

**LIMNOLOGY AND THE  
DISTRIBUTIONS OF NATIVE FISHES IN THE  
LITTLE COLORADO RIVER, GRAND CANYON, ARIZONA**

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*Abstract*—Four native fish species exist in the spring-fed, perennial lower 21 km of the Little Colorado River, but only speckled dace (*Rhinichthys osculus*) is present in the entire reach. The other three species—humpback chub (*Gila cypha*), bluehead sucker (*Pantosteus discobolus*) and flannelmouth sucker (*Catostomus latipinnis*)—are present only in the lower 14.2 km below Chute Falls. We sampled benthic algae and invertebrates and analyzed water chemistry in reaches above (Reach 1) and below (Reach 2) Chute Falls to determine whether the disparity in fish distributions could be attributed to these parameters. Algal biomasses (chl *a*) and densities and biomasses of invertebrates known to be food resources of the fishes were greater in Reach 2 than Reach 1. Dissolved oxygen, pH and specific conductance levels generally increased from Reach 2 to Reach 1, whereas alkalinity and free carbon dioxide decreased. To determine if native fishes other than speckled dace could survive above Chute Falls, we relocated age-0 and age-1 humpback chub and age-1 bluehead suckers from Reach 1 to three sites in Reach 2 and held them for three days. All age-1 fish survived the experiment, although some individuals of both species experienced short-term respiratory stress at the 20-km site. Age-0 humpback chub experienced significantly more mortalities, and exhibited more stress behaviors at the 20 km relocation site than at any other site. We conclude that food resources are not limiting to these native fishes in Reach 2, but that water chemistry (high free carbon dioxide levels) may restrict successful hatching and survival of age-0 individuals in much of that reach. Chute Falls is probably a physical barrier to upstream movement of these native fish species at base flow of the LCR. [Translocation of individuals to the reach above Chute Falls or breaching that barrier may be feasible management actions to increase available habitat for these fishes in the LCR.]

### Introduction

Native fish populations in the Southwest have declined since at least the early 1900s due to dams, water diversions, groundwater pumping, overgrazing, and effects of introduced nonnative fishes (Minckley and Douglas 1991). The Little Colorado River (LCR), a tributary to the Colorado River in Grand Canyon, is a prime example of a stream altered by such practices. Prior to 1900, the LCR was a perennial stream from its 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 that the river was almost as large as the 'Del Norte' (Colorado River) and was bordered by many groves of willows and poplars (Colton 1937). Whipple (1855) described the midportion of the LCR 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 LCR basin. By the early 1900s, the LCR became an intermittent stream between Holbrook, Arizona, and Blue Spring (a perennial, saline spring entering the LCR 21 km above its mouth; Figure 1) (Colton 1937, Hereford 1984). Due to the loss of perennial input, water

chemistry in the terminal 21 km of the LCR became dependent on the contributions of Blue Spring and other smaller source springs. Salinity and free carbon dioxide levels likely increased. 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 had perennial flows; however, very few fish surveys have been conducted in this reach. In the early 1900s, Colorado squawfish (*Ptychocheilus lucius*), bonytail chub (*Gila elegans*), and roundtail chub (*Gila robusta*) were present in plunge pools immediately below Grand Falls (Miller 1963, Smith et al. 1979, Minckley 1973). These three species are now extirpated from the Grand Canyon region. Razorback sucker (*Xyrauchen texanus*) has been collected sporadically at the mouth of the LCR, and it is rare in the Colorado River (Minckley 1990). Both bluehead sucker (*Pantosteus discobolus*) and flannelmouth sucker (*Catostomus latipinnis*) are presently found in East Clear Creek, a tributary of the LCR entering above Grand Falls, and in the lower 14.2 km of the LCR. Humpback chub (*Gila cypha*) also occurs in the lower 14.2 km. Speckled dace (*Rhinichthys osculus*), the only 'small-bodied' (maximum length <150 mm) native fish, is present in the LCR both above and below Grand Falls.

Within the perennial lower 21 km reach of the LCR, the four remaining native fish species have different distributions. All four inhabit the 14.2 km reach from the mouth of the LCR to Chute Falls, but only speckled dace is present from Chute Falls to Blue Spring (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 factors responsible for the disparate distributions of native fishes in the lower 21 km of the LCR, (i.e. why are four native fishes present in Reach 1, but only one in Reach 2?). Four hypotheses have been proposed to explain the present distributions (see also 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. In this study we concentrated on the first two hypotheses. An additional objective was to determine if the reach between Blue Spring and Chute Falls could be a potential site for augmentation of the LCR humpback chub population.

## Study Site

The study area was the perennial 21 km of the LCR immediately above its 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 nearly constant base flow of 6.3 m<sup>3</sup>/s (cms) at the mouth (Johnson and Sanderson 1968, Cooley et al. 1969). Blue Spring temperature is 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 flow downstream from Blue Spring, free carbon dioxide escapes to the atmosphere and calcite precipitates. Calcite precipitation increases turbidity, imparts a milky blue color to the water, and covers the stream bottom with a layer of uncemented particles. The precipitate eventually forms tufa, the source of 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 a close-order series of 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 Lower Atomizer Falls (13.6 km), Upper Atomizer Falls (13.9 km), and Chute Falls (14.2 km).

The LCR above Blue Spring temporally varies from dryness to large scale floods (U.S. Geological Survey 1954; estimated maximum ca. 3396 m<sup>3</sup>/s, Hereford 1984). Flood flows from winter snowmelt and summer convection storms cause seasonal fluctuations in water temperature in the study area (Kaeding and Zimmerman 1983, Clarkson et al. 1994).

