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FLOW–SEDIMENT–BIOTA RELATIONS: IMPLICATIONS FOR RIVER REGULATION EFFECTS ON NATIVE FISH ABUNDANCE

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Abstract. Alteration of natural flow regimes by river regulation affects fish distribution and assemblage structure, but causative pathways are not always direct and may go unrecognized. The Colorado River population of the endangered Colorado pikeminnow, *Ptychocheilus lucius*, suffers from low rates of recruitment and reduced carrying capacity. We hypothesized that availability of prey fish for this large-bodied native piscivore may, in part, be limited by reduced standing crops of periphyton and macroinvertebrates resulting from accumulation of fine sediment in the riverbed. We stratified the 373-km-long study area into 11 strata and sampled various physical and biological parameters in runs and riffles of three randomly selected 1- to 3-km-long study reaches in each stratum during base flows of spring and fall 1994–1995. Significant correlations were found between biomass of both chlorophyll *a* and macroinvertebrates and various physical metrics that described the degree of fine sediment accumulation in gravel–cobble substrates. Riffles were relatively free of fine sediment throughout the study area, but substrates of runs contained progressively more fine sediments with distance downstream. There was a corresponding longitudinal change in biota along the river continuum with greatest biomass of fish, invertebrates, and periphyton upstream. Adult pikeminnow were concentrated in upstream strata where potential prey fishes were most abundant. We suggest that fine-sediment effects on biota have increased in recent years as a result of river regulation. Historically, spring snowmelt frequently produced flows with magnitudes sufficient to mobilize the bed and winnow silt and sand from coarse substrates. Following regulation, the mean recurrence interval of such flows lengthened from 1.3–2.7 yr (depending on the stratum) to 2.7–13.5 yr, extending the duration of fine sediment accumulation and potentially depressing biotic production. Our results describe and help explain the spatial distribution of the Colorado River fish community and establish a link between flow, sediment, and the riverine food web supporting the community's top predator. To maintain intact native fish communities in this and other river basins, managers need to identify functional aspects of the natural hydrograph and incorporate these findings into river restoration efforts.

Key words: benthic macroinvertebrates; Colorado pikeminnow; Colorado River; fish distribution; flow regime; foodweb; interdisciplinary research; natural-flow-regime paradigm; *Ptychocheilus lucius*; river regulation; river restoration; sediment.

INTRODUCTION

Regulation of rivers and streams throughout North America during the twentieth century altered lotic ecosystems and contributed to the decline of many native fish populations (Petts 1984, Minckley and Douglas 1991, Hesse and Mestl 1993, Ligon et al. 1995, Naiman et al. 1995, Barinaga 1996, Poff et al. 1997). Often, the causes of rapid fish declines from dams and diversions were direct and readily apparent, e.g., drying of streams from water diversions, blockage of salmonid spawning runs by dams, or cold-water releases from dams into once warm-water fish habitats. However, alteration of flow regimes may affect fish indirectly and causal links to population health are often less appar-

ent. Nevertheless, the ultimate effects on fish populations may be profound (Wootton et al. 1996). Synthesis of accumulated evidence has recently led to the formulation of the “natural-flow-regime paradigm” wherein recreation of natural-hydrograph functionality is emphasized in foodweb and native fish restorative efforts (e.g., Power et al. 1996, Stanford et al. 1996, Poff et al. 1997).

Flow regime is an important factor influencing fish distribution and assemblage structure (Stevens and Miller 1983, Meffe 1984, Bain et al. 1988, Poff and Allen 1995, Mion et al. 1998, Petersen and Kwak 1999), and its modification affects aquatic biota at the population and community levels (Schlosser 1991, Marchetti and Moyle 2001). Past attempts to relate flow to fish production have been based largely on fish preferences for physical habitat variables (Bovee 1986,

Fausch et al. 1988), yet many studies suggest that biotic factors such as food availability may be more important (Cada et al. 1987, Filbert and Hawkins 1995, Hughes 1998, Nislow et al. 1999). With the exception of the flood-pulse concept, wherein main-channel productivity is enhanced by the entrainment of floodplain nutrients and carbon (Junk et al. 1989, Bayley 1995, Power et al. 1995), few investigations have attempted to link flow effects to availability of food for fishes.

To restore native fish populations in regulated rivers, management strategies must be based on an understanding, not only of the fishes' life-history attributes, but also of the ecosystem that sustains them (Power et al. 1995, Stanford et al. 1996, Wootton et al. 1996). Petts (1991) identified the need for integration of interdisciplinary research that approaches the study of regulated rivers on a longitudinal basis and in a hierarchical manner: hydrology and geomorphology to describe the influence of flow regime and sediment sources on river structure, and ecology to link these influences to riverine fauna. However, large-scale riverine processes are inherently difficult to study (Schlosser 1991, Johnson et al. 1995, Peterson and Kwak 1999). With some exceptions, experimental studies are generally not possible (Power et al. 1995, Poff et al. 1997), so correlative empirical approaches are required to discern linkages among flow, sediment, and biota.

The Colorado River, in southwestern United States, is one of the most regulated rivers in North America (Fradkin 1981). Nearly all of the pathways by which regulation can alter or degrade native aquatic fauna are represented, supplying diverse challenges for the applied ecologist. Driven by the mandates of the Endangered Species Act, resource managers need solutions to ecologically complex problems (Stanford 1994, Holling and Meffe 1996). Herein, we report the results of our investigations concerning physical habitat and trophic relations in a contiguous portion of the upper Colorado River inhabited by all life stages of *Ptychocheilus lucius* Girard (Colorado pikeminnow), an endangered piscivorous cyprinid. For this population, low recruitment and low adult carrying capacity are two primary constraints that limit population viability (Osmundson and Burnham 1998, Osmundson et al. 1998). In addition to the obvious effects of reduced range from instream barriers, we hypothesized that the capacity of the system to support adult pikeminnow may have declined from a reduction in food availability due to increased persistence of fine sediment (particles <2 mm), a possible effect of river regulation.

We used an interdisciplinary approach to investigating the role of flow regime in riverine trophic structure, integrating geomorphology with studies of fish community structure and biomass of lower trophic levels (Petts 1991, Johnson et al. 1995). We first described the distribution of physical habitat and biota on a longitudinal basis throughout the present and historical range of Colorado pikeminnow in the upper Colorado

River mainstem. Then, using empirical relations, we sought links among sediment distribution, standing crops of primary producers, consumers, and the principal piscivore (Colorado pikeminnow). The relation between flow and sediment movement was next assessed through standard geomorphological analyses. Utilizing these empirical relations and historical flow records, we evaluated the potential for reduced predator food availability as affected by functional changes in flow. Our goal was to assess links among flow, sediment, and biota in a large river system and determine if such linkages might provide a food-mediated pathway by which flow regime alteration affects fish assemblage structure. We discuss the implications for native fish restoration efforts in general and provide management recommendations for conservation of Colorado pikeminnow in the upper Colorado River.

SPECIES OVERVIEW AND STUDY AREA

Colorado pikeminnow

The Colorado pikeminnow, a large, long-lived piscivore, along with three other large-river, warm-water fish species (two chubs, *Gila cypha* Miller and *G. elegans* Baird and Girard, and one sucker *Xyrauchen texanus* Abbott) endemic to the Colorado River Basin, are classified as endangered under the Endangered Species Act (U.S. Fish and Wildlife Service 2000). All four once occurred throughout the basin, ranging from Wyoming south to the Gulf of California (Miller 1961). Due primarily to extensive dam construction during the 1930s to 1960s, populations of Colorado pikeminnow were extirpated in the lower sub-basin (downstream of Lee's Ferry) by the 1970s and today occur only upstream of Glen Canyon Dam, primarily in the states of Utah and Colorado (Minckley and Deacon 1968, Minckley 1973). In the upper sub-basin, the range of this species was reduced early in the century by diversions built for local irrigation projects, and additionally by the more recent (1960s–1980s) construction of several large dams. Lotic environments were converted to lentic habitats, downstream water temperatures were reduced by hypolimnetic releases, and migration routes were blocked (Ono et al. 1983). After a 75% basin-wide loss of range, a viable population occurs today only in the Green River system (Gilpin 1993). A smaller, less viable population occurs in the mainstem Colorado River and its Gunnison River tributary (Osmundson and Burnham 1998). Populations of *Ptychocheilus lucius* appear to require an extensive length of river with an array of habitat types to meet the changing needs of different life stages. Larvae hatched in gravel–cobble substrates of high-gradient reaches drift 100–200 km downstream to low-gradient reaches where backwaters formed in silt–sand bars provide ideal nursery habitat (Haynes et al. 1984, Tyus and Haines 1991). Insectivory is largely replaced by piscivory during the first year (Vanicek and Kramer

1969, Muth and Snyder 1995), and abundant nonnative minnows (*Cyprinella*, *Notropis*, and *Pimephales*) provide ample forage for the next several years. As Colorado pikeminnow mature (6–9 yr), the need for larger forage fish is not met in lower reaches of the Colorado River mainstem where native prey fish are scarce. Low body condition prompts many Colorado pikeminnow to disperse to upper reaches and tributaries where larger prey (suckers and chubs) are more abundant (Osmundson et al. 1998). This progressive dispersal pattern results in relatively segregated life stages and adult densities are surprisingly clumped near the upstream margins of their range.

The amount (kilometers) of suitable adult habitat in the Colorado River is substantially less than that available in the Green River system and this accounts in part for the difference in size of the respective populations. Additionally, the spring hydrograph of the Green River mainstem downstream of the Yampa River confluence more closely approximates natural conditions than does the hydrograph of the mainstem upper Colorado River. Although a population estimate is not yet available for the Green River system, Osmundson and Burnham (1998) estimated only 300–400 adult pikeminnow (≥ 500 mm long) in the mainstem Colorado River during 1991–1994 and considered the population vulnerable to extirpation.

The Colorado River in the upper basin

Setting.—The 373-km-long study area, situated in western Colorado and eastern Utah, encompasses the past and present range of the Colorado pikeminnow in the mainstem Colorado River upstream of the Green River confluence (Fig. 1). River locations are herein described in river kilometers (rk) upstream of this confluence (rk 0.0). The upstream-most 76 rk is a transition zone between warm- and cold-water fish communities and historic usage of this area by Colorado pikeminnow is unknown. Today, upstream range of pikeminnow is truncated by a diversion structure at rk 303 that has blocked upstream fish movements since 1911. Excluded from study were the Gunnison and Dolores rivers, two primary tributaries entering the Colorado River within the study area. Headwaters of the three tributaries are located in the Rocky Mountains and the Colorado Plateau. The annual hydrograph is dominated by spring snowmelt that typically begins in late April, peaks in late May or early June, and recedes in July. Most runoff is derived from high-elevation basins underlain by erosion-resistant rocks, whereas most of the sediment is derived from surface erosion of sedimentary rocks, primarily shale, in low-elevation basins (Iorns et al. 1965, Liebermann et al. 1989). Common, localized, summer thunderstorms dramatically increase river turbidity but generally have little effect on mainstem discharges (Van Steeter and Pitlick 1998). Drainage area upstream of the Gunnison River

confluence is $\sim 22\,700$ km²; $\sim 46\,200$ km² upstream of the Dolores River confluence, and $\sim 70\,000$ km² upstream of the Green River confluence. Within the study area, the river flows southwesterly, bisecting the Roan Mesa and Paradox Basin physiographic provinces of the Colorado Plateau (Liebermann et al. 1989). The gradient varies considerably (Fig. 1) and open valleys with floodplains (strata 4, 6, 8, 9, and 11) alternate with canyons (strata 1, 2, 3, 5, 7, and 10). Habitat richness is generally highest in floodplains where multichannel segments are common; in more confined sections, single-channel segments predominate. Gravel–cobble substrates comprise the channel bed in most areas, although silt and sand dominate in some low-gradient areas.

