ECOLOGY OF GRAND CANYON BACKWATERS

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INTRODUCTION

The closure of Glen Canyon Dam in 1963 turned a river that was characteristically warm and muddy into a cold clear one, and greatly affected the biota of the river corridor, particularly the native fishes (Valdez and Ryel 1995). Native fishes extirpated from the system include Colorado squawfish (*Ptychocheilus lucius*), bonytail chub (*Gila elegans*), and roundtail chub (*Gila robusta*). Razorback sucker (*Xyrauchen texanus*), if still present, is extremely rare and probably not reproducing (Minckley 1991). Viable populations of only four native species remain (Minckley 1991): humpback chub [(*Gila cypha)* listed as endangered (U.S. Fish and Wildlife Service 1990)]; flannelmouth sucker (*Catostomus latipinnis*); bluehead sucker (*Catostomus discobolus*); and speckled dace (*Rhinichthys osculus*). Humpback chub and flannelmouth sucker are species of special concern in Arizona (AGFD in preparation). Environmental changes in the mainstem Colorado River have largely restricted spawning of native fishes to tributaries, thus greatly reducing the available rearing habitat for these species.

The controlled daily fluctuations in the relatively clear Colorado River of today differ greatly from pre-dam conditions. Prior to impoundment by Glen Canyon Dam, the Colorado River, laden with sediment, underwent large, seasonally predictable floods, peaking in May and June (Valdez and Ryel 1995). These floods probably created and maintained a system of backwaters similar to those created by high discharge in the system today (Rubin et al. 1990; Schmidt 1990). Pre-dam mean annual maximum flow was 86,617 cfs (Stevens 1983) and reached 300,000 cfs (Carothers and Dolan 1982).

Water in the Colorado River through Grand Canyon is now largely supplied from hypolimnial discharge from Lake Powell through Glen Canyon Dam, which operates as a peaking power hydropower facility. Post-dam mean annual maximum flow is 27,898 cfs, ranging from 1,000 - 31,500 cfs (Stevens 1983). Post-dam flows fluctuate on a daily basis, instead of a seasonal basis, with a peak flow and low flow within every 24-hour period. Since closure of the dam, in 1963, through July 1991, daily discharge release patterns fluctuated widely with no restrictions on ramping rates (Figure 1). Discharge peaked in the early afternoon and could reach 31,500 cfs. Low discharge occurred during the early morning and could reach 1,000 or 3,000 cfs, depending on the time of year. On 1 August 1991, interim operations were implemented, restricting daily flow fluctuations to a range of 5,000 - 20,000 cfs. Maximum discharge is now 20,000 cfs and the minimum cannot drop below 8,000 cfs from 0700h to 1500h and 5,000 cfs at night (Figures 2-4). Ramping rates are also restricted to 2,500 cfs per hour up and 1,500 cfs per hour down. From June 1990 through 1994, low steady flows have been released periodically for research purposes.

Tributaries also contribute to the discharge of the Colorado River in Grand Canyon and provide spawning areas for native fishes. Most notable is the Little Colorado River (LCR), which joins the mainstem Colorado River at river mile 61.5 (river mile [RM]) is distance downstream from Lee's Ferry = RM 0). Since closure of the dam, the LCR and Paria River (RM 0.9) are the major sources of sediment input into the system (Andrews 1991). Floods in these tributaries can cause high discharges of sediment-laden water into the Colorado River and result in the formation of numerous sand deposits and associated backwaters (Schmidt and Graf 1990). However, these backwaters are generally temporary and are usually formed in the mainstem just downstream of the source tributary. The Paria River (RM 0.9), Bright Angel Creek (RM 87.62), Shinumo Creek (RM 108.6), Kanab

Creek (RM 143.5) and Havasu Creek (RM 156.93) are other major tributaries which provide spawning areas for native fishes. However, these tributaries are not as conducive to rearing of larval and juvenile native fishes due to limited accessibility, high numbers of predators, and/or declining conditions during the summer.

Backwaters are pockets of quiet water connected to the mainchannel with little or no flow, and are usually formed in eddies where scouring occurs during high flows. As water levels drop, a reattachment sand bar is exposed, partially isolating the eddy return channel and forming the backwater [refer to Rubin et al. (1990), Schmidt (1990), and Schmidt and Graf (1990) for detailed discussions on backwater formation and sediments in the Colorado River, Grand Canyon]. Backwaters and other slow water habitats add to the diversity of the riverine environment (Chart and Bergersen 1992). Due to changes in mainstem habitat caused by dams, particularly decreased water temperature, backwaters have become increasingly important as rearing areas for larval and juvenile native fishes in the Colorado River system (Holden 1978; Valdez and Clemmer 1982; Carter et al. 1985; Maddux et al. 1987) because they provide sheltered habitats with warmer water that contains greater densities of food than the mainchannel (Cole and Kubly 1976; AGFD 1994). However, fluctuations in dam releases can inundate or dewater backwaters, reducing their ability to support juvenile fish. These fluctuating flow regimes force small fish into the mainchannel where they are stressed by cold temperatures and high velocities and are more susceptible to predation (Lupher and Clarkson 1994).

The studies addressed herein use a number of sampling protocols and gear types. Six general objectives were addressed in an attempt to understand the effects of Glen Canyon Dam on the ecology of the fish communities and their habitats in the Colorado River, Grand Canyon.

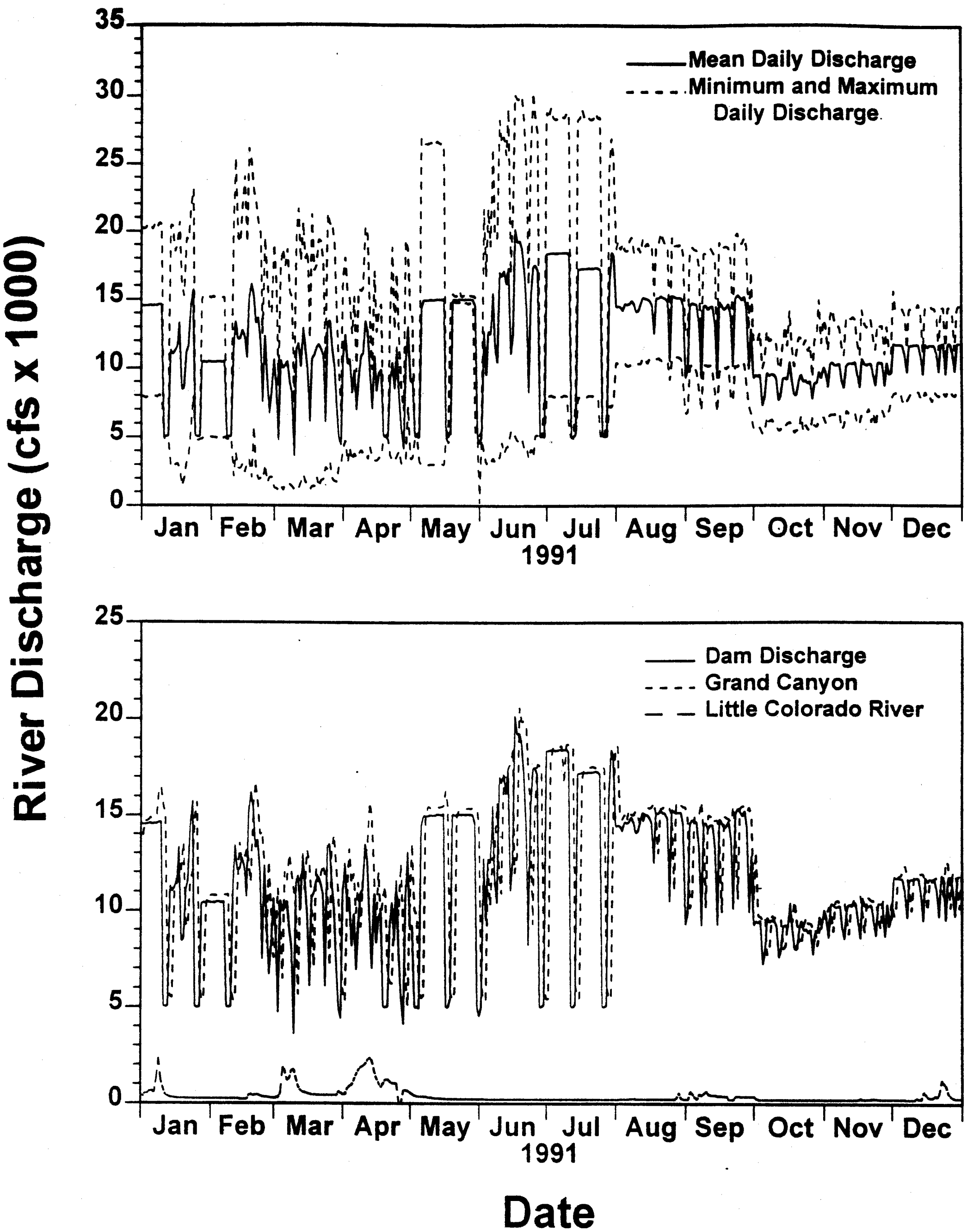

Fig. 1. Mean, minimum and maximum daily discharge from Glen Canyon Dam (top) and mean daily stream discharge in the Colorado River at Lee's Ferry and Grand Canyon (Phantom Ranch) and from the Little Colorado River (bottom) during 1991.