## Methods

### *Limnology*

We divided the LCR into two reaches: Reach 1 = 0-14.2 km (mouth to Chute Falls), and Reach 2 = 14.2-21 km (Chute Falls to Blue Spring), and established six sampling sites, three in each of the two reaches. Sampling sites at 21 (Blue Spring), 20, 15, 10, 5, and 0.6 km were sampled for water chemistry once during each season: October 18-21, 1991 (autumn); January 23-26, 1992 (winter); June 4-7, 1993 (spring); and August 3-8, 1993 (summer). We also sampled water chemistry immediately below AFC at 13.6 km in October 1991 and January 1992. Water temperature, conductivity, pH, and dissolved oxygen were measured with a Hydrolab Surveyor 3 datalogger and H2O transmitter. A Hach Model AL-36 digital titrator kit was used 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.

Periphyton biomass samples were collected from two broad substrate categories--fines (clay, silt and sand) and cobble (64-256 mm)--at the five lower sites during June and August 1993. 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. At each transect point, one (June) or three pooled (August) samples were collected from fine substrates using a mini-core sediment sampler (4.15 cm<sup>2</sup> cross sectional area). Equivalent epilithon samples were collected from cobble using a 4.15 cm<sup>2</sup> 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 opportunistically during autumn 1991 and winter 1992.

Periphyton biomass samples were wrapped in aluminum foil, frozen on dry ice in the field, and then kept in a freezer until laboratory chlorophyll analysis could be performed. Chlorophyll *a* content of the samples was determined by methanol extraction (Tett et al. 1975). Differences in chlorophyll *a* content between the two reaches were assessed with a Kruskal-Wallis (K-W) test.

Benthic invertebrates were collected using a Hess Sampler (0.09 m<sup>2</sup>) at the five lower sites. At each site, one perpendicular-to-flow transect was opportunistically 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 in Reach 2 (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 each of the four study sites: 12.5 (control site), 15, 17.5, and

20 km. 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  $\mu$ m 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 when noticed. At conclusion of the experiment (June 17, 1994), 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 limnology. At each site free carbon dioxide and alkalinity were measured at 6-12 h intervals. Temperature, pH, dissolved oxygen, and conductivity were monitored hourly at each site. Turbidity was measured at 1.25 km intervals from 11.25 to 20 km on June 16. Site differences in water chemistry parameters were analyzed with a one-way ANOVA and the Tukey-Kramer multiple comparison test.

## Results

### *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 small runoff (6.76-6.88 cms). Water temperature was relatively constant between reaches in all months but January, when temperatures were generally lower in Reach 1 than Reach 2.

Except for phosphate, longitudinal gradients in water chemistry were consistent across seasons. Pronounced water chemistry gradients were evident in the lower LCR; Reach 1 differed from Reach 2 (Figure 2). Dissolved oxygen, pH, and conductivity increased, and free carbon dioxide decreased throughout Reach 2, with the sharpest changes from Blue Spring to 20 km. In Reach 1 dissolved oxygen, pH, conductivity, and free carbon dioxide became relatively stable. Alkalinity decreased throughout Reach 2 and Reach 1. Nitrate levels increased

from Blue Spring to 20 km, then decreased downstream throughout the remainder of Reach 2 and throughout Reach 1. No gradient was evident in phosphate levels.

Turbidity increased from Blue Spring downstream throughout Reach 2 and until 10 km (Reach 1), then decreased towards the mouth. Turbidity was greater overall during October 1991 than the two 1993 sampling periods (base flow conditions during all three trips). 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.

Chlorophyll *a* biomass was significantly greater in Reach 2 than in Reach 1 ( $H=39.71$ ,  $p<0.001$ ; Figure 3). It did not vary significantly between the two sample periods ( $H=1.89$ ,  $p=0.17$ ), or between the two substrate types ( $H=1.15$ ,  $p=0.28$ ).

One hundred and thirteen algal taxa (see 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 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 (Ephydriidae, Simuliidae, Corydalidae, Hydrophiidae, Saldidae, Veliidae, Copepoda, and Nematoda) were found only in Reach 2. Ostracods, trichopterans, ephemeropterans, and larval and 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*

The only marked difference in fish survival and behavior was at the 20 km site. At this site, most fish exhibited stress behaviors and there was a high mortality rate for age-0 humpback chub.

Mortality of relocated age-0 humpback chub differed among sites ( $G=13.70$ ,  $p<0.01$ ); i.e., 70%, 0%, 30%, and 20% at the 20.0, 17.5, 15, and 12.5 km sites respectively. No

mortality occurred at the 17.5 km site, and no stress behavior was observed. 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 normally.

All of the age-1 humpback chub ( $n = 40$ ) and bluehead suckers ( $n = 15$ ) at each of the sites survived the 72 h experiment. Age-1 humpback chub behaved normally during the entire experiment, except for those at the 20 km site. All ten humpback chub at the 20 km site became hyperactive at the start of the tempering process. After 30 min of tempering they became lethargic and were gulping for air. These humpback chub were still behaving this way when first placed into the river, but one fish also lost equilibrium. After 24 h and 48 h, three humpback chub were acting normally. By the last observation, 70 h after being placed in the river, six fish were behaving normally.

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

Results of water chemistry analysis during the relocation experiment (Figure 4) were similar to those obtained from longitudinal limnological sampling (Figure 2). There were significant differences among sites for most water chemistry parameters (Table 5). For instance, conductivity and pH differed for all pairwise comparisons among sites. For alkalinity and free 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 17.5 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), however water temperature 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

The initial changes in magnitude of water chemistry parameters from Blue Spring to 20 km were similar to those of Mattes (1993), and likely due to shifts in chemical equilibria with atmospheric exposure. The mechanical action of the AFC and other rapids and falls in the 2 km immediately downstream may release carbon dioxide to the atmosphere, resulting in large amounts of calcium carbonate precipitate (Johnson and Sanderson 1968). Turbidity patterns indicated that calcite precipitation peaked within the 10-13.6 km reach below the major falls. Higher turbidity in 1991 than during both sampling periods in 1993 was 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 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 results in the observed drop in alkalinity immediately below AFC. The decrease in alkalinity and the increase in conductivity from Blue Spring to Chute Falls 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  $\text{Na}^+$ ,  $\text{SO}_4^-$ , and  $\text{Cl}^-$  are nearly twice as great in several downstream springs than in the waters of Blue Spring (Cooley 1976).