Regulation history.—Three mainstem, low-head, diversion dams built just upstream of Palisade, Colorado between 1883 and 1916 collectively divert ~ 43 m³/s from the river during the irrigation season (April through October) and $\sim 80\%$ of this water is returned through groundwater and numerous drains entering the river at various sites for 70 km downstream. Sediment plumes are normally observed at the mouths of return canals during the irrigation season. The middle and upper dams block all upstream fish migration. In the headwaters of the Colorado mainstem, 15 dams with individual capacities $>6.2 \times 10^6$ m³ were constructed, most between 1943 and 1968 (Liebermann et al. 1989). Collectively, the water volume stored in these reservoirs is equal to about one half of the mean annual streamflow of the upper Colorado River. Many of these were designed to serve transbasin diversions to the east side of the Rocky Mountains, and today, a mean of 14% (7–30% range) of the annual streamflow of the upper Colorado River is lost from the basin. In addition, reservoirs store runoff in the spring and release it slowly over the rest of the year to generate power and satisfy irrigation demands. This results in a flatter hydrograph, with lower spring runoff flows and higher summer and winter base flows (Van Steeter and Pitlick 1998). Earlier in the century (1902–1942), the median peak discharge (highest annual day) of the Colorado River (rk 298) upstream of the Gunnison River confluence was 838 m³/s; in more recent years (1969–1999), it was only 411 m³/s, a decline of 51%. Similarly, major dams in the Gunnison River basin were constructed primarily during 1937–1966 and the median peak flow upstream of the confluence with the Colorado River declined from 489 m³/s during 1897–1936 to 216 m³/s during 1967–1999, a 56% decline (synthesis of U.S. Geological Survey [USGS] gauge data). Median peak discharge of the Dolores River near its mouth (historically about 195 m³/s), also declined following the construction of McPhee Reservoir in 1984, but only by $\sim 6\%$. While spring flows in the Colorado River have declined, sediment inputs have probably not. Thus, suspended sediment that was once

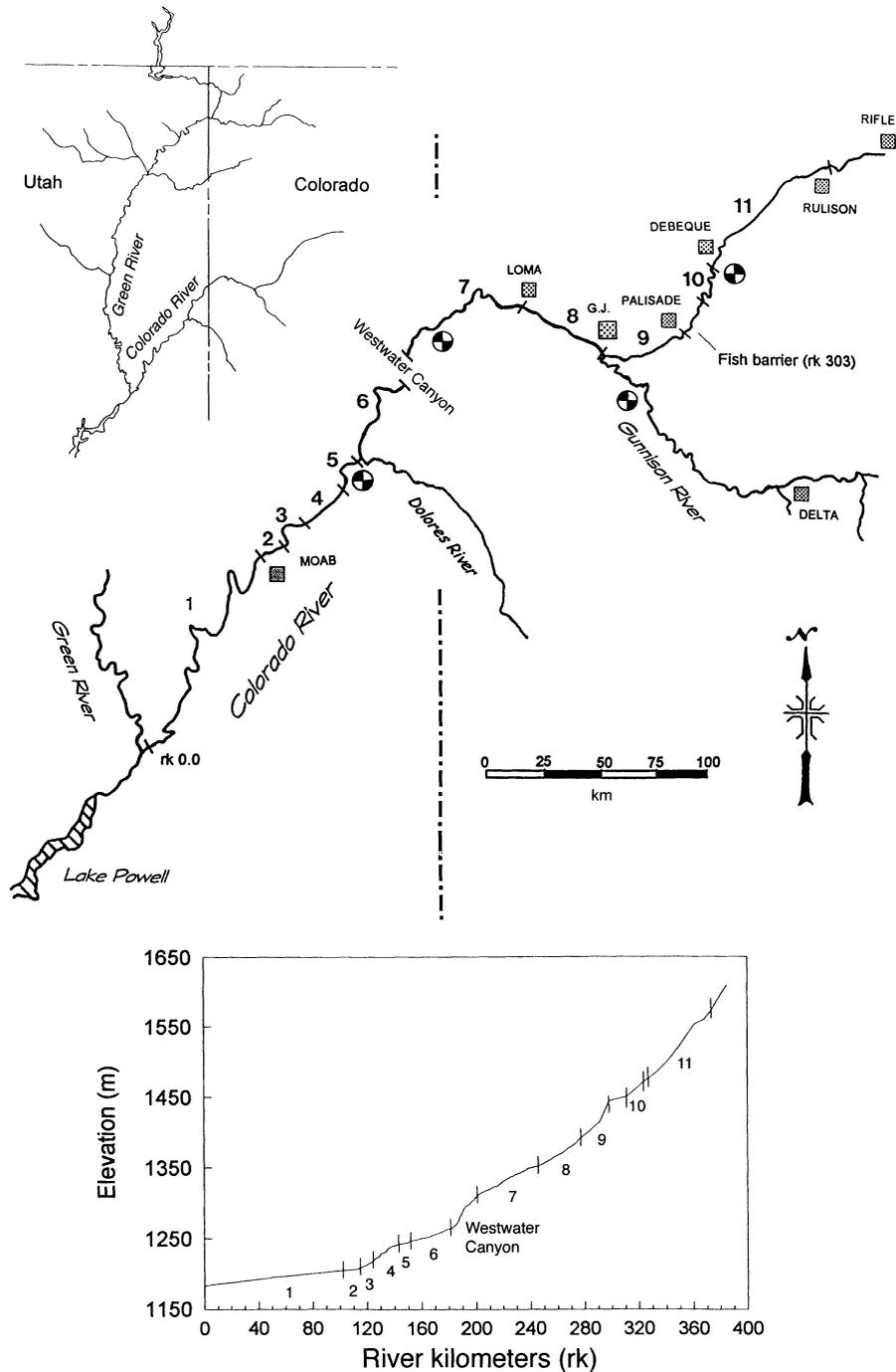


FIG. 1. Map (top) and longitudinal profile (bottom) of the upper Colorado River with numbered (1–11) study strata. Downstream and upstream river-kilometer (rk) boundaries of the 11 study strata are: 1, 0–103; 2, 103–113; 3, 113–126; 4, 126–142; 5, 142–151; 6, 151–182; 7, 201–248; 8, 148–275; 9, 275–298; 10, 312–323; 11, 328–373. The locations of current U.S. Geological Survey gauging stations are marked with crossed circles. The city of Grand Junction is abbreviated as G.J.

carried downstream and through the system now has a greater tendency to accumulate on the riverbed and channel margins. As a result, the channel (wetted area at base flow) has narrowed and backwater and side-

channel area has declined by 25% in the 51-km Grand Valley area (from Loma to Palisade) and 31% in the 58-km DeBeque-to-Rifle segment (Van Steeter and Pitlick 1998, Pitlick and Cress 2000).

METHODS

Study design

We used a stratified random-sampling approach to characterize physical and biotic attributes along the river and test for relationships between physical and biological metrics. The river was first stratified by differences in channel morphology and mean gradient. Four strata were omitted from study because they were either transitional, anomalous (Westwater Canyon), or similar to an adjacent stratum. Eleven study strata comprised 335 km, or 90% of the study area. Using aerial photographs, we divided each stratum into reaches consisting of one meander sequence (1.0–3.1 km long) with the top of each demarcated by the upstream end of a riffle. From these, three study reaches were selected from each stratum using a random numbers table, for a total of 33 reaches.

With three exceptions (studies of geomorphology, sediment dynamics, and Colorado pikeminnow), the study was conducted over a two-year period (1994–1995), with sampling conducted in early spring (March and April) prior to runoff and in fall (September and October) following the summer thunderstorm season. These represented two distinct seasonal periods when discharge levels were relatively stable. The first period (spring 1994) was largely a pilot effort and only strata 4, 6, 9, and 11 were sampled. All study strata were sampled in subsequent periods. Most analyses included only the three periods with complete data sets, although the spring 1994 samples were included when statistically appropriate.

Geomorphology

To characterize channel morphology, we surveyed main-channel cross-sections during 1995–1997 at evenly spaced, 1.6-km intervals from rk 77 to rk 363 (except two reaches and a few sites too difficult to access or survey) using an electronic theodolite (total station) and a motorized rubber raft outfitted with a depth sounder. Mean river slopes were calculated from USGS 7.5-min topographic maps (1:24 000 scale) and global-positioning surveys. Point counts of the surface bed material and bulk samples of the subsurface sediment were used to characterize substrate within each stratum. Sieves were used to size 100 or 200 randomly selected particles from the surface layer and 100–150 kg of underlying subsurface sediment. A total of 56 surface samples and 27 subsurface samples were taken from exposed bars at low flow. The median grain size (D_{50}) for each stratum was derived from composite samples obtained by grouping data from 3–10 individual sites per stratum.

Fine sediment is winnowed from the riverbed when flows reach sufficient magnitude to dislodge coarse framework particles and move the surficial armor layer. Estimates of discharges required to transport bed material were made by combining several conventional

flow and sediment transport equations, solved and calibrated with the aid of flow and sediment data described above (see Pitlick and Van Steeter 1998). Assessment of coarse sediment transport frequency was derived from stream-flow records from four USGS gauging stations (Fig. 1).

Total depth of free space (DFS: absolute distance from the top of surficial rocks to the point where rocks are embedded in fine sediment) and relative DFS (free-space depth scaled to median rock size) was monitored over six years (1996–2001) in strata 9 and 8 to provide insight into the temporal dynamics of fine sediment intrusion in the armor layer. These strata were selected for monitoring because of high numbers of fish, relatively clean substrate during the initial 1994–1995 study, and the immediate upstream and downstream proximity to a major inflow and potential sediment source (the Gunnison River). Twenty DFS measurements were taken per sampling effort at each of 16 permanent monitoring sites. In each stratum, four sites were in run habitats, four were in riffles. Each measurement consisted of laying one hand flat across the top of the substrate surface while using the extended fingers of the other hand to probe the substrate until the layer of embeddedness was reached. The distance from the finger tip of the probing hand to the perpendicular palm of the first hand was measured with a rule to the nearest 0.5 cm. Sampling was conducted 2–4 times annually during base flows of summer and fall (August through October). To derive relative DFS, individual values of total DFS were divided by the median rock width of the respective site (once annually during base flow, the *b*-axis of each of 100 rocks [≥ 8 mm] sampled from an underwater transect at each site was measured to the nearest 1 mm with a vernier caliper).

Other physical parameters

A representative riffle and run were selected within each study reach as consistent sites for additional measurements; there were 66 such sites (11 strata \times 3 reaches \times 2 habitats). Within each, the following measurements were made at five locations parallel to shore at a standardized water depth of ~ 30 –45 cm, independent of substrate: total DFS, percentage of embeddedness (portion of aerial surface area consisting of fines), interstitial void volume, and percentage of surface layer consisting of fines (< 2 mm). A 0.134-m² Hess sampler (50 cm high) was used to circumscribe the five samples for total DFS, percentage embeddedness, and void volume. Percentage embeddedness (surface area within the Hess sampler) was visually estimated before the Hess-enclosed substrate was disturbed. Total DFS within the Hess sampler was measured once using the method previously described for DFS monitoring. Void volumes were then derived from water displacement: all rocks above the embeddedness layer within the Hess sampler were placed in a tub of

the same dimensions, covered with water, and the water volume measured. To derive the percentage of substrate <2 mm, five interstitial substrate samples (500 mL) were collected near the Hess samples with a 3 cm diameter, clear, PVC, core tube; oven dried in the lab at 68°C; and sieve separated into size fractions. Mid-column water velocity was measured at each Hess sample location with a Model 201 portable water current meter (Marsh McBirney, Gaithersburg, Maryland, USA). To derive median substrate particle size (total D_{50} and D_{50} of particles ≥ 2 mm), substrate size distributions were quantified from pebble counts (Wolman 1954); one count was made parallel to shore at each run and riffle sampling site in the vicinity of the Hess sampling site described above.