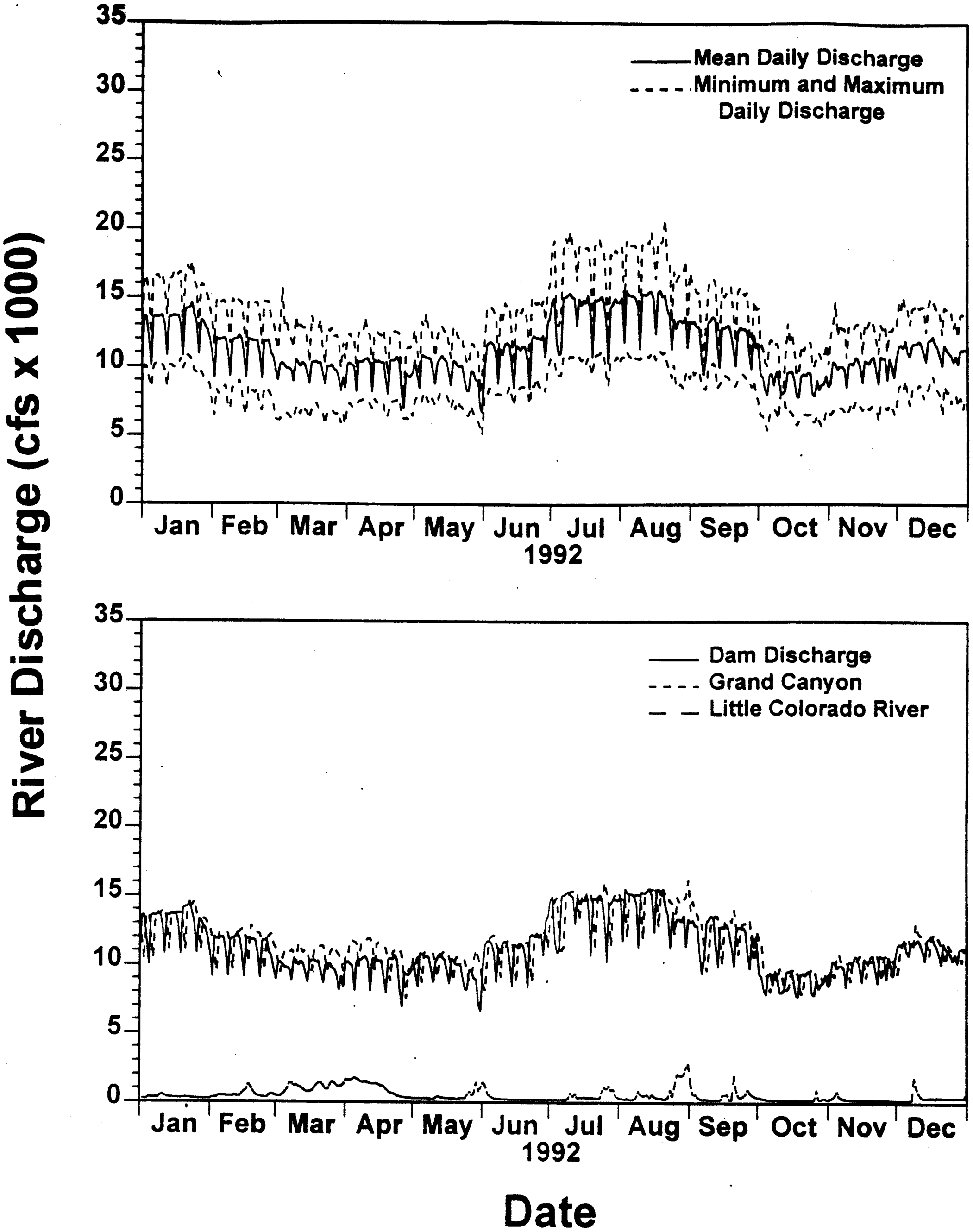

Fig. 2. Mean, minimum and maximum daily discharge from Glen Canyon Dam (top) and mean daily stream discharge in the Colorado River at Lee's Ferry and Grand Canyon (Phantom Ranch) and from the Little Colorado River (bottom) during 1992.

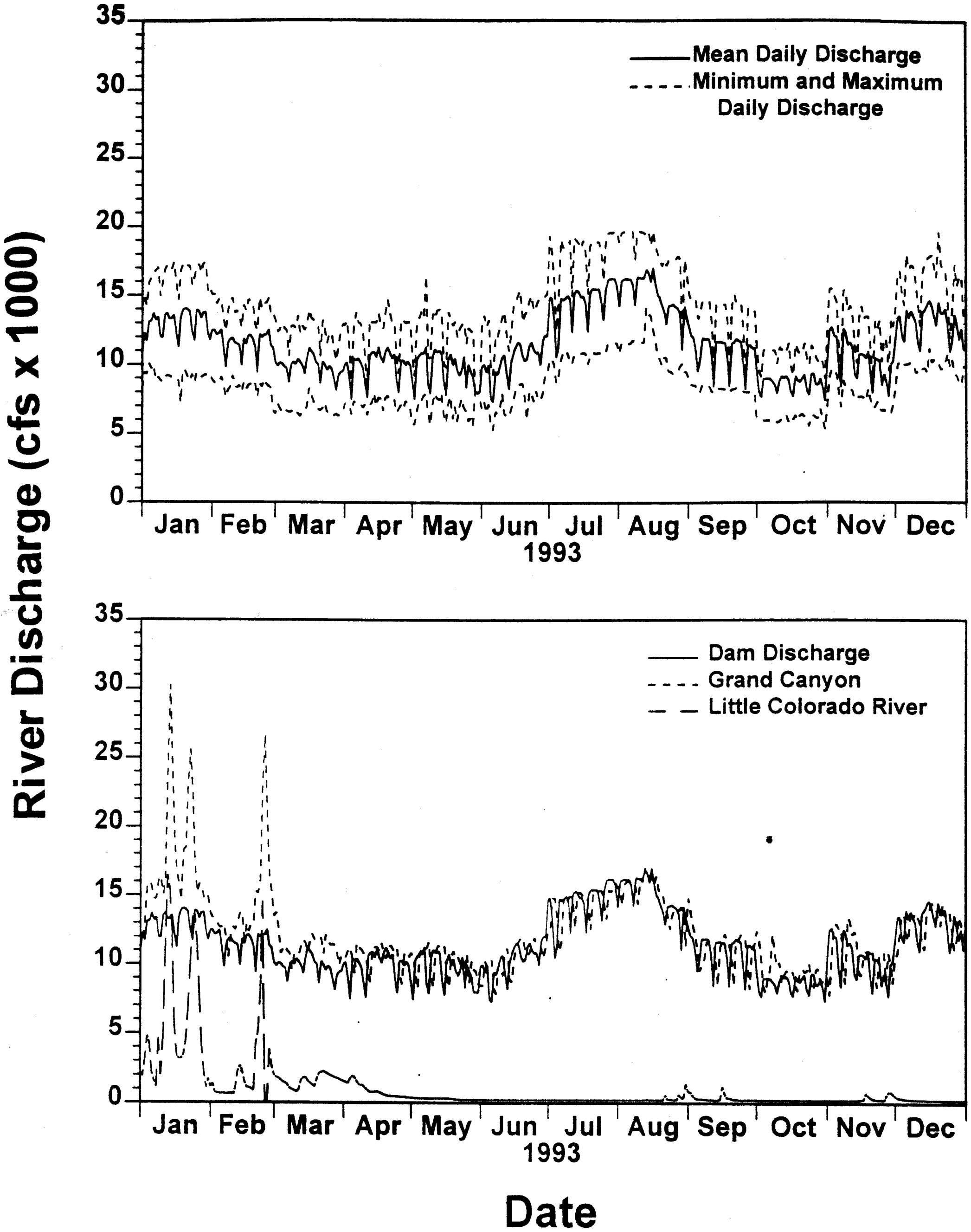

Fig. 3. Mean, minimum and maximum daily discharge from Glen Canyon Dam (top) and mean daily stream discharge in the Colorado River at Lee's Ferry and Grand Canyon (Phantom Ranch) and from the Little Colorado River (bottom) during 1993.