The output of Blue Spring during base flow results in fairly consistent water temperatures downstream. The decrease in water temperature from Blue Spring downstream in 1992 was likely due to mixing of cold, snowmelt waters with the warm waters of Blue Spring. Further decreases in temperature towards the mouth may be attributable to low solar radiation input during this month.

Although there is a difference in water chemistry between Reach 1 and Reach 2, and native fishes are likely sensitive to chemical gradients (Hoglund 1961), we do not believe that water chemistry alone prevents humpback chub and bluehead sucker from inhabiting Reach 2. This conclusion is based on: 1) humpback chub and bluehead sucker survival from the relocation

experiment, and 2) speckled dace are common below 20 km, and fathead minnow and common carp were recently reported in Reach 2 (Kaeding and Zimmerman 1983, Mattes 1993).

High carbon dioxide levels during periods of base flow may inhibit the large-bodied native fishes from entering the reach above Chute Falls (Mattes 1993). Our studies indicate that age-0 and age-1 humpback chub, and age-1 bluehead sucker, can acclimate to the carbon dioxide concentrations in the 2.5 km reach immediately above Chute Falls. It is likely that free carbon dioxide concentrations at the 20 km site (348 mg/l) were very near the lethal limit for age-0 humpback chub, however, since the mortality rate was high for these fish and all behaved stressfully. The free 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. 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<sub>2</sub> vary with species and environmental conditions such as temperature and oxygen concentrations (Powers 1937, Black et al. 1954, Alabaster 1957, Takeda and Itazawa 1983). Free carbon dioxide concentrations at the 15 km (192 mg/l) and 17.5 km (196 mg/l) sites are well below the lethal limits reported by Black et al. (1954) for fathead minnows (293 mg/l CO<sub>2</sub> at 20.4 °C for 50 g fish) and common white suckers (*Catostomus commersoni*; 260 mg/l CO<sub>2</sub> at 17.1 °C for 265 g fish).

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 navigate the AFC in the past. However, the extent to which they occupied the reach above the Chute Falls is unknown. The additional perennial discharge above Blue Spring may have been sufficient to allow fish to navigate the falls complex, and the travertine dams may have been smaller in the past. The loss of perennial input 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 floods may dilute chemical concentrations (i.e., CO<sub>2</sub>) and eliminate the vertical barrier of the falls. Four consecutive days of 283-464 cms mean flows were recorded at the Cameron gauge during a flood in January 1993. None of the native large-bodied fishes have been observed above Chute Falls since this flood to indicate that they moved through the falls into Reach 2; however, fish sampling above Chute Falls has been sporadic. Upstream movement through the falls would most likely occur during an extended high stage flood concurrent with the spawning season, when humpback chub are hypothesized to migrate upstream (Mattes 1993).

It is possible that during base flow, unfavorable water quality (i.e., high free carbon dioxide concentrations) and the physical obstacle of Chute Falls limits the distribution of the three large-bodied native fishes to Reach 1, 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, dissolved oxygen concentrations were near saturation immediately below (12.5 km site, 94.55%) and above Chute Falls (17.5 km site, 95.40%), and free carbon dioxide concentrations were lower at the 12.5 km site (179 mg/l) than at the 15 km site (192 mg/l). These oxygen and free carbon dioxide concentrations may negatively affect 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 move through the AFC. Therefore, the physical aspect of the falls in conjunction with high carbon dioxide levels at near-saturation oxygen levels may limit the upstream movements of humpback chub and bluehead and flannelmouth suckers.

Our results indicated 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, free carbon dioxide and 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 promoted 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 abundance in the two reaches, we 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 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 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' (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 Spring reach.

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

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TABLE 1. Mean densities (numbers/m<sup>2</sup>) of invertebrates by site (km) from fine substrates, Little Colorado River, 1993.

	Kilometer Above the Mouth				
	Reach 1			Reach 2	
	0.6	5	10	15	20
<i>June</i>					
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
Ephydriidae	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	37.04	3.70	7.41
Oligochaeta	0	0	3.70	0	0
Total	188.88	248.14	759.25	11459.26	1996.30
<i>August</i>					
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				
	Reach 1			Reach 2	
	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<sup>2</sup>) of invertebrates by site (km) from cobble substrates, Little Colorado River, 1993.

	Kilometer Above the Mouth				
	Reach 1			Reach 2	
	0.6	5	10	15	20
<i>June</i>					
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
<i>August</i>					
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				
	Reach 1			Reach 2	
	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
<b>Chironomidae</b>						
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*
<b>Ceratopogonidae</b>						
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
<b>Empididae</b>						
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
<b>Trichoptera</b>						
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
<b>Ephemeroptera</b>						
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*
<b>Ostracoda</b>						
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
<b>Chironomidae</b>						
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*
<b>Other Diptera</b>						
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*
<b>Trichoptera</b>						
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*
<b>Ephemeroptera</b>						
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*
<b>Ostracoda</b>						
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
<b>Other Taxa</b>						
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
<b>Total</b>						
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. One-way 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	Reach 1	Reach 2			F	p
	12.5 km	15.0 km	17.5 km	20.0 km		
Water temperature ( $^{\circ}\text{C}$ )	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 $\text{CaCO}_3$ )	594.65*	672.30	671.53	740.48*	335.00	<0.001
Carbon dioxide (mg/L)	178.67*	192.15	195.93	347.96*	585.55	<0.001
Dissolved Oxygen (mg/L)	7.48	8.34*	7.57	6.62*	106.62	<0.001
Conductivity ( $\mu\text{S}/\text{cm}$ )	4762.57*	4545.74*	4493.70*	4468.71*	505.26	<0.001