Mapping was used to quantify the surface area, within each reach, of seven major mesohabitat types (riffles, runs, shoals, backwaters, low velocity, slack water, and vegetated), with two to six possible subtypes. This was done once during base flows of fall 1996. Habitats were drawn in the field on hard copies of airborne videography, orthorectified, and transferred to a GIS base map for interpretation.

Additional parameters were measured during a synoptic survey that immediately preceded each sampling period, and included light extinction, dissolved or suspended nutrients, and turbidity. This survey was conducted in one day and data were collected at one site within each sample stratum. Light was measured at multiple depths with a model LI-193SA spherical quantum sensor (LICOR, Lincoln, Nebraska, USA) that collected scattered as well as surface light. Water samples were collected from midchannel at a depth of ~15 cm. One 1-L water sample was split into two parts: one part was filtered in the field with a 0.45- μ m mesh type HA Millipore filter for ammonia, nitrate, nitrite, and orthophosphorous analyses; the other part remained as a whole-water sample for total nitrogen and total phosphorous analyses. All water samples were acidified with concentrated sulfuric acid. Time between collection and laboratory analysis varied but was always within holding periods specified in Standard Methods (American Public Health Association et al. 1992). All nutrients were analyzed in the laboratory with a Spectronic 301 (Milton Roy Company, Rochester, New York, USA), utilizing a 5-cm cell. Methodologies for nutrient analyses followed Standard Methods. Turbidity was measured in situ (midchannel) with a Hydrolab Surveyor 3 (Hydrolab, Austin, Texas, USA). Main-channel temperatures were monitored year-round at seven sites within the study area (strata 1, 6, 7, 8, 9, 10, and 11) as part of another study and methods and results were previously reported by Osmundson et al. (1998).

Biological parameters

Biomasses of periphyton, benthic macroinvertebrates, and benthic detritus were estimated at each riffle

and run sample location. Benthic macroinvertebrates were collected at the same five Hess-sample sites described in the preceding section. All substrate particles above the level of embeddedness were dislodged or rubbed by hand to loosen macroinvertebrates as particles were removed from the Hess sampler for the interstitial void volume analysis described above. In the laboratory, formalin-preserved samples were sorted and dry mass of invertebrates was estimated from displacement volumes using family-specific regression equations developed for this study. Detritus, or coarse particulate organic matter (CPOM), collected with the invertebrate samples was oven dried at 68°C and weighed with an analytical balance.

Chlorophyll *a* was used as a relative index to live periphyton biomass (Stemann Nielsen and Jorgensen 1962); this was because periphyton samples contained dead tissue, detritus, and deposited silt particles that could not be easily separated. Five cobble-sized rocks adjacent to each Hess sample were selected to provide periphyton samples. Periphyton scraped from a 2.5 cm diameter circle (5 cm²) scribed on each rock was covered in tin foil to exclude light, frozen in the field with dry ice, and stored frozen until analyzed in the lab. Chlorophyll *a* concentrations were measured with a Model 111 fluorometer (Turner Associates, Palo Alto, California, USA) within 30 d of collection.

Electrofishing catch rates were used as an index of relative abundance of main-channel fish species. We assumed these rates were proportionally related to the total fish biomass within a study reach. Only fish ≥ 100 mm in total length (TL) were targeted under the assumption that pikeminnow ≥ 550 mm TL require forage items of at least this size (Osmundson et al. 1998). Within each study reach, both shorelines were electrofished in a downstream direction with a 5 m long, hard-bottomed, electrofishing boat. In reaches containing rapids, a 5-m rubber raft outfitted for electrofishing was sometimes used. Each craft was equipped with a Coffelt VVP-15 (Coffelt Manufacturing, Flagstaff, Arizona, USA) that produced pulsed DC. In strata 7–11, where fish were abundant, two people were required to dipnet stunned fish from the bow of the boat; in strata 1–6, where fish were few, only one person was needed to net all fish. Each shoreline within each reach was treated as a separate sample, resulting in six samples per stratum.

Netted fish were transferred to one of two live wells on the boat and held until a shoreline sample was completed: fishes from run habitats went in one and fishes from riffles went in the other. Elapsed shocking time (*s*) through each habitat type (counted on the VVP meter) was recorded. Fishes were identified, measured for TL (to the nearest 1 mm), weighed with an electronic balance (to the nearest gram), and released.

Adult Colorado pikeminnow densities per stratum were derived from mean annual population estimates (see Osmundson and Burnham 1998 for methods), the

proportion of captured individuals ≥ 550 mm TL, and correction factors based on stratum-specific catch-per-effort values and kilometers per stratum. Because of the rarity of this species, all available data (1991–1994 and 1998–1999) were used to characterize population distribution including years outside of the 1994–1995 study period.

Comparisons of fish body condition among strata also were used as a means to assess food availability. Only the three dominant large-bodied native species were analyzed: *Catostomus discobolus* Cope (bluehead sucker), *C. latipinnis* Baird and Girard (flannelmouth sucker), and *Gila robusta* Baird and Gerard (roundtail chub). Relative condition (K_r) is the observed mass of a given fish divided by the expected mass for a fish of its length (Le Cren 1951). The expected mass is calculated using constants (slope and intercept coefficients) derived from regressing log-transformed mass as a function of length (see Osmundson et al. 1998). We used length and mass of all captured individuals from the last three sample periods to develop one length–mass relationship for each species that could then be used as a standard for among-strata comparisons.

Statistical procedures

Various statistical procedures were used including analysis of variance (ANOVA), analysis of covariance (ANCOVA), Pearson correlation, multiple regression, and principal component analysis (PCA). All statistical analyses were performed using NCSS (2000). In the results, the test used for each analysis is stated along with the pertinent statistics and P values. For statistical analyses, log transformations ($\ln[x + 1]$) were used to increase normality in biological parameters; all analyses of chlorophyll a , macroinvertebrate biomass, and fish numbers and biomass are from \ln -transformed values. For ANOVA tests, the Tukey–Kramer multiple comparison test was used for post hoc testing among treatments ($P < 0.05$).

PCA was used to explore relationships among physical attributes of the riverbed. The PCA attempts to maintain the information of several variables with fewer independent variables (often one to three). Values (scores) of this reduced set of variables are calculated from transformed original data using loading coefficients (maximum absolute value = 1.0). Ranges in the scores of the resulting variables are useful in characterizing the original data set and relating to other variables. We used PCA to characterize sites relative to bed-sediment characteristics. The scores from the first principal component from seven physical variables were regressed against chlorophyll a and macroinvertebrate biomass to assess relationships between the physical environment and the lowest trophic levels. The seven physical variables were: fraction of the substrate < 2 mm, median particle size of the surface layer, volume of interstitial void space, fraction of the surface

area consisting of fines, total DFS, midcolumn water velocity, and CPOM dry mass.

RESULTS

Longitudinal variation

Physical characteristics.—River gradient increased almost exponentially in an upstream direction, varying from 0.028% in stratum 1 to 0.196% in stratum 11 (Fig. 1, lower). The overall mean gradient of 0.100% was equaled or exceeded in strata 7–11 and stratum 4. Bankfull depth of the river channel increased systematically downstream (Fig. 2a), whereas bankfull width varied greatly among strata but with no longitudinal trend. Mean bankfull depth doubled between strata 11 and 5 and reached a maximum in canyon-bound stratum 3; it then decreased through strata 2 and 1. Actual water depth at base flow was not measured. Habitat mapping indicated a steady, nearly linear, downstream decrease in surface area of riffles, varying from 12.9% of total surface area in stratum 11 to $< 0.1\%$ in stratum 1 (Fig. 2b).

Estimates of discharges necessary to initiate motion of coarse bed materials (characterized by sporadic motion of a few particles somewhere on the bed) at 50% of the cross sections increased with distance downstream, but were similar among strata bounded by the same major tributaries (Table 1; Fig. 1); in strata 2–11, these discharges averaged 40% of the bankfull discharge (Pitlick and Cress 2000). Discharges necessary to cause widespread bed mobilization at 50% of the cross sections also increased downstream (Table 1); in strata 6–11, these discharges were similar among strata bounded by the same major tributaries and corresponded to the bankfull discharge. Downstream of the Dolores River inflow (strata 1–5), some very high discharges are required to reach bankfull owing to large increases in either channel width or depth, and thresholds for widespread bed mobilization were assumed to occur at discharges less than bankfull.

Other physical habitat characteristics were estimated separately for riffle and run habitats. However, characterization of riffles was precluded in stratum 1 because of the near absence of this habitat type. For the whole study area, the mean D_{50} (median grain size) of riffle substrates was greater than that of run substrates (ANOVA, $F_{1,99} = 21.12$, $P = 0.00001$). Also, there was a fairly continuous and significant (ANCOVA, $F_{1,92} = 52.19$, $P < 0.00001$) downstream decrease in the D_{50} of runs, though not of riffles (ANCOVA, $F_{1,72} = 0.96$, $P = 0.33$). In riffles, the D_{50} increased in the three strata immediately downstream of stratum 6 (Fig. 2c). In contrast, when fine sediments were excluded from the analysis and only coarse substrate particles (≥ 2 mm diameter) were considered (Fig. 2d), mean grain sizes of riffle and run substrates were not significantly different (ANOVA, $F_{1,99} = 0.50$, $P = 0.48$), and mean grain sizes in runs did not decrease with distance down-

