,R,I	A,R,I	A,R
microcephala	A,R,C	A,R,I	A,R,I	A,R	A,R	A,R
palea	A,R,I,C	A,R,I	A,R,I	A,R,I	A,R	A,R,I
sigma	A,R	A,R	A,R,I	A,R,I,C	A,R,I	A,R,C
vermicularis	A	A	A	A	A	A,R
Pinnularia						
appendiculata	A,R	A,R	A,R,I	A,R,I	A,R	A,R,I
microstauron	A	A,R	A,R	A	A	A
substomatophora	A,R	A	A	A	A,R	A,R
sp.	A	A,R	A,R	A	A	A,R
Pleurosigma						
delicatulum	A,R	A	A,R	A	A,R	A,R
Rhopalodia						
gibba	A	A	A	A,R	A	A
gibba v *ventricosa*	A,R	A	A	A,R	A	A

TABLE A1. continued...

Species	21 km (n=5)	20 km (n=8)	15 km (n=6)	10 km (n=6)	5 km (n=6)	0.6 km (n=6)
gibberula v *vanheurckii*	A,R	A,R	A	A,R	A,R	A
Stephanodiscus						
astraea	A	A	A,R	A	A	A
Surirella						
ovalis	A,R	R,I	R,I,C	A,R,I	A,R,I	A,R
ovata	A	A	A	A,R	A,R	A
ovata v *pinnata*	A,R	A,R	A	A	A	A
striatula	A	A,R	A,R	A	A,R	A
Synedra						
acus	A,R	A	A,R	A,R	A,R	A,R
affinis	A	A	A	A	A,R	A
ulna	A,R	A,R	A,R,I	A,I	A,R,I	A,R,I
CYANOPHYTA						
Anabaena sp.	A,R,I	A,I	A,R	A,R,I	A,R,I,C	A,R,I
Calothrix sp.	A,R	A,R	A	A	A	A,R
Chroococcus sp.	A,R	A	A	A	A	A,R
Gloeocapsa sp.	A	A,R	A	A	A	A
Lyngbya sp.	A,I	A,R	A	A	A	A
Microcoleus sp.	A	A,R	A	A	A	C
Microcystis sp.	A	A,R	A	A	A	A
Nostoc sp.	A,I	A	A	A	A,R	A
Oscillatoria sp.	A,R,I,C	A,R,C	A,R	A,R,I,D	A,R,C,D	A,R,I
Pseudanabaena sp.	A	A,R	A	A	A,I	A