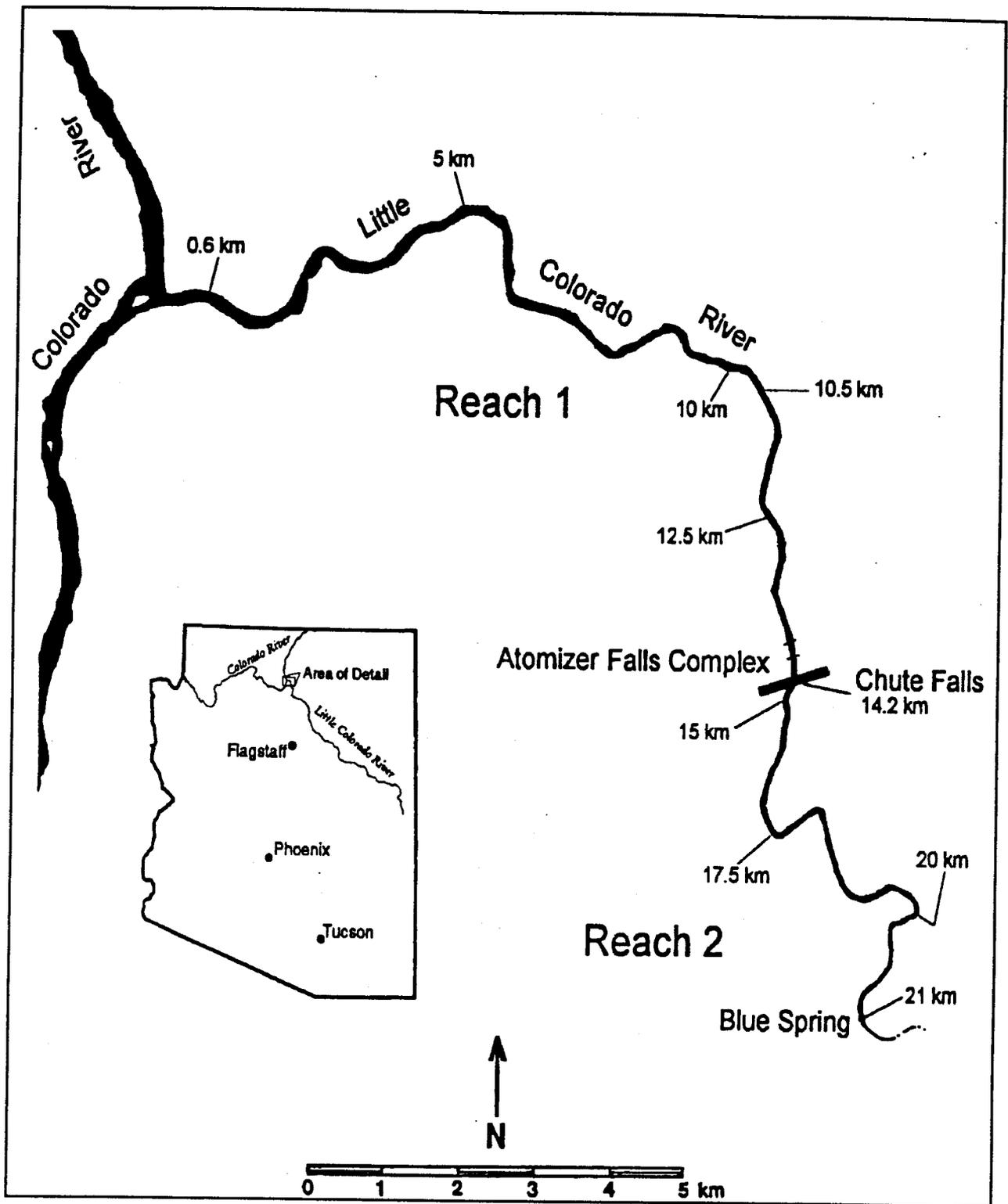


FIGURE 1. Map of the study area showing the location of the reaches and study sites in the terminal 21 km of the Little Colorado River.