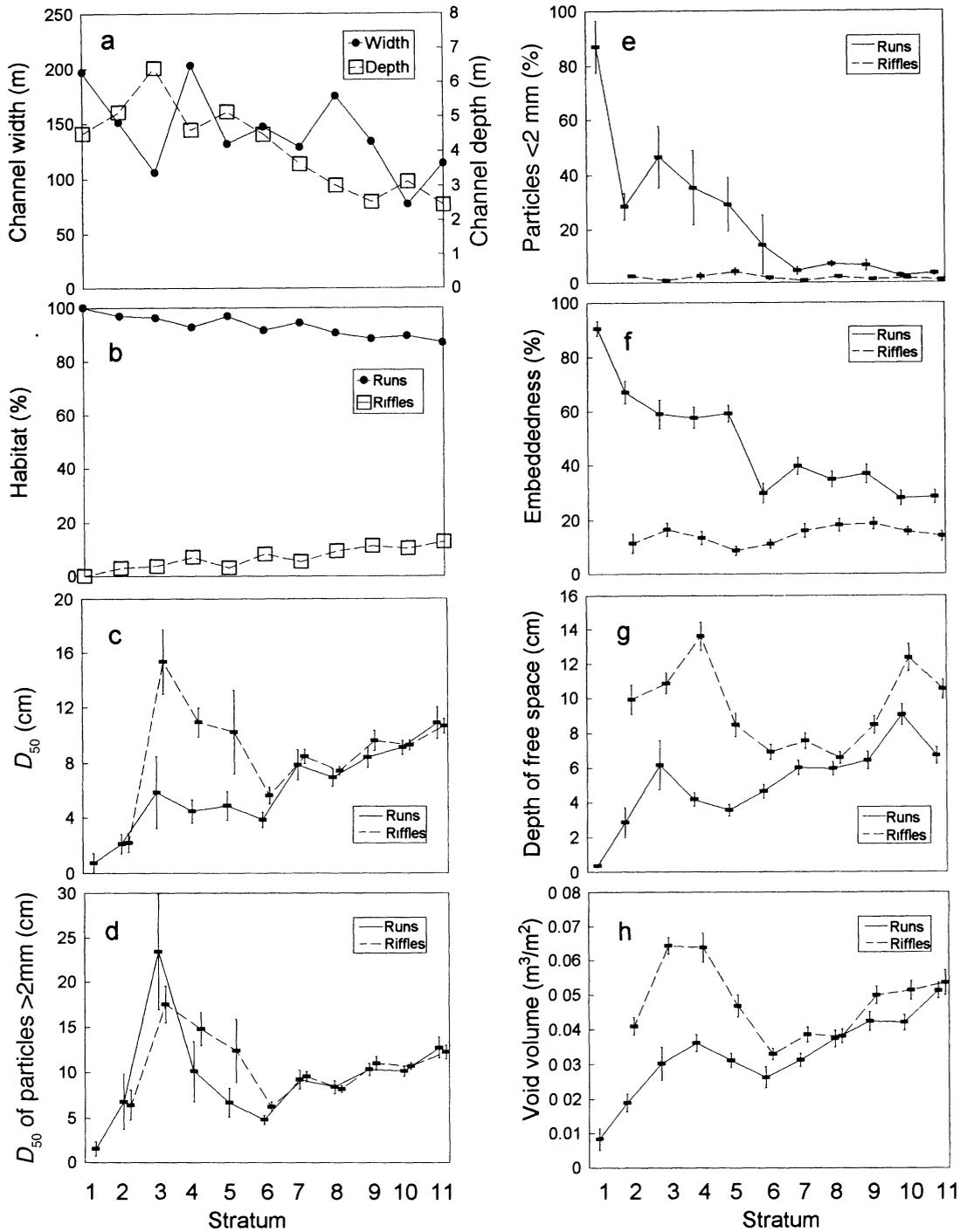


FIG. 2. Longitudinal pattern of physical parameters by study stratum: (a) bankfull width and depth of channel; (b) percentage of surface area of the dominant habitat types (run and riffle); (c) mean D_{50} particle size of riffle and run substrates; (d) mean D_{50} particle size of riffle and run substrates excluding particles < 2 mm; (e) fraction of riffle and run surface material consisting of particles < 2 mm; (f) percentage of embeddedness (aerial surface area composed of fines) of riffle and run substrates; (g) depth of free space within riffle and run substrates; (h) volume of void space within riffle and run substrates. Values plotted are means ± 1 SE.

TABLE 1. Threshold discharges (m^3/s) for initial motion of the bed (Q_c) and the bankfull discharge (Q_b) in the study strata.

Stratum	Q_c	Q_b
11	246	623
10	211	580
9	278	608
8	548	979
7	519	1021
6	497	1320
5	609	1429
4	650	2929
3	561	2012
2	659	1543
1	na†	1788

Notes: The threshold for full mobilization of the bed occurs at the bankfull discharge in strata 6–11, but probably at lower discharges in strata 1–5. Initial motion of the bed occurs at very low flows in stratum 1 due to the unconsolidated nature of the predominantly sand bed.

† Not applicable.

stream (ANCOVA, $F_{1,92} = 0.79$, $P = 0.38$). However, mean grain size of coarse material in riffles did significantly decrease (ANCOVA, $F_{1,70} = 4.22$, $P = 0.044$) in a downstream direction. Grain size of the gravel–cobble portion of the river bed declined downstream in both habitat types between strata 11 and 6, then increased downstream through stratum 3.

Differences between the longitudinal patterns of the D_{50} (all sediments) and those of the mean sizes of coarse particles (gravel–cobble) resulted from the varying proportion of fine sediment (<2 mm) present in the bed (Fig. 2e); this fine sediment fraction was greater in runs than in riffles (ANOVA, $F_{1,99} = 27.86$, $P < 0.00001$) and in runs it increased downstream (ANCOVA, $F_{1,95} = 54.69$, $P < 0.00001$), whereas in riffles it did not (ANCOVA, $F_{1,75} = 0.85$, $P = 0.36$). This fine sediment was responsible for a major increase in percent embeddedness in downstream runs (ANCOVA, $F_{1,486} = 209.4$, $P < 0.00001$). In contrast, percentage of embeddedness in riffles did not significantly change longitudinally (ANCOVA, $F_{1,724} = 2.77$, $P = 0.10$). Per-

centage of embeddedness (Fig. 2f) was higher in runs than in adjacent riffles (ANOVA, $F_{1,724} = 357.3$, $P < 0.00001$) and this difference increased substantially downstream of stratum 6.

The quantity of fine sediment in the streambed also was reflected in measurements of total DFS and interstitial void volume. DFS was less in runs than in riffles (ANOVA, $F_{1,719} = 154.7$, $P < 0.00001$). In runs, DFS decreased significantly (ANCOVA, $F_{1,478} = 70.25$, $P < 0.00001$) in a downstream direction (Fig. 2g). However, in riffles, although DFS declined between stratum 10 and 8, and was similar in strata 6–8, it increased downstream of stratum 6, and the overall downstream trend was not significant (ANCOVA, $F_{1,389} = 28.51$, $P = 0.28$). As expected, the longitudinal pattern of void volume resembled that of DFS (Fig. 2h), and void volume in riffle substrates was significantly greater (ANOVA, $F_{1,726} = 82.91$, $P < 0.00001$) than in run substrates.

Several physical parameters were highly correlated across riffles and runs (Table 2). Principal component analysis was used to characterize sites according to their streambed attributes (including detritus dry mass and midcolumn velocity) with a single variable to facilitate comparison with periphyton and invertebrate mass. The factor scores of the first principal component provided a single variable that contained 58% of the information of the original seven bed-sediment parameters (Table 3). Other principal components explained <17% of the variability in physical parameters (range 1.7–16.6%). The loadings of the first principal component variable suggest a strong positive relationship (all same sign) with D_{50} , void volume and total DFS, and a lesser positive relationship with midcolumn velocity and detritus dry mass (Table 3). Strong inverse relationships (inverse sign) with percentage of substrate <2 mm and percentage of embeddedness were also found for the first principal component variable. These relationships indicate that the score of the first principal component relate to the amount of sedimentation of the streambed at a location: higher scores

TABLE 2. Pearson correlation coefficients for various physical parameters, chlorophyll *a* concentrations (mg/m^3), and invertebrate dry mass (mg/m^2).

Parameter	Chl <i>a</i>	Invertebrates	Detritus	Sub <2 mm	D_{50}	Voids	% Embedded	DFS
Invertebrates	0.60							
Detritus	0.41	0.54						
Sub <2 mm	-0.50	-0.51	-0.45					
D_{50}	0.43	0.51	0.46	-0.83				
Voids	0.35	0.44	0.42	-0.76	0.91			
% Embedded	-0.35	-0.54	-0.47	0.76	-0.72	-0.70		
DFS	0.43	0.53	0.39	-0.76	0.79	0.76	-0.80	
Velocity	0.17 (0.016)	0.51	0.33	-0.37	0.28	0.22 (0.001)	-0.50	0.40

Notes: All data were \log_e -transformed for analysis. All correlations were significant at $P < 0.00001$ for $r = 0.0$, except the two indicated in parentheses. Parameters in order are: chlorophyll *a* concentration (Chl *a*), invertebrate dry mass (Invertebrates), detritus dry mass, fraction of substrate particles <2 mm (Sub <2 mm), median particle size of the surface layer (D_{50}), volume of interstitial void space within the substrate, percentage of the surface area consisting of fines (% Embedded), absolute depth of free space (DFS), and midcolumn water velocity.

TABLE 3. Factor loadings for the first factor from principal-components analysis using several attributes of the stream-bed.

Attribute	Loading
Substrate <2 mm	-0.835
D_{50}	0.857
Void volume	0.818
% Embedded	-0.832
Total DFS	0.876
Midcolumn velocity	0.465
Detritus	0.500

Notes: All data were \log_e -transformed for analysis. Attributes, in order, are percentage of substrate particles <2 mm, median particle size of the surface layer (D_{50}), volume of interstitial void space, percentage of the surface area consisting of fines (% Embedded), absolute depth of free space (DFS), midcolumn water velocity, and detritus dry mass.

indicating low amounts of fine sediment and lower scores indicating higher amounts. The size of the loading coefficients reinforce the strength of the interrelationships among these physical parameters.

Water-quality parameters.—Nutrient analyses indicated high variability among samples, but NO_3 , NO_2 , total inorganic N, total N, and total P increased significantly (ANCOVA, $P < 0.00001$ for all) with distance downstream (not shown). NH_3 and orthophosphorus did not display significant increases downstream (ANCOVA, $P > 0.15$), but strata 10 and 11 had among the lowest concentrations. General observations during the study period indicated turbidity was highly variable over time. Our data, representing only a few snapshots in time, are therefore not particularly instructive. From the three days in which it was measured, the mean significantly increased with distance downstream (ANCOVA, $F_{1,64} = 19.60$, $P = 0.00004$), but strongly displayed this pattern only during the spring 1995 survey.

Biological parameters.—Chlorophyll *a*, our index of active periphyton biomass, declined downstream. This decline was significant in riffles (ANCOVA, $F_{1,391} = 136.8$, $P < 0.00001$) and runs (ANCOVA, $F_{1,423} = 133.3$, $P < 0.00001$), with the decline in runs especially pronounced (Fig. 3a). Although chlorophyll *a* was greater in riffles than in runs (ANOVA, $F_{1,701} = 68.34$, $P < 0.00001$), differences occurred only downstream of stratum 9. In strata 9–11, chlorophyll *a* was essentially the same in runs and riffles. Invertebrate biomass also declined downstream in both riffles (ANCOVA, $F_{1,391} = 201.5$, $P < 0.00001$) and runs (ANCOVA, $F_{1,486} = 337.5$, $P < 0.00001$) and was also higher in riffles than in runs (ANOVA, $F_{1,726} = 269.0$, $P < 0.00001$). However, unlike chlorophyll *a*, invertebrate biomass was much higher in riffles than in runs of strata 9–11 (Fig. 3b). Detritus showed a less precipitous decline with distance downstream (Fig. 3c), but the declines were still significant for riffles (ANCOVA, $F_{1,391} = 69.57$, $P < 0.00001$) and runs (ANCOVA, $F_{1,486} = 57.05$, $P < 0.00001$). Riffle substrates generally con-

tained a greater biomass of detritus than did run substrates (ANOVA, $F_{1,726} = 126.9$, $P < 0.00001$).

Catch rates of all fish declined with distance downstream when expressed as either number caught (Fig. 3d; ANCOVA, $F_{1,196} = 191.2$, $P < 0.00001$) or as biomass caught (not shown) (ANCOVA, $F_{1,196} = 147.9$, $P < 0.00001$). Subsets of the total catch rate (numbers caught), presumably more relevant to pikeminnow food availability, displayed similar trends: the catch rate of forage-sized (100–300 mm) individuals (excluding spined species) declined downstream (ANCOVA, $F_{1,196} = 74.88$, $P < 0.00001$); catch rates of the three dominant soft-rayed, fusiform, native fish species: roundtail chub (Fig. 3d), flannelmouth suckers (Fig. 3e), and bluehead suckers (Fig. 3f) also declined downstream (ANCOVA, all $F_{1,391} > 60.0$, $P < 0.00001$). For all species (all sizes), catch rates were highest in strata 7–9 and 11; for forage-sized fish, catch rates were similar among strata 7–11 (Fig. 3d). For total fish, native fish, and forage-sized fish, catch rates were consistently much lower downstream of stratum 7.