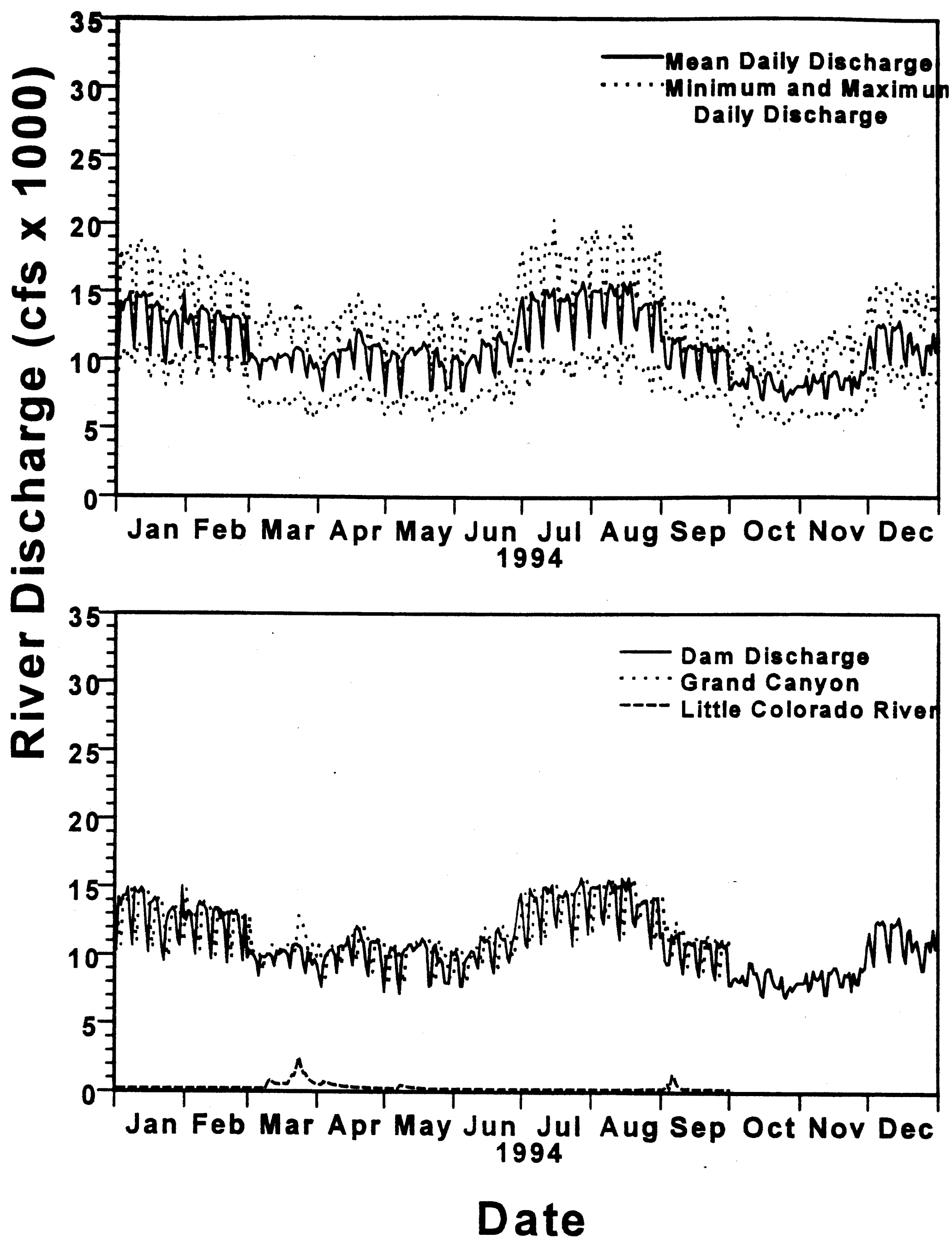

Fig. 4. Mean, minimum and maximum daily discharge from Glen Canyon Dam (top) and mean daily stream discharge in the Colorado River at Lee's Ferry and Grand Canyon (Phantom Ranch) and from the Little Colorado River (bottom) during 1994.

SAMPLING AREA AND PROTOCOLS

During Phase I of Glen Canyon Environmental Studies (Maddux et al. 1987) the Colorado River, Grand Canyon, from Lee's Ferry to Diamond Creek was divided into four sampling reaches (Table 1; Figure 5). The number of backwaters and their characteristics varied greatly within each reach and over the four years of sampling.

Three different sampling protocols, Type A, Type B, and Opportunistic sampling, were used for backwater, mainchannel, and tributary mouth sites. In addition, Quarterly Samples (consisting of benthic invertebrate, zooplankton, and sediment samples) were collected from one location within each reach. Datasondes (DataSonde II, Hydrolab Corporation) were also opportunistically placed in mainchannel and backwater sites. Appendix 1 summarizes all of the sampling sites and the types of samples collected at each site. Specific methods are provided for each objective later in this report.

Type A Sampling

Type A sampling was implemented at backwater sites. This intensive protocol was designed to assess environmental conditions and fish population size at the existing river stage and estimated discharge. Environmental parameters of velocity, depth, turbidity, temperature, pH, conductivity, ambient light, and backwater size were measured and recorded, and substrates were characterized in the foot, center, and mouth of each backwater. Fish collections were made by seining which included multiple passes for calculation of a population estimate for the backwater by depletion (Youngs and Robson 1978; Van Deventer and Platts 1983; 1989). Seine hauls, substrate characterization, and environmental parameter measurements were also taken along the mainchannel beachface adjacent to the backwater. Also, a plane table map and/or a total station survey was conducted at each site to quantify total backwater area and areas of depth contours, substrates, and structure within the backwater. Seining effort was recorded in m^2 of water surface area seined and catch-per-unit-effort (CPUE) calculated as: CPUE = number of fish caught / 100 m^2 seined. Sampled fish were identified to species, measured (total length [mm] and weight [g]), and released at the site of capture.

Type B Sampling

This sampling protocol was used in backwaters and tributary mouths in an attempt to determine presence of fish and changes in habitat characteristics under various stages of river discharge. Fish were collected in 30-50 minnow traps deployed at each site. At backwater locations, traps were placed in the adjacent mainchannel, mainchannel eddy, and return channel eddy, as well as the backwater proper. At each tributary mouth, traps were deployed in the mainstem Colorado River and upstream in the tributary as far as the estimated high water zone under maximum mainstem discharge. Traps were checked approximately four to five times per day over a three day period and during ascending, steady high, descending, and steady low flow stages, whenever possible. During each trap check, water velocity, depth, water temperature, and substrate type were recorded at each trap, as well as species and total length of fishes captured. Benthic invertebrate, zooplankton, and sediment samples were also collected in conjunction with these samples. One datasonde was deployed in each of a backwater and its adjacent mainchannel to record changes in pH, temperature, dissolved oxygen, specific conductivity, and relative depth at 15-30 minute intervals for the duration of the sampling period at that site.

Table 1. Reach designations, their upper and lower boundaries and a general description of the number and characteristics of backwaters within each reach.

	Reach Boundaries		
Reach	Upper	Lower	General Reach Characterization
20	Lee's Ferry RM 0	Little Colorado River RM 61.50	A few moderately-sized backwaters, with silty substrates, that persisted at all flow levels within the interim flow limits and numerous smaller backwaters that appear only at lower flows.
30	Little Colorado River RM 61.50	Bright Angel Creek RM 87.62	Numerous backwaters, with silty substrates, between the LCR and Unkar Rapid formed as a result of the floods of January and February, but most of these became smaller or disappeared over the course of the year. Essentially no backwaters in the Upper Granite Gorge portion of this reach (RM 85.5 - 87.62).
40	Bright Angel Creek RM 87.62	National Canyon RM 166.40	Very few backwaters in this reach, and those present are very small, with sandy substrates, and subject to inundation at higher flows.
50	National Canyon RM 166.40	Diamond Creek RM 225.60	A few well-defined backwaters with sandy substrates, especially below Lava Falls. Subject to complete or partial inundation at higher flows.