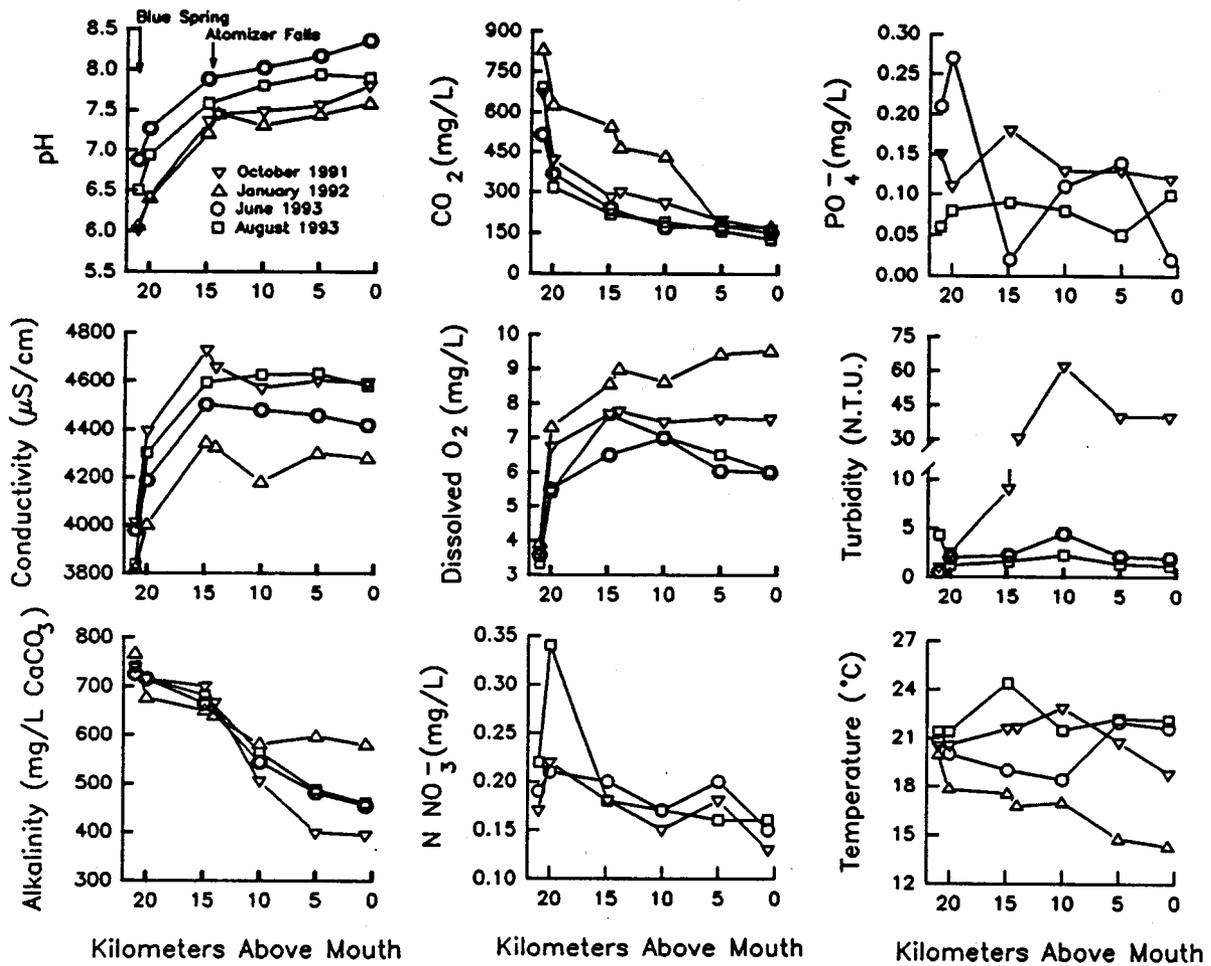


FIGURE 2. Longitudinal patterns of water quality parameters measured at 6 to 7 sites from the Little Colorado River, October 1991 through August 1993.

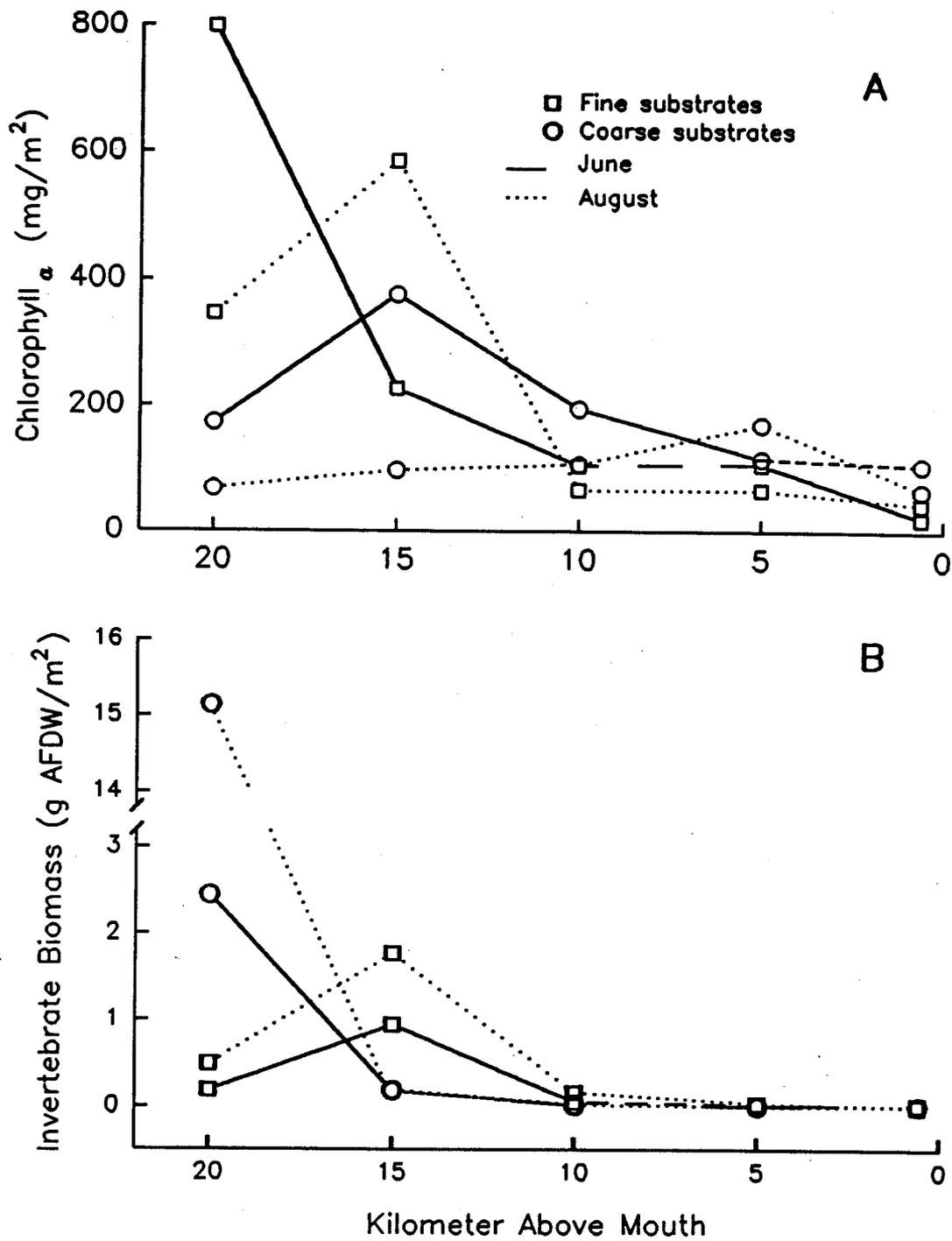


FIGURE 3. Means of chlorophyll *a* concentrations (A) extracted from algal samples, and (B) invertebrate biomass, collected at 5 sites from coarse and fine substrates, Little Colorado River, 1993.