Catch rates of all sizes of the two dominant native fish species, flannelmouth sucker and particularly bluehead sucker, were significantly higher in riffles than in runs on a river-wide basis (Fig. 3e and f). For bluehead sucker in strata 10 and 11, catch rates in the two habitat types were nearly identical, but rates were significantly higher in riffles than in runs in strata 5–9 ($P < 0.05$). Although bluehead suckers made up a majority of forage-sized fish in downstream strata 2–6, very few were captured from run habitats. On a river-wide basis, catch rates of bluehead sucker from riffles were higher than from runs (ANOVA, $F_{1,363} = 84.09$, $P < 0.00001$). Flannelmouth suckers were similarly distributed, with greater catch rates from riffles than from runs (ANOVA, $F_{1,363} = 20.25$, $P < 0.00001$); however, no within-stratum differences were significant ($P > 0.05$). For roundtail chub, catch rates in the two habitat types were similar (ANOVA, $F_{1,363} = 1.39$, $P = 0.24$), and only a few fish were found downstream of stratum 7 (Fig. 3d).

Relative body condition (K_r) of both sucker species and roundtail chub decreased downstream (regression, for all: $N = 405$ – 3203 ; $P < 0.0003$), with the lowest condition exhibited by bluehead sucker in the three most downstream strata (Fig. 3g).

Densities of adult Colorado pikeminnow ≥ 550 mm TL also decreased in a downstream direction (Fig. 3h). Densities were highest in strata 8 and 9, declined exponentially between strata 8 and 5, and were consistently low in strata 1–5. Because of instream barriers at the top of stratum 9, pikeminnow did not occur in strata 10 and 11.

Interrelationships

Physical habitat–periphyton/macrobenthic biomass relationship.—Highly significant correlations were found between both chlorophyll *a* and inverte-

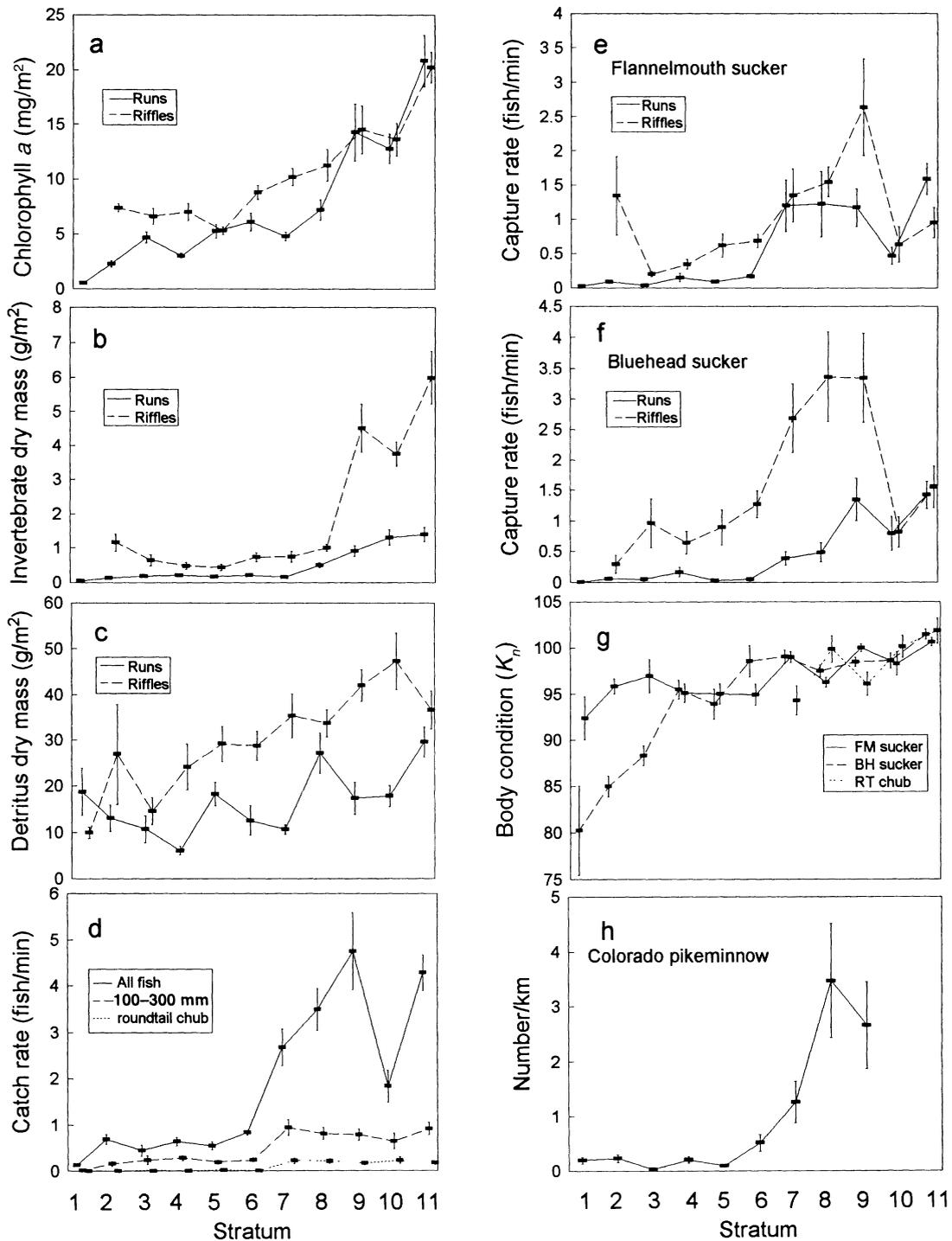


FIG. 3. Longitudinal pattern of biological parameters by study stratum: (a) chlorophyll *a* concentration on riffle and run cobbles; (b) dry mass of invertebrates in riffle and run substrates; (c) accumulated coarse particulate organic matter (detritus) in riffles and runs; (d) electrofishing catch-per-effort (CPE) of all fish (except pikeminnow), fish 100–300 mm long (potential pikeminnow forage), and native roundtail chub; (e) electrofishing CPE of native flannelmouth sucker by habitat type; (f) electrofishing CPE for native bluehead sucker by habitat type; (g) body condition index (K_n) of flannelmouth (FM) sucker, bluehead (BH) sucker, and roundtail (RT) chub; (h) estimated densities of adult Colorado pikeminnow ≥ 550 mm TL. Values plotted are means ± 1 SE.

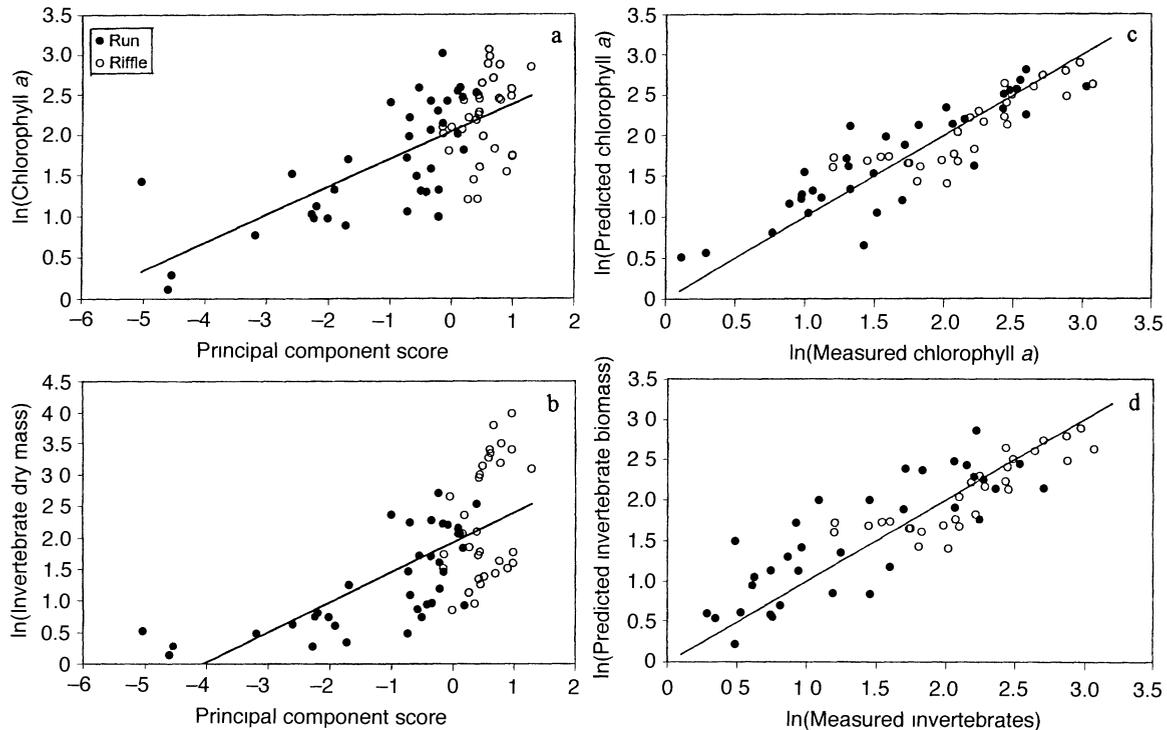


FIG. 4. Interrelationships among physical and biological parameters. Solid lines represent regression lines in (a) and (b) and 1:1 line in (c) and (d). (a) Relationship between $\ln(\text{chlorophyll } a \text{ biomass})$ and principal component score based on physical habitat parameters; (b) relationship between $\ln(\text{invertebrate biomass})$ and principal component score based on physical habitat parameters; (c) predicted and measured $\ln(\text{chlorophyll } a \text{ biomass})$, regression based on principle component score and rk location; (d) predicted and measured $\ln(\text{invertebrate biomass})$, regression based on principle component score and $\ln(\text{chlorophyll } a \text{ biomass})$.

brate biomass and the physical variables that characterize the riverbed (Table 2). Positive correlations were found with variables reflecting less sedimentation (DFS , D_{50} , void volume) and higher detrital content and water velocity, while inverse relationships were found with variables reflecting higher sedimentation (percentage of embeddedness and percentage of substrate $< 2 \text{ mm}$).

The high degree of correlation among physical parameters (Table 2) made it difficult to determine which parameters most related to standing crops of primary producers and invertebrate consumers. Hence, PCA factor scores were used to assess relationships between physical habitat and measures of benthic biota. Factor scores for the first principal component for each riffle and run were calculated using the factor loadings in Table 3 for each sample reach and regressed against the corresponding values for chlorophyll a and biomass of invertebrates. Biological parameters at each sample reach were averaged over the three sample periods. The analysis combined riffles and runs because physical habitat differences were included in the factor score. Highly significant relationships were found between both chlorophyll a ($F_{1,66} = 57.8$, $P < 0.0000001$, $r^2 = 0.47$) and invertebrates ($F_{1,66} = 50.3$, $P < 0.0000001$, $r^2 = 0.43$) and the principal component scores (Fig. 4a,

b). Regression relationships were improved by adding additional variables to the regressions containing the factor scores. Because a highly significant ($F_{1,66} = 130.2$, $P < 0.0000001$, $r^2 = 0.66$) relationship was also found between chlorophyll a and invertebrate biomass (Fig. 5a), and longitudinal relationships were found for both chlorophyll a and invertebrates, addition of these elements was evaluated. By including the distance upstream (rk) of the Colorado and Green River confluence, the regression relationship (Fig. 4c) for chlorophyll a improved ($F_{2,59} = 104.6$, $P < 0.00001$, $r^2 = 0.78$), and the multiple regression analysis indicated no collinearity problems (condition number = 3.11; Belsley et al. 1980). The relationship also improved for invertebrates (Fig. 4d) when chlorophyll a was included ($F_{2,65} = 69.9$, $P < 0.00001$, $r^2 = 0.68$); however, when rk location was added, the resulting condition index of 17.4 suggested collinearity problems, probably reflecting the relationship between chlorophyll a and rk location.