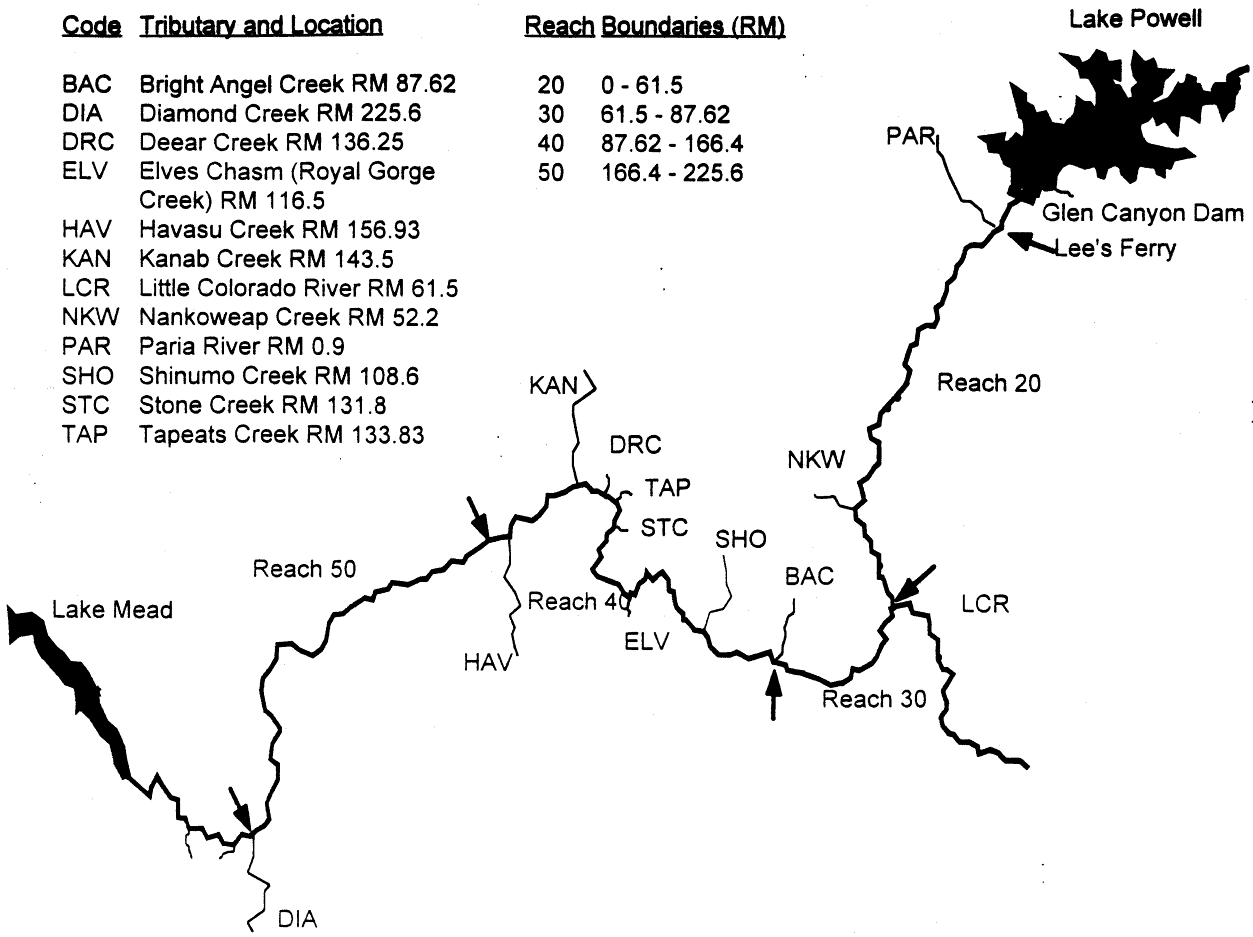

Fig. 5. Sampling reach and tributary locations in the Colorado River, Grand Canyon. RM = river miles below Lee's Ferry.

Opportunistic Sampling

Opportunistic sampling was conducted to obtain a quick, qualitative, point-in-time characterization of a site. This protocol was conducted largely at sites where population estimates by depletion were not feasible (e.g., beachfaces, side channels, tributaries, tributary mouths, and extremely deep backwaters) or gear other than seines were used. Fish were captured using a single pass through the site using either a straight or bag seine, or using minnow traps, hoop nets, dip nets, or kick seines in selected locations. Effort was recorded in m^2 seined (seines) or hours set (minnow traps and hoop nets) and CPUE was calculated as: CPUE = number of fish caught / 100 m^2 seined or 12h trap set. Sampled fish were identified, measured, and released. The same habitat information was collected for each site as was for Type A samples, but the data were recorded from only one location within each site.

Invertebrate and Sediment Samples

Benthic invertebrate, zooplankton, and sediment samples were collected in association with Type A and Type B samples. These samples were collected from each Type B site, quarterly from four or five Type A sites during 1991-93, and at each Type A site during all four trips in 1994. Quarterly samples were collected from between three and five different Type A backwaters, representing each reach, during each quarterly trip: one above the Little Colorado River (Reach 20); one or two locations immediately downstream of the LCR (Reach 30); one location in the Blacktail area (RM 119, Reach 40) (except Trips 14 and 17, when no backwaters suitable for sampling could be found due to river flow conditions); and one below Lava Falls (Reach 50). We sampled backwaters that we thought would persist at different flows (to allow repeated sampling) and were representative of backwaters in the respective reaches. However, because different river flows and shifting substrates often resulted in inundation, desiccation or shrinkage of backwaters, different sites (or no sites) occasionally had to be sampled instead.

Benthic invertebrate, zooplankton, and sediment samples were collected at two or three locations within each site. Benthic invertebrate samples were collected using a Petite Ponar dredge. Plankton samples were taken by pouring 50 L of water through an 80 µm mesh plankton net. All organisms were identified to the Family level. Sediment core samples were collected using a 50 cm^3 minicore sampler. Sediments were separated into sand, silt, and organic components.

Datasondes

Datasondes were placed in selected locations along the river to monitor changes in water temperature, pH, dissolved oxygen, conductivity, and relative depth. These samples were taken in conjunction with Type B samples and opportunistically at other sites. Recordings were made every 20 minutes. Sondes were generally deployed overnight but were occasionally deployed for up to 96 hours (Type B samples).

OBJECTIVES

This study entailed several diverse objectives dealing with populations of fish and their habitat and those factors that might limit their populations and distributions. Small fish inhabit backwaters, tributary mouths, and other nearshore habitats and include larval and juvenile stages of larger species (e.g., humpback chub, bluehead sucker, flannelmouth sucker, and rainbow trout [Oncorhynchus mykiss]) and all life stages of smaller species (e.g., speckled dace, fathead minnow [*Pimephales promelas*], and plains killifish [*Fundulus zebrinus*]). Primary objectives concern the behavior, diet and growth of these fish. Other objectives concern their nearshore and tributary habitats and the availability of food (benthic and planktonic) in these areas.

These studies were part of a larger study of the fishes of the Colorado River and its tributaries in Grand Canyon conducted by the Arizona Game and Fish Department, Arizona State University, Bio/West, Inc., Hualapai Tribe, University of Arizona, and the U. S. Fish and Wildlife Service. Each agency had responsibility for a specific set of objectives to learn more about this system and its aquatic biota. The following is a list of the specific AGFD objectives of this portion of the study.

Objective 3.1. Continue the AGFD monitoring and research program for native fishes of the Colorado River and its tributaries in the Grand Canyon.

This objective acknowledges the importance of continuing to collect information on fish populations in the Colorado River, Grand Canyon, that was started with Phase I of the Glen Canyon

Environmental Studies (Maddux et al. 1987). This section addresses fish distribution and composition throughout the Colorado River, Grand Canyon, and the lower section of important tributaries. These data were analyzed to examine changes in distribution and catch-per-unit-effort (CPUE) over the period of this study (1991-94) and compare them with previous studies. They will also serve as a baseline for future studies. A continuous database of fish collections is of vital importance to monitor the populations of fish in the Grand Canyon.

Objective 3.2. Identify the temporal and spatial distribution patterns and movements of early life stages of fishes in the Little Colorado River and other tributaries.

> *Objective 3.2.a.* **Determine the timing and duration of reproductive activity for different fish species by the evaluation of otoliths and length-frequency distributions.**

This section addresses fish distribution in tributaries of the Colorado River, Grand Canyon. These objectives were designed to provide information on the timing of spawning in these fish, the environmental cues that induce spawning, and residence times of larvae and juveniles in these tributaries. An index of catch-per-unit-effort (CPUE) was also calculated for comparison with previous and future studies and for use in long-term monitoring. This information will be important when deciding to manipulate discharge from Glen Canyon Dam.

Objective 3.4. Determination of the changes in environmental conditions in mainstream and tributary confluence zone native fish rearing habitats under different flow regimes.