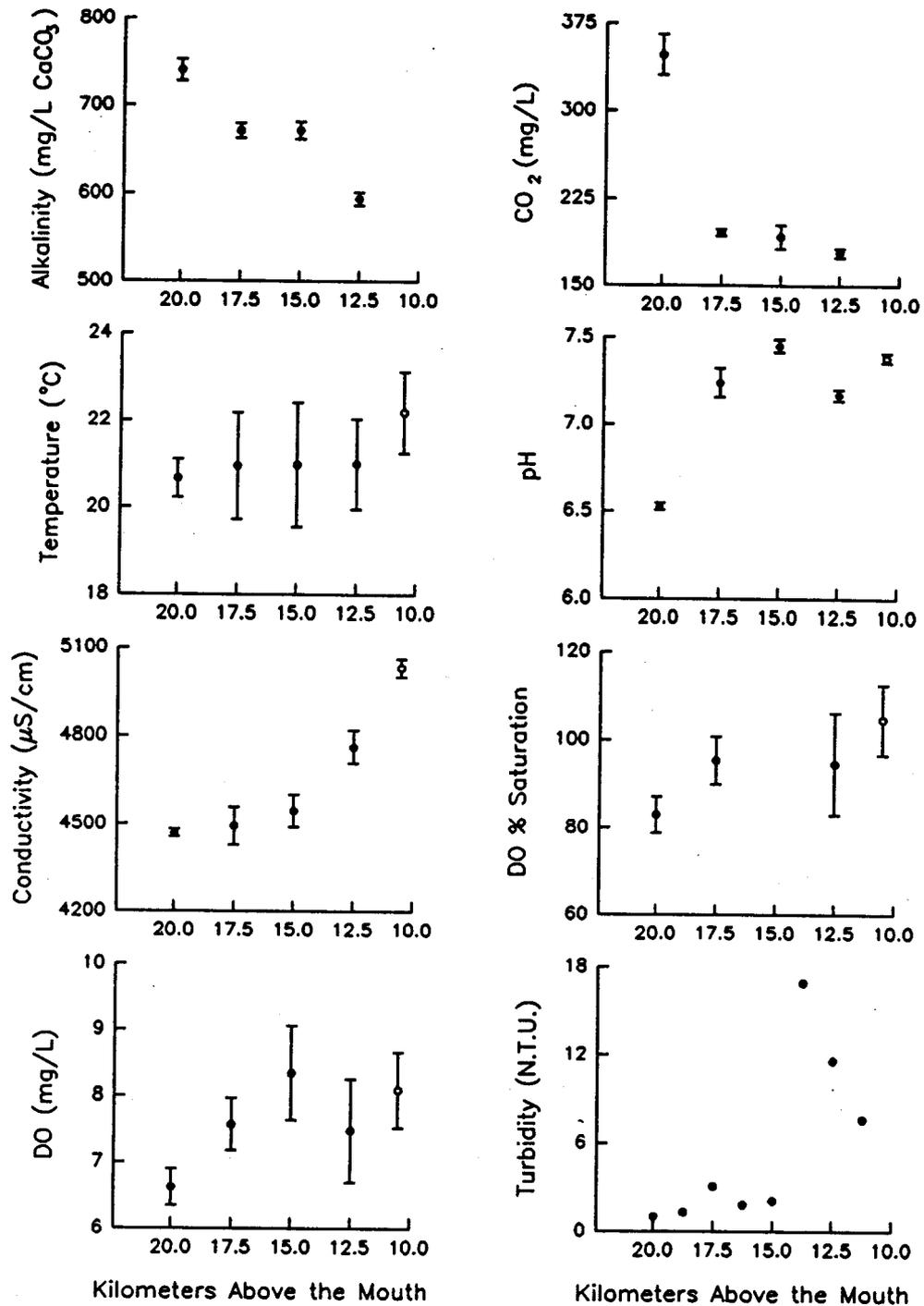


FIGURE 4. Means and standard deviations of water chemistry parameters measured at 5 sites during the humpback chub relocation experiment, Little Colorado River, June 1993. Turbidity, measurements, at 1.25 km intervals, were not replicated.