Algal/invertebrate biomass–fish biomass relationship.—Highly significant relationships were found between fish biomass (expressed as catch rates) and chlorophyll a (Fig. 5b; $F_{1,31} = 35.2$, $P < 0.00001$, $r^2 = 0.53$), invertebrate biomass ($F_{1,31} = 26.3$, $P = 0.00001$, $r^2 = 0.46$), and combined chlorophyll a and inverte-

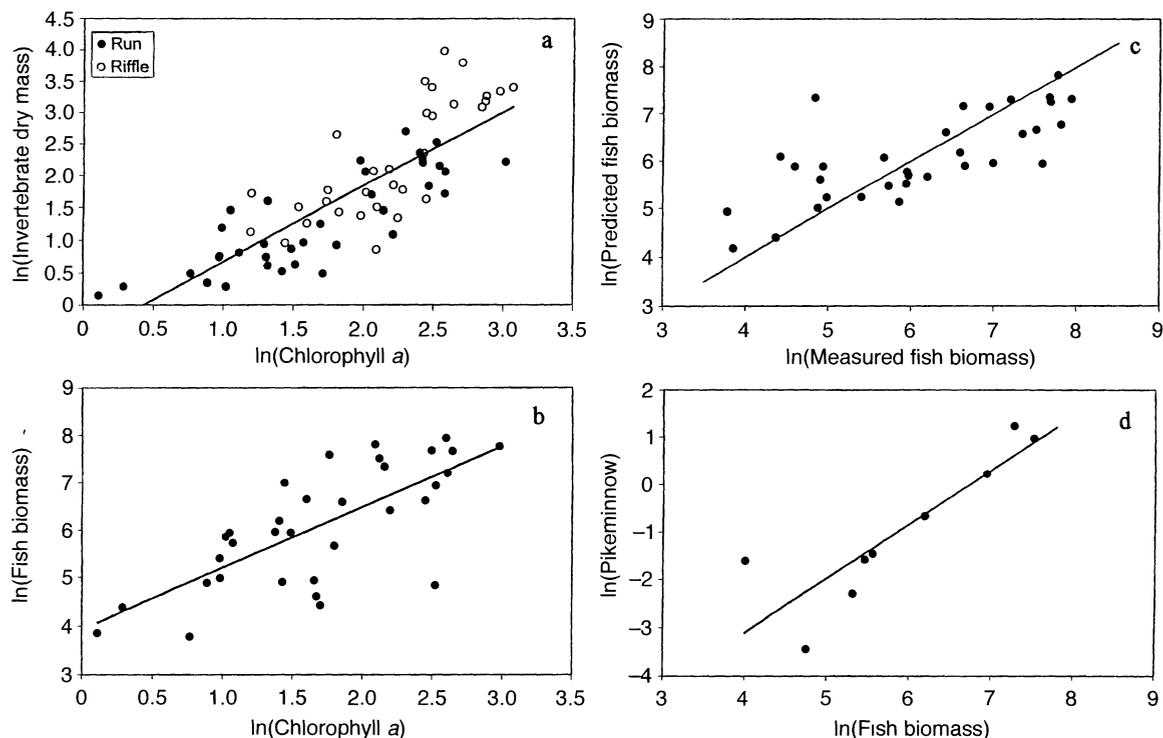


FIG. 5. Interrelationships among biological parameters. Solid lines represent regression lines in (a), (b), and (d), and 1:1 line in (c). (a) Relationship between $\ln(\text{chlorophyll } a \text{ biomass})$ and $\ln(\text{invertebrate biomass})$; (b) relationship between $\ln(\text{chlorophyll } a \text{ biomass})$ and $\ln(\text{fish biomass})$; (c) predicted and measured $\ln(\text{fish biomass [as catch rate]})$, regression based on $\ln(\text{chlorophyll } a \text{ biomass})$ and $\ln(\text{invertebrate biomass})$; (d) relationship between $\ln(\text{pikeminnow density})$ and $\ln(\text{fish biomass [as catch rate]})$.

brate biomass (Fig. 5c; $F_{2,30} = 17.75$, $P < 0.00001$, $r^2 = 0.54$). These regressions improved substantially when two outlying points were removed ($r^2 = 0.66$, 0.72 , and 0.74 , respectively). The multiple regressions were conducted by sample reach using mean values over the three sample periods. The weighted means (weighted by the fractions of riffle and run area in each reach) of chlorophyll a and invertebrate biomass were regressed against fish numbers and biomass. Highly significant regressions also were found for numbers of all fish ($F_{2,33} = 25.8$, $P < 0.00001$, $r^2 = 0.61$) and for numbers of soft-rayed, native fish ($F_{2,33} = 24.1$, $P < 0.00001$, $r^2 = 0.59$) when regressed against chlorophyll a and invertebrate biomass. Both regressions improved when the two outlying points were removed ($r^2 = 0.81$ and 0.79 , respectively). A less significant relationship ($F_{2,33} = 5.6$, $P = 0.008$, $r^2 = 0.25$) also was found between the numbers of forage-sized fish (100–300 mm) and chlorophyll a and invertebrate biomass. Removing the same outlying points resulted in an improved relationship ($r^2 = 0.45$).

Body condition (K_n) was averaged by strata over all sample periods and compared with averages of chlorophyll a and invertebrate biomass. K_n of both bluehead sucker and flannelmouth sucker was significantly correlated with chlorophyll a ($r^2 = 0.77$ and 0.70 , respectively; $P = 0.0015$, $n = 11$) and invertebrate bio-

mass ($r^2 = 0.58$ and 0.67 , respectively; $P = 0.007$, $n = 11$). Similar relationships were found for roundtail chub Kn, but these were not significant (chlorophyll a , $P = 0.24$, $r^2 = 0.42$; invertebrate biomass, $P = 0.19$, $n = 5$, $r^2 = 0.49$), likely reflecting that only five strata could be included in the analysis (too few roundtail chub downstream of stratum 7).

Fish biomass–adult pikeminnow densities relationship.—Significant relationships were found between densities (individuals/km) of adult pikeminnow and catch rates of other fish that might serve as forage. Catch rates of other fish within sample reaches were averaged by stratum and again averaged over the three sample periods. Significant regression relationships were found between density of adult pikeminnow and number of soft-rayed, native fish ($F_{1,7} = 27.6$, $P = 0.001$, $r^2 = 0.80$) and number of forage-sized (100–300 mm) soft-rayed native fish ($F_{1,7} = 12.8$, $P = 0.009$, $r^2 = 0.65$). Density of adult pikeminnow was also highly correlated with biomass of all fish (Fig. 5d; $F_{1,7} = 22.4$, $P = 0.002$, $r^2 = 0.76$).

To determine whether the availability of physical habitat might help explain the observed variation in pikeminnow densities, regressions were conducted using the areas of riffles, runs, and combined other non-riffle/run habitats present in each stratum. Of these, only riffles had a significant relationship with densities

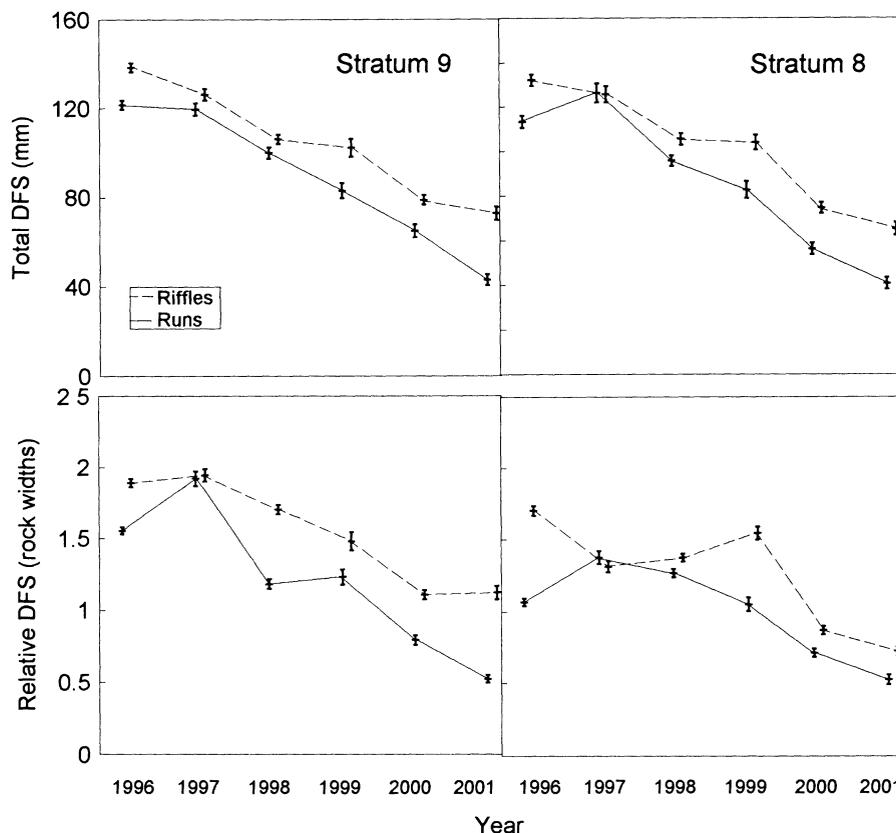


FIG. 6. Mean total (top) and mean relative (bottom) depth-of-free-space (DFS) in run and riffle substrates of stratum 9 (left) and stratum 8 (right) during base flows of 1996–2001. Total DFS is the absolute distance from the top of surface rocks to the level of embeddedness; relative DFS scales absolute distance to the median rock width (measured across the b -axis) at each site.

of adult pikeminnow ($F_{1,7} = 8.0$, $P = 0.025$, $r^2 = 0.53$), an expected result because of the strong relationship between biomass of all fish and riffle area ($F_{1,7} = 20.6$, $P = 0.001$, $r^2 = 0.70$). The stronger relationships of adult pikeminnow with numbers and biomass of other fish suggests that food availability is more important than the physical habitat provided by riffles.

Given that food availability was most important, the regression for adult pikeminnow densities with biomass of other fish was extended to include area of runs and area of nonriffle/run habitats. This was conducted to assess if the area of other habitats, when combined with food availability (which strongly correlated with riffles), further explained the variability in adult pikeminnow densities. This regression was highly significant ($F_{3,5} = 84.1$, $P = 0.0001$, $r^2 = 0.98$), with all independent factors significant ($P < 0.02$) and no evidence of multicollinearity (condition number = 4.05). When the regression was conducted in a stepwise manner, biomass of other fish explained 76% of the variation in density of adult pikeminnow while the other two factors explained 65% of the residual variation, suggesting that habitat heterogeneity and total wetted area (as reflected by the major habitat type, runs) may

also influence adult pikeminnow distribution when overlain on food resources. This interpretation of the importance of total wetted area was assessed with a similar stepwise regression using biomass of other fish and total wetted area ($F_{2,6} = 66.3$, $P = 0.0008$, $r^2 = 0.96$). Total wetted area explained 65% of the residual variation in density of adult pikeminnow when regressed against biomass of other fish.