> *Objective 3.4.a.* **Measure water depth, temperature, pH, dissolved oxygen, specific conductance and redox potential at each backwater, tributary mouth and adjacent mainstream sites under a variety of controlled GCES Research flows and interim operations.**

> *Objective 3.4.c.* **Collect sediment cores from the tributary mouths, backwaters and mainchannel and analyze for constituents of environmental importance.**

> *Objective 3.4.d.* **Map and identify each area of study.**

These objectives examine changes and differences in the backwater and mainchannel habitats of small fish. This section of this report examines environmental conditions in these areas, as compared to the mainchannel, and their variation under different flow regimes. The various anthropogenic and natural disturbances in the Colorado River greatly affect these habitats. These changes may be beneficial or deleterious and may be short-term or long-lasting. This information will also be important when deciding to change the operations of Glen Canyon Dam.

Objective 3.5. Determine invertebrate standing crops and their relative contributions to diets of young native fishes in tributary, backwater and mainchannel habitats under different flow regimes.

> *Objective 3.5.a.* **Determine the exchange of zooplankton, drift organisms and particulate organic matter between backwaters and mainchannel and tributary mouths.**

***Objective 3.5.b.* Determine the changes in zooplankton communities during the GCES Research and Interim flows in the backwaters.**

***Objective 3.5.c.* Sample benthic invertebrates in rearing habitats both within and without the fluctuating flow regime impact areas.**

***Objective 3.5.d.* Sample larval to juvenile native fish from backwaters, tributary confluences, tributaries above the confluence zone and outlying mainchannel habitats for analysis of digestive tracts.**

These objectives examine the diet of small fish and the availability of food. Zooplankton and benthic invertebrates comprise the majority of the diet of these fish. Under peaking power dam operations (prior to August 1991), fluctuations in water depth caused cycles of inundation and/or desiccation of backwater habitats within the study area. The institution of interim flows caused backwaters habitats to become relatively stable with most experiencing minor daily flushing, thus, providing refugia for larval and juvenile fish, as well as aquatic invertebrates. This section examines benthic invertebrate density and biomass and zooplankton density in backwaters and associated mainchannel beachfaces in the Colorado River, Grand Canyon, from 1991 to 1994. The primary objectives of this portion of the study were to describe the benthic and planktonic community composition and determine the effect of flow regime on invertebrate densities. The secondary objective was to examine the diet of native and non-native fish and the relationship between their diet and relative abundance of prey items. Changes in the operation of the dam are likely to affect invertebrate populations and, therefore, the fish.

Objective 3.6. Determine the behavioral responses of larval to juvenile native fishes to changing environmental conditions in rearing habitats.

***Objective 3.6.a.* Measurement of the associated behavioral responses by young fish to different flow regimes.**

***Objective 3.6.c.* Capture and mark selected fish and track their habitat use over controlled flow sequences.**

***Objective 3.6.d.* Collect and analyze stomach and otolith samples from selected fish.**

This objective addresses the behavior of juvenile fishes to environmental conditions caused by Glen Canyon Dam. Fluctuating flows have the potential to force juvenile fish out of backwaters or tributaries into the mainchannel Colorado River, where the water is usually colder and velocities greater. The use of mainstem (mainchannel and backwater) habitats under different discharges and flow stages is examined. Unfortunately, Objective 3.6.a proved to be unworkable. Objective 3.6.d was addressed in other parts of this and other reports.

Objective 3.9. Determine the extent to which limnological factors, with emphasis on water chemistry and aquatic productivity, potentially limit the distribution and abundance of native fishes in the Little Colorado River and other tributaries which might serve as streams for augmentation of humpback chub in Grand Canyon.

Objective 3.9.a. **Evaluation of water chemistry and hydrologic events as they affect distribution and abundance of fishes directly and secondarily through impacts on productivity of algae and invertebrate food resources.**

This objective addresses the feasibility of introducing a new population of humpback chub into another tributary of the Grand Canyon. This concept was addressed in the Glen Canyon Dam Environmental Impact Statement and is being considered in order to prevent a complete loss of humpback chubs in the Grand Canyon in the event of a catastrophe in the Little Colorado River. The streams in question are Bright Angel Creek, Shinumo Creek, Kanab Creek and Havasu Creek. Humpback chub have been captured in the mouth or vicinity of each of these streams (AGFD 1993; this report) and it is possible that breeding attempts have been made there. However, no evidence of successful reproduction has been found in any tributary other than the LCR.

This report summarizes data collected by the Arizona Game and Fish Department (AGFD) during 25 research trips conducted on the Colorado River from 1991-94. It provides information concerning how changes in habitat may affect the distribution and relative abundance of native fishes and their food in the Colorado River, Grand Canyon, Arizona. The information in this report, along with data collected by AGFD during GCES Phase I studies, will provide baseline data for evaluating the long-term effects of Interim or Modified Low Fluctuating Flows, proposed habitat building and habitat maintenance flows, and the effects of thermal modification should those studies materialize in the future.

Objective 3.1. Continue the AGFD monitoring and research program for native fishes of the Colorado River and its tributaries in the Grand Canyon.

This section addresses distribution and composition of small (<150 mm) fish throughout the Colorado River, Grand Canyon, and the lower section of major tributaries. These data were analyzed to examine changes in distribution and catch-per-unit-effort (CPUE) over the period of this study (1991-94) and compare them with previous studies. These data will also serve as a baseline for future studies.

METHODS

The mainstem Colorado River in the Grand Canyon was partitioned into the same four reaches that were used during Phase I studies (Figure 5; Maddux et al. 1987). Five major tributaries, Little Colorado River and Bright Angel, Shinumo, Kanab, and Havasu Creeks were also sampled regularly.

Fish were collected by a variety of sampling gears and methodologies, designed to be effective in specific habitats. Habitats sampled included backwaters, their associated mainchannel beachfaces, and tributary mouths.

Seines were the standard gear type used for collections from backwaters, where the entire area to be sampled can be blocked off, and along mainchannel beachfaces. Seines were preferred, particularly in backwaters, since they are an active capture gear (less dependent upon species behavior) and are selective mostly by mesh size (Hayes 1983). The seine most commonly used was 9 m x 3 m x 3.2 mm mesh with a 3 m x 3 m bag. In small backwaters or areas where larval fish were suspected to be present, a smaller seine with 0.79 mm mesh was used. Seining was employed under two sampling protocols: Type A and Opportunistic. Opportunistic samples employed a single seine pass through the selected habitat. Backwaters were seined from the mouth to the foot. Type A samples included multiple seine passes through a backwater and a single pass through the associated mainchannel beachface. Under the Type A protocol, backwaters were first blocked off using a straight seine to prevent escape of fish between seine hauls. At least two and as many as four seine hauls permitted the calculation of a population estimate by depletion for each species in Type A backwaters. Maximum likelihood population estimates (Van Deventer and Platts 1983) were calculated using MicroFish 3.0 (Van Deventer and Platts 1989) for each native species, the two common exotic species (fathead minnow and rainbow trout), and total catch. Fish density was calculated as the estimated population size / 100 m^2 surface area of the backwater. Areas of backwaters were determined from plane table maps drawn as part of the Type A protocol. Catch-per-unit-effort (CPUE; number of fish caught / 100 m^2 seined) was calculated as an index of fish abundance for all seined sites, Type A and Opportunistic. If more than one seine haul was taken at a site only the first seine haul was used to calculate CPUE.

Most other gear types used were passive, and thus were both size selective (based on size of mesh or net opening) and species selective (based on behavior of fish; Hubert 1983). Minnow traps were used in backwaters, mainchannel, and tributary habitats - mostly areas in which seining was not feasible. Minnow traps tend to select against benthic species and for those species seeking cover (Hubert 1983). Hoop nets were used in tributary mouths and in the vicinity of tributaries in the mainstem. These nets, especially those with leads, were very effective in capturing adults moving into tributaries, particularly during spawning runs. Minnow trap and hoop net CPUE's were calculated as number of fish captured / 100 hours of trapping time. These collections were designed to provide a single sample of the species using these areas at a given time, or to collect fish for diet analysis and replicate samples were rarely taken. Therefore, little analysis has been performed on these data.

Total length (mm) was recorded for all bluehead suckers, flannelmouth suckers, and humpback chub. Total length was also recorded for other species, except, on occasions when large numbers were captured, at which times counts were made. During Trips 1-21, weight (g) was recorded for fish large enough (about 5 g) to be accurately weighed with our scale. During Trips 22-25 a more precise scale was used which allowed all fish to be weighed to 0.1 g.