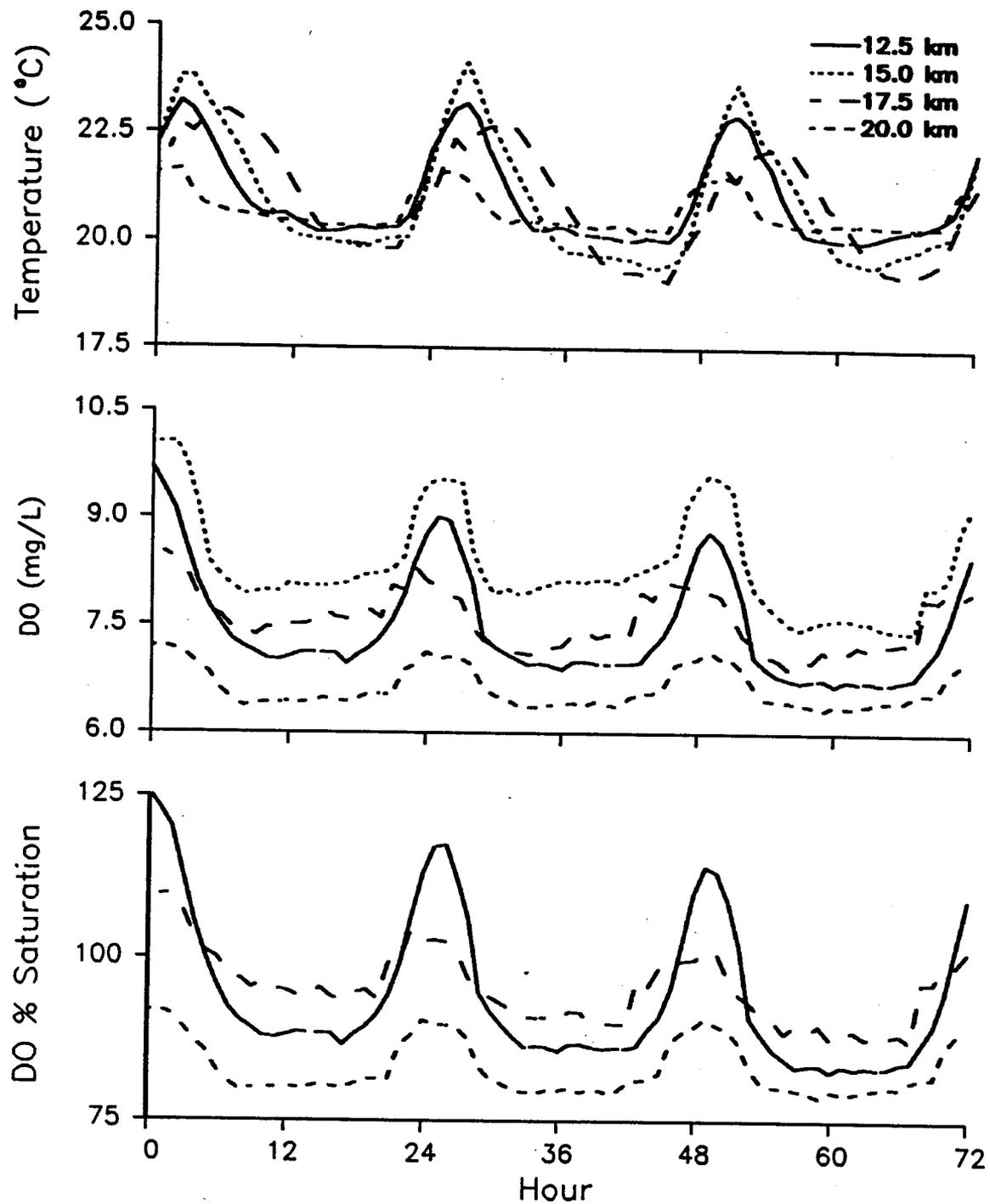


FIGURE 5. Hourly levels of temperature and oxygen at each of the relocation sites, Little Colorado River, 1993. Hour 0 = 1200 h June 13, 1993.

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	Reach 1			Reach 2		
	0.6 km (n=6)	5 km (n=6)	10 km (n=6)	15 km (n=6)	20 km (n=8)	21 km (n=5)
CHLOROPHYTA						
<i>Cladophora</i>						
<i>glomerata</i>	A,R,D	A,D	A,I,D	A	A	A
<i>Microspora</i> sp.	A,R	A	A	A,R	A,R,I,D	A
<i>Oedogonium</i> sp.	A,R	A	A	A,R	A	A,R
<i>Rhizoclonium</i> sp.	A,R	A	A,R	A,R	A	A,I
<i>Spirogyra</i> sp	A,R,D	A	A,D	A,I,D	A,R	A,R,I
<i>Ulothrix</i> sp.	A,R,I	A	A,I	A,R,I	A,C	A,I,C,D
CHRYSOPHYTA						
XANTHOPHYCEAE						
<i>Tribonema</i> sp.	A,R	A	A	A	A,I	A,D
<i>Vaucheria</i> sp.	A	A	A,C	A,D	A,I	A
BACILLARIOPHYCEAE						
<i>Achnanthes</i>						
<i>affinis</i>	A,R,I,C	R,I,C	A,R,I,C	R,C	R,I,C	A,R,I,C
<i>deflexa</i>	A,R	A,R	A	A	A	A
<i>lanceolata</i>	A,R	A,R	A,R,I	R,I,C	I,C	R,I
<i>lanceolata v omissa</i>	A,R	A	A	A,I	A	A,I
<i>linearis</i>	A,R	A,I	A,R	A,R	A,R	A
<i>minutissima</i>	A	A	A	A,R	A	A
<i>Amphora</i>						
<i>coffieformis</i>	A,R	A,R,I	A,R,I	A,R,I	A,R	A,R
<i>ovalis</i>	A,R	A,R	A,I	A,R,I	A	A,R
<i>veneta</i>	A	A	A	A,R	A	A

TABLE A1. continued...

Species	Reach 1			Reach 2		
	0.6 km (n=6)	5 km (n=6)	10 km (n=6)	15 km (n=6)	20 km (n=8)	21 km (n=5)
<i>Anomoeoneis</i>						
<i>vitrea</i>	A,R	A,R,I	A,R	A	A	A
<i>Bacillaria</i>						
<i>paradoxa</i>	A,R	A,R	A,R	R,I	A,R	A,R
<i>Biddulphia</i>						
<i>laevis</i>	A	A	A,R	A,R	A,R,I	A,R
<i>Caloneis</i>						
<i>amphisbaena</i>	A	A	A,R	A	A,R	A,R
<i>bacillaris v thermalis</i>	A	A	A,R	A	A	A
<i>bacillum</i>	A,R	A	A	A,R	A,R	A,R
<i>clevei</i>	A,R	A,R	A	A	A	A
<i>ventricosa v truncatula</i>	A	A	A	A	A,R	A
<i>Cocconeis</i>						
<i>diminuta</i>	A,R	A	A	A	A	A
<i>placentula</i>	A,R	A,R	A,R	A,R	A,R	A
<i>Cyclotella</i>						
<i>meneghiniana</i>	A,R,I	A,R	A,R	R,I	A,R	A,R
<i>Cymbella</i>						
<i>minuta</i>	A,R,I	A,R	A,R,I	A,I	A,R	A
<i>Denticula</i>						
<i>elegans</i>	A,R,I,C	A,R,I	A	A,R	A,R	A,R
<i>Diatoma</i>						
<i>hiemale v mesodon</i>	A	A	A	A	A,R	A
<i>Diploneis</i>						
<i>elliptica</i>	A	A	A	A,R	A	A,R
<i>oblongella</i>	A,R	A,R,I	A,R	A,R	A,R	A,R

TABLE A1. continued...