Sediment dynamics

Depth of free space.—Total DFS monitored in strata 8 and 9 during 1996–2001 showed significant declines in both runs and riffles (Fig. 6) corresponding to declines in annual peak flow (Fig. 7). Mean annual total DFS was positively correlated with peak discharge in runs ($P = 0.005$, $r^2 = 0.86$) and riffles ($P = 0.03$, $r^2 = 0.70$) of stratum 8 and in runs ($P = 0.02$, $r^2 = 0.69$) and riffles ($P = 0.04$, $r^2 = 0.60$) of stratum 9. Declines occurred in both habitat types in both strata in years following 1997, the last year when the thresholds for widespread bed mobilization were exceeded. These declines occurred despite thresholds for initial motion having been exceeded in stratum 9 in 1998–2000 and in stratum 8 in 1998.

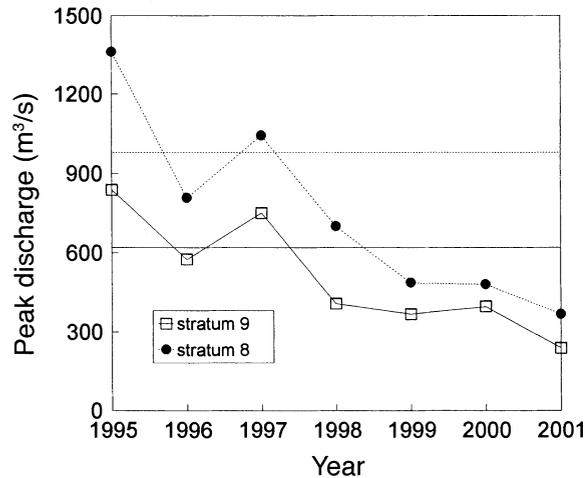


FIG. 7. Peak discharge (highest mean daily discharge of the year) in strata 8 and 9 during the DFS monitoring years of 1996–2001. The antecedent peak flow of 1995 is also shown. Horizontal lines indicate thresholds for widespread bed mobilization in stratum 8 (upper line) and stratum 9 (lower line).

Because total DFS can vary by rock size, relative DFS (scaled to median rock diameter) was examined as a means to isolate changes in DFS attributable to changes in fine sediment accumulation alone. By fall 2001, 4 yr following the relatively high flows of 1997, mean relative DFS had declined from 1.4 to 0.5 rock diameters (rd) in runs of stratum 8, and from 1.9 to 0.5 rd in stratum-9 runs. Relative DFS also declined in riffles, though values were generally higher than in runs. In 2001, relative DFS in stratum-8 riffles averaged 0.7 rd; in stratum 9, 1.1 rd (Fig. 6). Relative DFS was also significantly ($P < 0.05$) correlated with peak discharge in both runs and riffles of stratum 9 and runs of stratum 8. No correlations were found between total or relative DFS and the mean August to October base flow discharge.

Frequency of substrate-mobilizing flows.—Because deposits of fine sediment were found to accumulate in the bed over time, we were most interested in potential changes in the mean interval between flushing events. Pitlick and Van Steeter (1998) found that the minimum flow necessary to produce widespread bed mobilization in strata 7, 8, and 9 corresponded with the bankfull flow, and results from our study indicate this to be the case for strata 10 and 11 as well (see Pitlick and Cress 2000). Because of geomorphic similarities, we assumed this is also true for stratum 6. However, downstream of the Dolores River confluence (strata 1–5), discharge thresholds for widespread bed movement have not yet been determined and these strata were therefore not included in our analysis of flushing-flow frequencies. Relatively large blocks of years are required for calculating mean recurrence intervals, and we were fortunate that gauge records for annual peak flow for strata 6–11 were available back to 1908. The early period

was characterized by a series of wet years (1908–1930) followed by dry years (1931–1940); the latter period, also had wet (1982–1987) and dry periods (1988–1992) but were of shorter duration (N. Doeskin, *personal communication*).

For our comparison of mean recurrence intervals, we assumed that thresholds for bed-mobilizing discharges were similar between historic and recent periods. However, because these calculated thresholds were based on recent channel and substrate characteristics, we preface our results with the caveat that recent threshold discharges are only approximations of historic thresholds. If the bankfull channel was historically wider or the substrate coarser than today, historic thresholds for bed mobilization would have been higher, likely lengthening average recurrence intervals. Although we know that wetted area of the main channel at base flow has narrowed by a mean of 15% in strata 8–10 since 1937 (Van Steeter and Pitlick 1998), historic bankfull channel width and historic substrate size distributions are unknown.

The frequencies of flows necessary for initial motion and for widespread mobilization of the bed in strata 6–11 were evidently much lower during recent years than during the early half of the century prior to most river regulation. During the preregulation period of record (1908–1942), mean recurrence intervals of widespread bed mobilization (assuming current discharge thresholds) were 1.2–1.4 yr in strata 9–11 (upstream of the Gunnison River confluence); this increased to 2.7–3.6 yr in the “post-development” period (1966–2000). Between the inflows of the Dolores and Gunnison rivers (strata 6–8), the mean interval during 1908–1942 was 1.4–2.7 yr and during 1966–2000, 4.6–13.5 yr (Fig. 8). Most of the difference between periods can be attributed to water development, although the numbers may also have been influenced by climate to some unknown degree (snowpack records for the Colorado basin did not begin until around 1950).

DISCUSSION

Longitudinal trends

Abundance of adult pikeminnow, and other main-channel native fish, generally declined in a downstream direction. Differences in food resource availability can explain much of this observed pattern. Our study identified three important patterns related to longitudinal changes in lower trophic level structure: (1) benthic biomass in both riffles and runs decreased downstream, (2) riffle substrates contained more biota and detritus than run substrates of a similar water depth, and (3) the total surface area of riffles (the most productive habitat type) decreased downstream.

Principal component analysis showed a strong positive relationship between biomass of both primary producers and invertebrate consumers and the degree to which the substrate was free of fine sediment. The

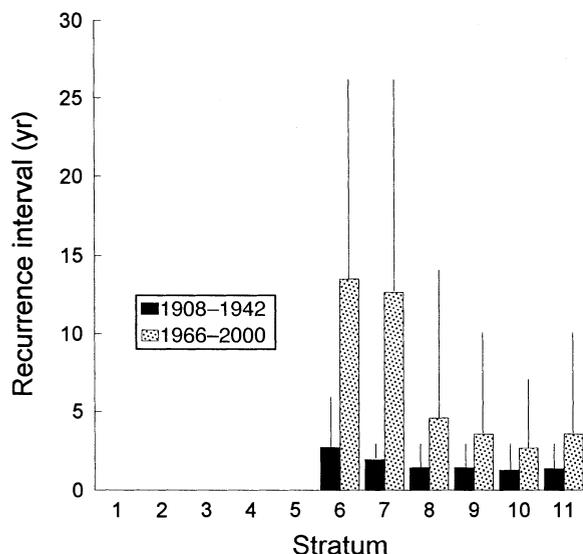


FIG. 8. Mean recurrence intervals (bars) of discharges necessary to produce widespread streambed mobilization in strata 6–11 during recent (1966–2000) and preregulation (1908–1942) periods. Lines above bars indicate the maximum recurrence intervals.

downstream decline of biomass in riffles, even though fine sediment in riffles was fairly consistent, suggests involvement of additional factors. Also, the highly significant multiple regressions of chlorophyll *a* and invertebrates with both PC score and river kilometer indicated that both cleanness of the bed and factors associated with longitudinal location were important.

Possible factors varying longitudinally include water clarity, water velocity, nutrients, water quality, water temperature, and detritus. Our measurements of turbidity, although very limited, suggested a downstream decrease in light penetration which could affect primary productivity. Although not measured, mean water velocity may decline downstream due to the general attenuation of gradient. If so, surficial sediment deposition, expected to be more prevalent in areas with low base-flow velocities might explain the weak correlation found between water velocity and chlorophyll *a* and invertebrate biomass. Concentrations of nitrogen and phosphorus tended to increase downstream, and there was no correspondence between higher nutrient concentration and higher biomass. Lower nutrients in the upper river may have reflected greater uptake in the more productive strata. Although oxygen was not monitored, bed samples provided no indication of anaerobic conditions. Contaminant concentrations were not evaluated, but we would expect levels to be highest in upstream strata where urban and agricultural areas border the river (elevated selenium levels have been reported in off-channel habitats within strata 8 and 9 [Osmundson et al. 2000]). Water temperatures increase with distance downstream (Osmundson et al. 1998), but did not reach levels that would inhibit primary or

secondary production. Detritus declined downstream and the weak correlation with invertebrate biomass suggests a possible food linkage, but does not explain higher standing crops of periphyton. The downstream decline of detritus probably resulted from corresponding periphyton declines (an instream source) and the distance from upstream terrestrial sources (i.e., from alluvial reaches where riparian zones were most extensive). While difficult to ascertain from this study, it appears that water clarity, water velocity, and detritus were factors that declined downstream and may have, in addition to bed sediment effects, influenced standing crops of primary producers and invertebrate consumers.

Riffles were more productive than runs primarily because riffle substrates generally contained less fine sediment than adjacent run substrates. In addition, riffles generally had higher velocities and contained more detritus than runs, variables that were weakly correlated with chlorophyll *a* and invertebrate biomass. Detritus, a food for many invertebrates, may have been significantly higher in riffles because of more periphyton biomass and better detritus-collecting properties of “clean” substrate. Also, increased velocities in riffles may have benefited suspension feeders by increasing encounter rates with drifting detritus.

The downstream decrease in surface area of riffles likely contributed to downstream declines in fish biomass. Runs were found to be increasingly less productive than riffles downstream, increasing the importance of riffles in supporting stratum-wide fish numbers, yet the surface area of riffles decreased downstream as run area increased. Hence, downstream fish not only had less total periphyton and invertebrate biomass available per unit area, but also less total area of the more productive habitat type.

Factors related to the longitudinal patterns of biota in the upper Colorado River were generally consistent with observations reported by various stream investigators. Increased sedimentation has been shown to reduce insect diversity, density, and species richness in streams (Chutter 1969, Bjornn et al. 1977, Lenat et al. 1981). Lab studies have demonstrated macroinvertebrate preference for substrates with unembedded cobble over those with half-embedded cobble, and cobble completely embedded in sand is unacceptable to most species (Brusven and Prather 1974). Factors underlying these relationships are fairly well established: rock surfaces provide attachment sites for periphyton; algal filaments in turn provide food and effective microenvironments for some invertebrate species (Brusven and Prather 1974); crevices among coarse substrate particles shelter invertebrates and collect detritus (Rabeni and Minshall 1977). Schlosser (1982) reported a positive influence of increased algal and invertebrate production on growth, reproductive success, and recruitment of stream-dwelling fish. Berkman and Rabeni (1987) found that feeding guilds of stream fishes most

affected by sedimentation were those most specialized to feed from the substratum; in their study, both benthic insectivores and herbivores decreased in abundance as the percent of fine substrate increased. Our results support this last observation: native suckers were generally more abundant in riffles (the more sediment-free habitat) than in runs. Nearly equal usage of the two habitat types by suckers in stratum 10 and 11 suggest they are not tied to riffles by some physical habitat preference. Riffles were likely more attractive than runs in most strata because of higher periphyton biomass (downstream of stratum 9), invertebrate biomass, and detritus biomass—variables associated with cleanness of the bed.