A large number of gear types were used in this study, each with different selectivity biases. Minnow traps were the most commonly used gear type in 1991 and 1992. In 1993 and 1994, seines were the preferred gear type. Hoop nets were used during all years (mostly in tributary mouths), but were used selectively. Also, the degree to which hoop nets and minnow traps were used and the effort expended varied widely among years, reaches, and habitat types. This was particularly true in tributaries where effort was usually comprised of a single gear set on a given trip. This lack of consistency and replication makes it difficult to interpret comparisons of species composition between years, reaches, and habitats. Therefore, only qualitative examination of trap data is reported.

Differences in species distribution for collections made by seining among habitats and reaches were tested using CPUE data from seine collections from 1993 and 1994. These changes were tested by multiple ANOVA (α=0.05) and the Ryan-Einot-Gabriel-Welch Multiple F test (Day and Quinn 1989). Differences in CPUE among years was not statistically tested due to wide variations in effort and changes in protocol.

RESULTS

Fifteen species of fish were captured during 1991-94 (Table 2). All four remaining native species were at least locally abundant. Eleven exotic species were captured, but only fathead minnow, plains killifish, channel catfish (*Ictalurus punctatus*), rainbow trout, and brown trout were commonly captured. Examination of species abundance data showed that species varied among reaches and habitats.

Table 2. Common name, scientific name, and families of all native and exotic fish species captured during this study.

Common Name	Scientific Name	Family
Native Species		
Bluehead Sucker	*Catostomus discobolus*	Catostomidae
Flannelmouth Sucker	*Catostomus latipinnis*	Catostomidae
Humpback Chub	*Gila cypha*	Cyprinidae
Speckled Dace	*Rhinichthys osculus*	Cyprinidae
Exotic Species		
Common Carp	*Cyprinus carpio*	Cyprinidae
Fathead Minnow	*Pimephales promelas*	Cyprinidae
Red Shiner	*Cyprinella lutrensis*	Cyprinidae
Plains Killifish	*Fundulus zebrinus*	Cyprinodontidae
Green Sunfish	*Lepomis cyanellus*	Centrarchidae
Striped Bass	*Morone saxatilis*	Percichthyidae
Channel Catfish	*Ictalurus punctatus*	Ictaluridae
Black Bullhead	*Ameiurus melas*	Icatluridae
Brook Trout	*Salvelinus fontinalis*	Salmonidae
Brown Trout	*Salmo trutta*	Salmonidae
Rainbow Trout	*Oncorhynchus mykiss*	Salmonidae

Species Composition by Reach

Native species dominated the catch in Reaches 20, 40, and 50 (Figure 6; Table 3) and in all tributaries (Figure 7; Table 4). Rainbow trout were the most abundant exotic species above the Little Colorado River (LCR). Fathead minnows were most common down river, particularly in Reach 30 where they were the most common species captured. Figure 8 shows the percentage of the catch comprised by bluehead sucker, flannelmouth sucker, humpback chub, speckled dace, fathead minnow, and rainbow trout in mainstem habitats (mainchannel and backwaters) of Reaches 20, 30, 40, and 50 during 1991-94.

Reach 20

Speckled dace (39% of the catch) were the most common species found in backwaters of Reach 20, followed by flannelmouth sucker (27%), rainbow trout (15%), and fathead minnow (13%). In the mainchannel of Reach 20, rainbow trout (61%) was the most common, followed by speckled dace (15%), flannelmouth sucker (14%), and humpback chub (11%). Speckled dace comprised 63% of the catch in Reach 20 in 1992 but only 11% in 1994 (Figure 8). Flannelmouth sucker comprised only 15% of the catch in Reach 20 in 1992 but 29% of the catch in 1991 Rainbow trout were more commonly caught in 1991-93 (19-23%) than in 1994 (11%). Fathead minnows were uncommon in Reach 20 in 1991 (9%) and rarely caught in 1992 and 1993 (0% and 1%) but comprised 42% of the catch in 1994.

Reach 30

Fathead minnows were the most common species caught in backwaters (42%) in Reach 30, with humpback chub also being common (29%). Bluehead sucker (12%), speckled dace (8%), and flannelmouth sucker (7%) were also commonly caught. In the mainchannel, humpback chub were the most commonly caught species (45%). Fathead minnow (22%), speckled dace (18%), and bluehead sucker (8%) were also commonly captured. The percentage of the catch comprised of fathead minnow in Reach 30 varied greatly, ranging from 18% in 1993 and 21% in 1991 to 60% in 1994 and 79% in 1992. Conversely, humpback chub comprised a larger percentage of the catch in 1993 (45%) and 1991 (44%) than in 1994 (15%) and 1992 (9%). Prevalence of bluehead sucker in the catch from Reach 30 was relatively constant, ranging from 2% in 1992 to 11% in 1994. The percentage of flannelmouth sucker in the catch from Reach 30 was also relatively constant, ranging from 3% in 1992 and 1994 to 6% in 1991 and 8% in 1993.

Reach 40

In Reach 40, bluehead sucker was the most common species collected in backwaters (45%). Fathead minnow (22%), speckled dace (17%), and flannelmouth sucker (10%) were also caught in backwaters. In the mainchannel, fathead minnow was the most common species (30%). Bluehead sucker (26%), speckled dace (16%),rainbow trout (15%), and flannelmouth sucker (6%)were also common. Percent composition of bluehead suckers in Reach 40 increased over the study period from 12% in 1991 to 49% in 1994. Percent composition of speckled dace also increased from 7% in 1991 to 23% in 1994. Prevalence of humpback chub in the catch in Reach 40 decreased over the same period, from 14% in 1991 to 1% in 1994. The percentage of flannelmouth suckers in the catch remained relatively constant, ranging from 5% in 1994 to 17% in 1993. The percentage of fathead minnow in the catch from Reach 40 was relatively constant and ranged from 20% in 1991 to 33% in 1992. The percentage of the catch comprised of rainbow trout in Reach 40 decreased dramatically from 27% in 1991 to 1% in 1994.

Reach 50

Speckled dace (37%) was the most commonly caught species in backwaters in Reach 50. Fathead minnow (22%), bluehead sucker (21%), and flannelmouth sucker (19%) were also commonly caught. In the mainchannel, speckled dace (45%) was also the most common species captured, followed by flannelmouth sucker (24%), fathead minnow (14%), and bluehead sucker (11%). Speckled dace was the most common species captured in Reach 50, but its composition of the catch decreased from 62% in 1991 to 26% in 1994. Bluehead sucker composition in the catch increased from 4% in 1991 to 33% in 1994. Flannelmouth sucker percent composition also increased, but more modestly, from 8% in 1991 to 22% in 1994. Fathead minnow prevalence in Reach 50 was quite constant, ranging from 14-18% in 1991, 1993 and 1994, except for an increase in 1992 when this species comprised 38% of the catch. Humpback chub were rarely caught in Reach 50 and always comprised <1% of the catch there. However, 26 humpback chub were caught in Reach 50, many of which were larvae and small juveniles.

Little Colorado River

In the mouth of the Little Colorado River, humpback chub dominated the catch (47%). Bluehead sucker (29%) and speckled dace (13%) were also common, with flannelmouth sucker comprising 4% of the catch. Interestingly, all native species were captured more frequently than any exotic species in the mouth of the LCR.

Bright Angel Creek

In Bright Angel Creek, speckled dace were the only species commonly caught (89%). Rainbow trout (6%), brown trout (2%), fathead minnow (2%), bluehead sucker (1%), and humpback chub (1%) were also collected.

Shinumo Creek

Speckled dace were also the most commonly caught species in Shinumo Creek (90%). Bluehead sucker (3%), fathead minnow (3%), rainbow trout (2%), flannelmouth sucker (1%), humpback chub (1%), and brown trout (<1%) were also captured.

Kanab Creek

In Kanab Creek, speckled dace (40%) also dominated the catch, but less so than in Bright Angel and Shinumo Creeks. Also commonly caught were flannelmouth sucker (22%), fathead minnow (21%), bluehead sucker (12%), and plains killifish (5%). Most of the suckers were spawning adults captured in the spring and early summer. Common carp, rainbow trout, channel catfish, striped bass, humpback chub, and brown trout, combined, comprised 1% of the catch in Kanab Creek.

Havasu Creek

Speckled dace (47%) dominated the catch in Havasu Creek, as well. Bluehead sucker (33%) and flannelmouth sucker (18%) were also commonly caught, which mostly consisted of spawning adults captured in the spring and early summer. Humpback chub, common carp, fathead minnow, and rainbow trout, combined, comprised 1.5% of the catch from Havasu Creek.