Species	Reach 1			Reach 2		
	0.6 km (n=6)	5 km (n=6)	10 km (n=6)	15 km (n=6)	20 km (n=8)	21 km (n=5)
<i>Entomoneis</i>						
<i>alata</i>	A,R	A	A,R	A,R	A,R,I	A,R,I
<i>paludosa</i>	R,I,C	R,I,C	A,R,I,C	R,I	A,R,I	R,I
<i>Fragilaria</i>						
<i>brevistriata v inflata</i>	A,R	A	A	A	A	A,R
<i>crotonensis</i>	A,I	A,R	A	A	A	A
<i>vaucheriae</i>	A,R	A,R	A,R	A,R	A,R	A
<i>Frustulia</i>						
<i>vulgaris</i>	A,R	A,R	A,R	A	A	A
<i>Gomphonema</i>						
<i>affine</i>	A	A	A	A	A,R	A,R
<i>angustatum</i>	A,R,I	A,R	A	A,R,I	A,R	A,R
<i>olivaceum</i>	A,I	A,R	A,R	A,R	A	A
<i>parvulum</i>	A,R	A,R	A,R	A,R,I	A,R,I	A,R,I
sp.	A	A	A,R	A	A	A
<i>Gyrosigma</i>						
<i>spencerii</i>	A,R	A,R	A,R	A,R	A	A,R
<i>Mastogloia</i>						
<i>elliptica v danseii</i>	A	A,I	A,R,I	A	A	A,R
<i>Melosira</i> sp.	A	A	A	A	A	A,R
<i>Navicula</i>						
<i>cryptocephala</i>	A,R,I,C	A,C	R,I,C,D	A,I,C	A,C,D	A,C
<i>cryptocephala v veneta</i>	A,R,I	A,R,I,C	A,I,C	A,R,I,C	A,I,C	A,R,C,D
<i>cuspidata</i>	A	A	A	A	A	A,R
<i>gregaria</i>	A,R	A,R	A	A,R	A,R	A,R
<i>seminulum v hustedtii</i>	A,R,I	A,R,I	A,I	A,R	A	A

TABLE A1. continued...

Species	Reach 1			Reach 2		
	0.6 km (n=6)	5 km (n=6)	10 km (n=6)	15 km (n=6)	20 km (n=8)	21 km (n=5)
<i>tripunctata</i>	R,I,C	R,I,C	A,I,C	A,R,I,C	A,R,I,C	A,R
<i>Nitzschia</i>						
<i>acicularis</i>	A	A	A	A,R	A	A
<i>apiculata</i>	A	A	A,R	A,R	A	A,R
<i>dissipata</i>	A	A	A	A,R	A	A
<i>filiformis</i>	A	A	A	A,R	A	A
<i>fonticola</i>	A	A	A,R	A	A,R	A,R
<i>frustulum</i>	A	A	A	A,R	A	A
<i>frustulum v perpusilla</i>	A,R	A	A,R	A,R	A,R,I	A,R
<i>gracilis</i>	A	A	A	A	A,R	A
<i>hungarica</i>	A	A,R	A,R	A,R,I	A	A,R
<i>longissima v closterium</i>	A,R	A,R,I	A,R,I	A,R,I	R,I	R,I
<i>microcephala</i>	A,R	A,R	A,R	A,R,I	A,R,I	A,R,C
<i>palea</i>	A,R,I	A,R	A,R,I	A,R,I	A,R,I	A,R,I,C
<i>sigma</i>	A,R,C	A,R,I	A,R,I,C	A,R,I	A,R	A,R
<i>vermicularis</i>	A,R	A	A	A	A	A
<i>Pinnularia</i>						
<i>appendiculata</i>	A,R,I	A,R	A,R,I	A,R,I	A,R	A,R
<i>microstauron</i>	A	A	A	A,R	A,R	A
<i>substomatophora</i>	A,R	A,R	A	A	A	A,R
sp.	A,R	A	A	A,R	A,R	A
<i>Pleurosigma</i>						
<i>delicatulum</i>	A,R	A,R	A	A,R	A	A,R
<i>Rhopalodia</i>						
<i>gibba</i>	A	A	A,R	A	A	A
<i>gibba v ventricosa</i>	A	A	A,R	A	A	A,R

TABLE A1. continued...

Species	Reach 1			Reach 2		
	0.6 km (n=6)	5 km (n=6)	10 km (n=6)	15 km (n=6)	20 km (n=8)	21 km (n=5)
<i>gibberula v vanheurckii</i>	A	A,R	A,R	A	A,R	A,R
<i>Stephanodiscus</i>						
<i>astraea</i>	A	A	A	A,R	A	A
<i>Surirella</i>						
<i>ovalis</i>	A,R	A,R,I	A,R,I	R,I,C	R,I	A,R
<i>ovata</i>	A	A,R	A,R	A	A	A
<i>ovata v pinnata</i>	A	A	A	A	A,R	A,R
<i>striatula</i>	A	A,R	A	A,R	A,R	A
<i>Synedra</i>						
<i>acus</i>	A,R	A,R	A,R	A,R	A	A,R
<i>affinis</i>	A	A,R	A	A	A	A
<i>ulna</i>	A,R,I	A,R,I	A,I	A,R,I	A,R	A,R
CYANOPHYTA						
<i>Anabaena</i> sp.	A,R,I	A,R,I,C	A,R,I	A,R	A,I	A,R,I
<i>Calothrix</i> sp.	A,R	A	A	A	A,R	A,R
<i>Chroococcus</i> sp.	A,R	A	A	A	A	A,R
<i>Gloeocapsa</i> sp.	A	A	A	A	A,R	A
<i>Lyngbya</i> sp.	A	A	A	A	A,R	A,I
<i>Microcoleus</i> sp.	C	A	A	A	A,R	A
<i>Microcystis</i> sp.	A	A	A	A	A,R	A
<i>Nostoc</i> sp.	A	A,R	A	A	A	A,I
<i>Oscillatoria</i> sp.	A,R,I	A,R,C,D	A,R,I,D	A,R	A,R,C	A,R,I,C
<i>Pseudanabaena</i> sp.	A	A,I	A	A	A,R	A