Flood-flow aspects

Considerable research has focused on the role of physical disturbance from floods in structuring stream benthic communities (Cobb et al. 1992, Scarsbrook and Townsend 1993, Death and Winterbourn 1995, Poff and Allen 1995, Clausen and Biggs 1997, Blinn et al. 1999). Invertebrate density is reduced by flood disturbances (from shear stress removal and abrasion from moving particles), but these reductions are short-lived with numbers recovering in a few to several tens of days (Scrimgeour et al. 1988). Communities controlled by stochastic factors such as floods are characterized by high species turnover and rapid recolonization (Lake and Doeg 1985). However, rapid restoration after floods may be slowed in highly modified systems where alien assemblages adapted for more stable flow regimes have replaced native fauna, such as in the Grand Canyon downstream of Glen Canyon Dam (Shannon et al. 2001). Clausen and Biggs (1997) reported increases in invertebrate density with low to moderate flood frequencies (several events per year). Our study suggests a mechanism by which low flood frequencies (<1 flood/yr) in a partially modified system might depress invertebrate production; i.e., the accumulation of fine sediment in upper layers of the bed. This effect, in mid reaches of the upper Colorado River, might be expected in other systems where impoundments are located upstream of sources of fine sediment, resulting in a flow volume reduction without a corresponding reduction in fine sediment input.

Constraints of the physical environment

Standing crops of biota in the upper Colorado River are limited by characteristics of the physical environment. Some constraints are relatively permanent, while others are more subject to short-term external change. Influences of physical attributes of the river can be viewed as hierarchically organized within a spatiotemporal framework (Frissell et al. 1986, Scarsbrook and Townsend 1993). Within our study area, setting and morphology of the channel, dictated by geology and landform type (directional orientation, canyon vs. alluvial valley, etc.) affect depth and shading and con-

strain primary producers and consumers in each stratum to varying degrees. Overlain on this templet are the physical attributes of the riverbed. These attributes, dictated by sediment input and flow regime, also affect algal and macroinvertebrate production. Finally, water quality or clarity add yet another layer of potential constraint. Turbidity in the upper Colorado River varies seasonally (spring runoff), daily (summer thunderstorms), and longitudinally (irrigation and tributary inputs).

Dominant channel features set by landform and geology, such as the deep water and steep banks of confined canyon stretches (strata 2, 3, and 5), are long-term attributes with little potential for change. Coarse sediment inputs from tributaries and channel margins are also relatively long-term constants. Inputs of fine sediment, on the other hand, may have increased in the Colorado Plateau watershed during historic and recent times as a result of land-use practices (e.g., grazing, irrigation, road building, off-road vehicle use); such potential changes are difficult to quantify, and are in need of further study. The transport and distribution of sediment once it has entered the river is determined by the annual flow regime, and bed conditions are therefore subject to the short-term vagaries of both climate and human activities. From an applied perspective, the greatest opportunities for enhancing within-channel productivity appear to be through this flow–sediment link.

To what degree fine sediment may influence standing crops of benthic biota in strata 10 and 11 is difficult to discern because of the relatively clean conditions we observed there during our period of study. In these two strata large loads of fine sediment begin entering the river via small tributaries that drain erodible low-elevation watersheds, increasing suspended sediment loads of strata downstream. Thus, strata 1–9 are probably the most susceptible to problems associated with fine sediment accumulation. However, the bed of low-gradient stratum 1 has probably always consisted of sand and silt, and the productivity of strata 2–5 has likely always been constrained by the overriding limitations of channel morphology that limit autotrophy. The best opportunity for increasing main-channel food production appears to be in strata 6–9 and perhaps 10 and 11 as well.

Flow alteration effects

Periodic movement of surficial framework particles is required to remove fines below the surface layer (Milhous 1973, O'Brien 1987, Kondolf and Wilcock 1996, Wilcock et al. 1996). Suspended sediment makes up more than 98% of the total sediment load in our study area (Butler 1986, Van Steeter and Pitlick 1998). At low flows, the immobile surface layer acts as a sink for suspended sediment, which deposits in the interstices. The bed thus acts as a silt and sand reservoir. At high discharge, when the surficial gravel–cobble

framework is set in motion, the bed becomes a source of suspended sediment as fines are winnowed out. How much fine sediment accumulates in the bed is a function of sediment load, local velocity, and the period of time separating bed-mobilizing events.

Flows of sufficient magnitude to fully mobilize the bed now occur at a lower frequency than during historic times, largely due to river regulation. The result has been a lengthening of time between such events (Fig. 7). For strata 6–11, estimates of historic recurrence intervals averaged 1.2–2.7 yr, depending on the stratum. Our monitoring results of DFS in strata 8 and 9 indicate that sediment begins to accumulate in the bed within the first year following a flushing event and DFS continues to decline through at least the first four years if flows do not exceed the threshold for widespread bed mobilization. Flows reaching or exceeding the threshold for initial motion were ineffective at reversing declines in DFS. In the 34 yr since most water development projects were completed, mean duration separating flushing events doubled in strata 9–11, tripled in stratum 8 and increased fivefold in strata 6 and 7. From 1957 to 1983, strata 6 and 7 underwent a 26-yr period without a widespread mobilizing event. Similarly, stratum 8 lacked such flows during 1965–1978 (14 yr). Historically, the longest interval for strata 6–11 was 3 yr. Given the link between benthic biomass and fine sediment indicated here, we infer that in recent times these strata underwent artificially extended periods of lowered productivity with a corresponding negative effect on resident fish populations. This, coupled with range reduction and increases in nonnative fish of limited forage value, have almost certainly reduced the capacity of the upper Colorado River to support adult Colorado pikeminnow.

Management implications

Spatial distribution of the community's primary piscivore was related to the relative abundance of potential prey fish. Our results also indicated that total surface area of the river and the availability of non-riffle/run mesohabitats (pools, eddies, backwaters, etc.) positively influenced adult pikeminnow densities in combination with food availability. Relationships with food availability were stronger than with habitat area alone. Hence, traditional instream flow methodologies that strive to increase standing stocks of target species by emphasizing the importance of preferred physical habitat and the manipulation of base flows may be met with limited success in the upper Colorado River and perhaps in other similarly regulated rivers. Such efforts may prove beneficial, however, if coupled with management actions designed to enhance food availability. Our work provides a first step towards understanding how changes in flow regime in the upper Colorado River might affect the foodweb supporting the main-channel fish community.

To increase standing crops of primary producers and

consumers, strategies aimed at restoring the frequency of flushing events should be explored. Runs were the most pervasive habitat type in the river and the most in need of more frequent flushing of fine sediment. Riffles were relatively clean during our longitudinal study regardless of location; however, the 1994–1995 sampling may have represented a particularly "clean" period: discharges adequate to fully mobilize the bed occurred during 1993, a year preceding the start of our study, and again during 1995, just prior to our last sampling effort. Results of the 6-yr DFS monitoring in strata 8 and 9 showed that riffles, though generally more free of fine sediment than runs, can nonetheless accrue fines over time. In all strata, riffles made up a small percentage of the overall total area. Riffles were especially rare in downstream strata 1–5; there they apparently act as localized centers of bioproduction amid a channel dominated by unproductive runs.

It is difficult to surmise the degree to which the longitudinal distributions of fine sediment documented here deviate from the historical norm and the degree to which management efforts might be successful in enhancing conditions in some strata. Indeed, the period of our longitudinal study may have coincided with a relatively clean period, representing substrate conditions difficult to improve upon. Thus, benthic invertebrates, with their quick recovery time, might have been at near-optimum levels; however, fish populations, due to lag effects, may have required more time to respond to improved conditions. Hence, our fish abundance results may have reflected antecedent or long-term average conditions. Clearly, the main objective of providing flows that flush fines from the bed is to make runs more biologically productive more of the time.

Bankfull flushing flows serve other purposes beneficial to Colorado pikeminnow and to the native fish community in general. Such flows are often channel-forming flows that scour encroaching vegetation and maintain side channels (Van Steeter and Pitlick 1998), improve substrate conditions for spawning and reproductive success, entrain organic debris and perhaps negatively affect small non-native fish abundance (Stanford 1994, McAda and Ryel 1999). Complex river segments created by lateral channel movement in unconfined reaches produce mesofeatures of the channel such as riffles, and midchannel or shoreline bars, thereby providing a mosaic of productive littoral zones (Thorp 1992) juxtaposed with other mesohabitats (pools, eddies, and backwaters) preferred by Colorado pikeminnow and other native fish (Osmundson et al. 1995). Although the base-flow stage can be manipulated to maximize preferred mesohabitats and habitat heterogeneity, periodic flood flows are required to create or maintain the channel features that give rise to these base-flow habitats. These effects are important functions of the natural flow regime in the upper Colorado River. Restoring the frequency of bankfull events to near historical levels may yet be possible through

coordinated dam releases. Experimental releases of sufficient magnitude could be used to test whether the flushing function can be achieved with a short-term flow spike that would require less water than natural runoff flows of historic duration.

If factors that currently hamper reproductive success and recruitment of Colorado pikeminnow in the upper Colorado River can be identified and remedied, the system must have the capacity to support an enlarged adult population. In previous studies, mean body condition of adult pikeminnow was significantly lower in strata downstream of Westwater Canyon (strata 1–6) than in strata upstream (strata 7–9), and dispersal of young adults to upstream strata was interpreted as a response to downstream food limitations (Osmundson et al. 1998). Recent (1998–2000) declines in mean body condition of adults both upstream and downstream, coinciding with an increase in adult numbers (USFWS, unpublished data), suggest food limitations were experienced riverwide. Two methods to increase carrying capacity of the system are possible and both will be needed to maximize size of this population and thereby improve population viability: (1) extend the current upstream range to include historic habitat now unused by pikeminnow (i.e., provide fish passage and perhaps temperature augmentation where appropriate), and (2) enhance conditions for lower trophic levels in both off-channel (*sensu* Junk et al. 1989) and within-channel (this study) habitats. A combined approach would allow increases in both distribution and density of Colorado pikeminnow.

CONCLUSIONS

This study demonstrated a clear link between bed sediment and biomass of benthic organisms in the upper Colorado River. Numbers and biomass of fish corresponded with biomass of detritus, periphyton, and invertebrates, strongly suggesting that their numbers are limited by available food. The downstream decline in body condition of the dominant native fish species was consistent with this hypothesis. In this system, with large annual inputs of fine sediment, flows of sufficient magnitude are frequently required to winnow silt and sand from the bed and transport it downstream where it can be deposited on floodplains or channel margins. Peak flows from snowmelt runoff historically provided the energy needed to flush the bed. However, river regulation, primarily in the headwaters of the mainstem and Gunnison rivers, has reduced the magnitude of these flows during the past 50 yr and thereby reduced the frequency of flushing events.

The link between fine sediment and biomass of aquatic organisms, although demonstrated here via spatial empirical relationships, has an important temporal implication. Because fine sediment accumulates in the bed over time, the frequency of flushing flows may be a key variable influencing main-channel benthic production and ultimately the capacity of the river to sup-

port the native piscivore. Hence, our analysis suggests another pathway by which river regulation may depress native fish assemblages in large rivers, and in this case, place an additional constraint on population viability of an endangered species. The “natural-flow-regime paradigm” (Stanford et al. 1996, Poff et al. 1997) may prove a timely guide for managers of the upper Colorado River system. Our results support the concept that reestablishing functional roles of the natural flow regime are necessary if efforts to restore native fish communities in this and other regulated rivers are to succeed.

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