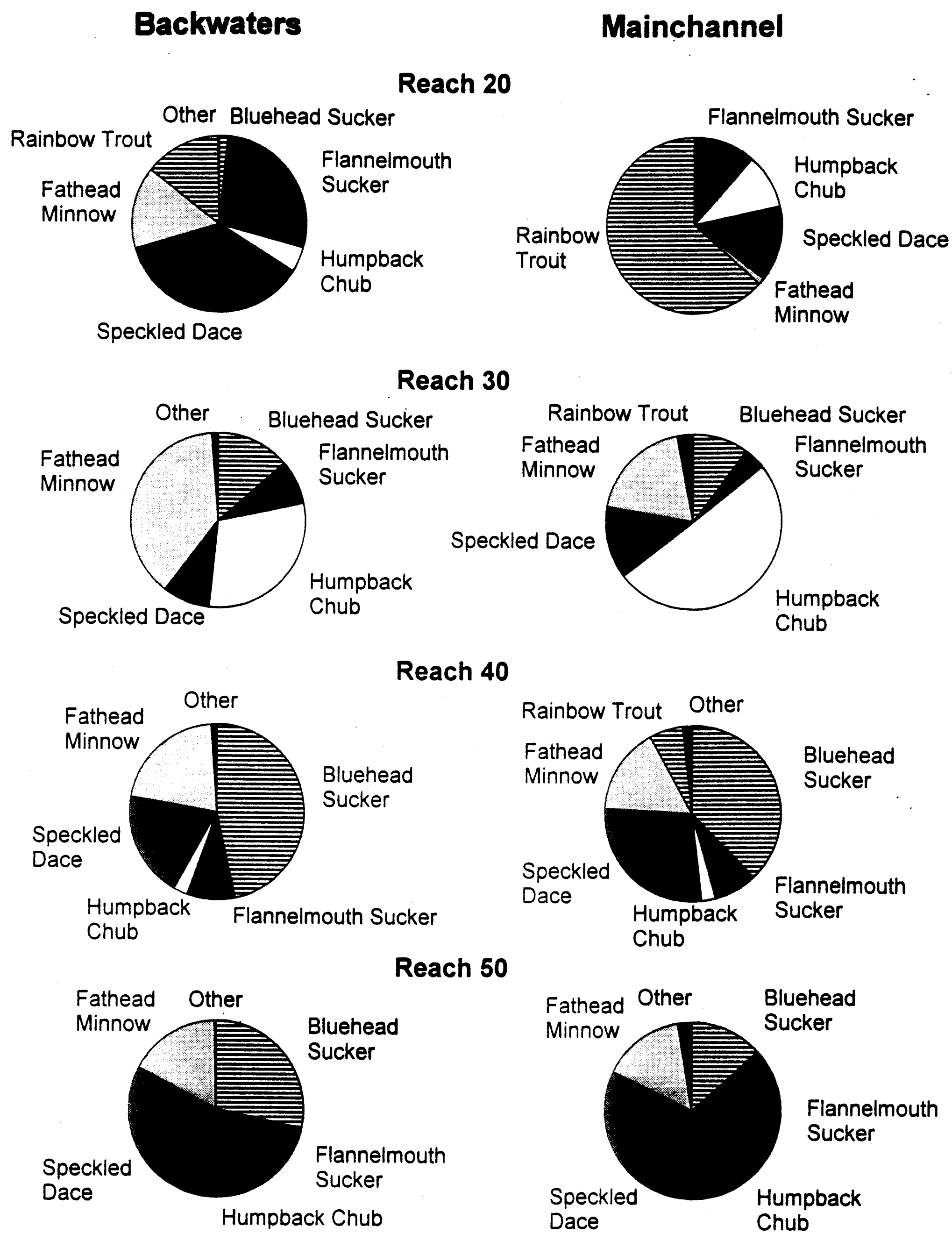

Fig. 6. Species composition of catch in backwater and mainchannel habitats of each reach of the Colorado River, Grand Canyon, during AGFD sampling trips, 1991-94.

Table 3. Number and percent composition of catch of each species in each reach from backwaters and mainchannel beachfaces of the Colorado River, Grand Canyon, during AGFD sampling trips, 1991-94.

Habitat/Species	Reach 20		Reach 30		Reach 40		Reach 50	
Backwaters								
Bluehead Sucker	26	1.4	1,532	12.3	1,510	44.8	2,613	21.1
Flannelmouth Sucker	517	27.1	920	7.4	343	10.2	2,336	18.9
Humpback Chub	73	3.8	3,545	28.5	90	2.7	26	0.2
Speckled Dace	743	38.9	1,048	8.4	575	17.1	4,563	36.9
Total Natives	1,359	71.1	7,045	56.6	2,518	74.8	9,538	77.2
Black Bullhead	0	0.0	0	0.0	0	0.0	1	0.0
Brown Trout	1	0.1	1	0.0	2	0.1	0	0.0
Channel Catfish	1	0.1	3	0.0	0	0.0	10	0.1
Common Carp	2	0.1	17	0.1	18	0.5	77	0.6
Fathead Minnow	253	13.2	5,203	41.8	754	22.4	2,689	21.8
Green Sunfish	1	0.1	0	0.0	0	0.0	0	0.0
Plains Killifish	2	0.1	81	0.7	7	0.2	20	0.2
Rainbow Trout	292	15.3	93	0.7	68	2.0	19	0.2
Total Exotics	552	28.9	5,398	43.4	849	25.2	2,816	22.8
Backwater Total	1,911	96.3	12,443	89.9	3,367	93.0	12,354	97.4
Mainchannel Beachfaces								
Bluehead Sucker	0	0.0	114	8.2	67	26.5	34	10.5
Flannelmouth Sucker	10	13.5	42	3.0	15	5.9	79	24.3
Humpback Chub	8	10.8	625	44.8	10	4.0	0	0.0
Speckled Dace	11	14.9	250	17.9	40	15.8	147	45.2
Total Natives	29	39.2	1,031	73.9	132	52.2	260	80.0
Brook Trout	0	0.0	1	0.1	0	0.0	0	0.0
Brown Trout	0	0.0	0	0.0	3	1.2	0	0.0
Channel Catfish	0	0.0	1	0.1	0	0.0	1	0.3
Common Carp	0	0.0	0	0.0	1	0.4	9	2.8
Fathead Minnow	0	0.0	311	22.3	76	30.0	44	13.5
Plains Killifish	0	0.0	1	0.1	1	0.4	0	0.0
Rainbow Trout	45	60.8	51	3.7	38	10.5	6	1.8
Red Shiner	0	0.0	0	00.	1	0.4	0	0.0
Striped Bass	0	0.0	0	0.0	1	0.2	5	1.2
Total Exotics	45	60.8	365	26.1	121	47.8	65	20.0
Mainchannel Total	74	3.7	1,396	10.1	253	7.0	325	2.6
Reach Total	1,985		13,839		3,620		12,679	

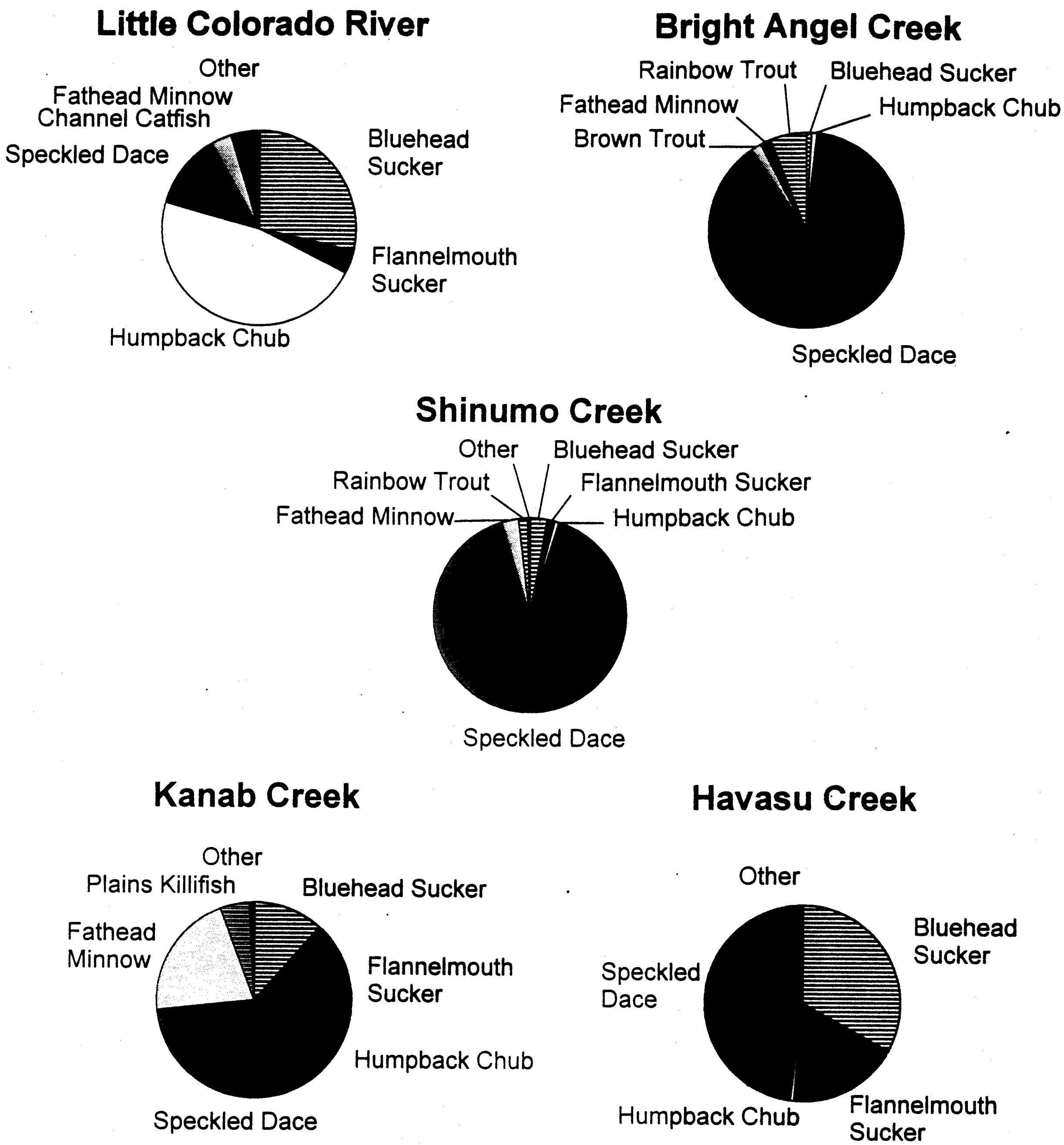

Fig. 7. Species composition of catch in mouths of tributaries of the Colorado River, Grand Canyon, during AGFD sampling trips 1991-94.

Table 4. Number and percent composition of catch of each species from mouths of tributaries of the Colorado River, Grand Canyon, during AGFD sampling trips, 1991-94.

Species	Tributary									
	Little Colorado River		Bright Angel Creek		Shinumo Creek		Kanab Creek		Havasu Creek	
Bluehead Sucker	285	28.6	1	0.9	67	3.0	165	11.6	154	33.0
Flannelmouth	38	3.8	0	0.0	30	1.3	304	21.3	85	18.2
Humpback Chub	465	46.8	1	0.9	16	0.7	1	0.1	3	0.6
Speckled Dace	124	12.5	103	88.8	2,046	90.3	573	40.1	220	47.2
Total Natives	912	91.8	105	90.5	2,159	95.2	1,043	73.1	462	99.1
Brown Trout	0	0.0	2	1.7	8	0.4	1	0.1	0	0.0
Channel Catfish	35	3.5	0	0.0	0	0.0	2	0.1	0	0.0
Common Carp	11	1.1	0	0.0	1	0.0	5	0.3	2	0.4
Fathead Minnow	32	3.2	2	1.7	64	2.8	302	21.2	1	0.2
Plains Killifish	0	0.0	0	0.0	1	0.0	69	4.8	0	0.0
Rainbow Trout	5	0.5	7	6.0	34	1.5	3	0.2	1	0.2
Striped Bass	0	0.0	0	0.0	0	0.0	2	0.1	0	0.0
Total Exotics	83	8.3	11	9.5	108	4.8	384	26.9	4	0.9
Total	995		116		2,267		1,427		466	

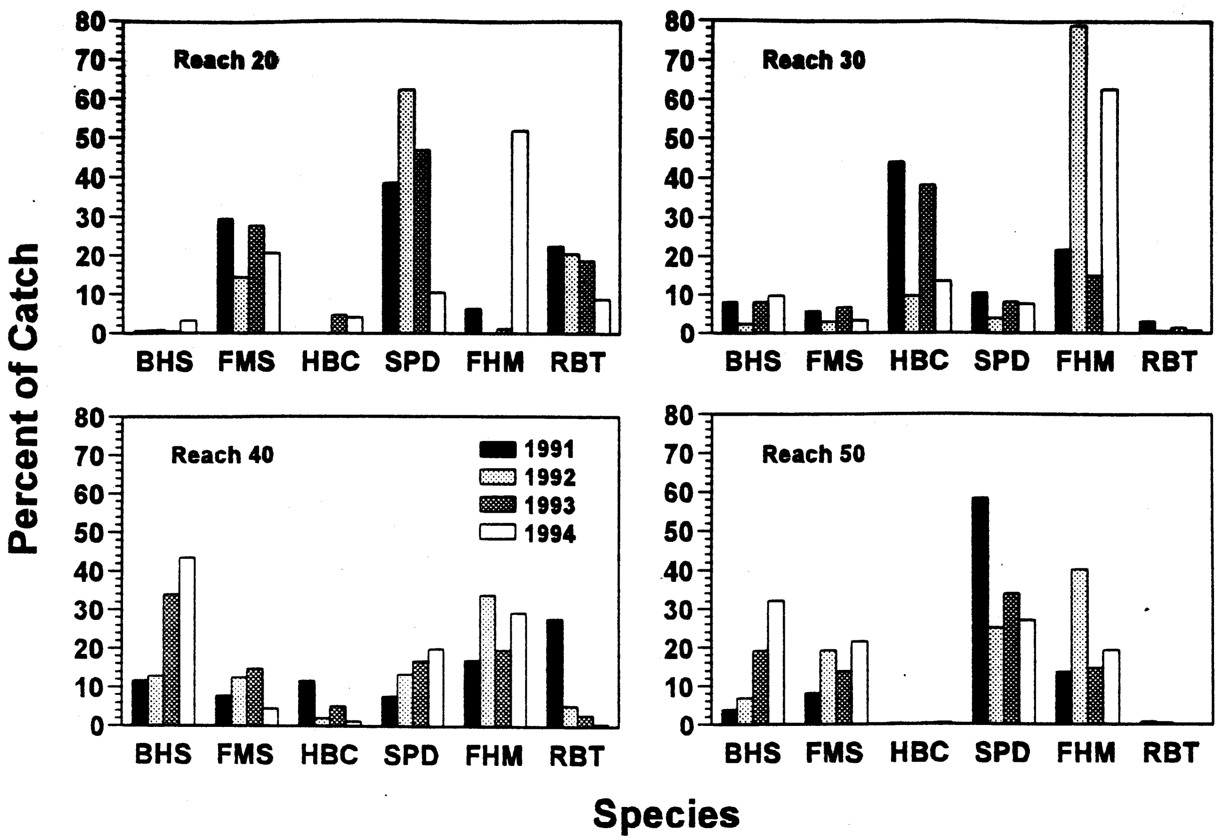

Fig. 8. Percentage of the catch comprised by bluehead sucker (BHS), flannelmouth sucker (FMS), humpback chub (HBC), speckled dace (SPD), fathead minnow (FHM), and rainbow trout (RBT) in mainstem habitats (mainchannel and backwaters) of Reaches 20, 30, 40, and 50 during 1991-94 of AGFD mainstem sampling in the Colorado River, Grand Canyon.

Species Distribution

Juvenile stages of all four native species were found predominantly near known or suspected spawning areas for those species. Catch-per-unit-effort for all species combined (total CPUE) was higher in backwaters than along mainchannel mainchannel beachfaces (P=0.0001). Mean total CPUE in backwaters in Reach 50 was higher (P=0.0001) than in all other reaches and higher in Reach 30 backwaters than in Reaches 20 and 40. There was no significant difference in total CPUE in the mainchannel among reaches (P=0.8646).

Bluehead Sucker

Bluehead suckers were found throughout the river between the LCR and Diamond Creek with the highest percentages being found in Reach 50 (43%; Figure 9). Bluehead suckers were also prevalent in reaches 30 (32%) and 40 (25%). Only 24 (<1%) bluehead suckers were captured in Reach 20, with most of them being captured just above the LCR, the upper boundary of Reach 30. Mean CPUE for bluehead suckers in backwaters was higher in Reach 50 than any other reach (P=0.0001). In the mainchannel, mean CPUE for bluehead suckers was higher in Reaches 50 and 40 than in Reach 20 (P=0.0224). Bluehead suckers spawn in the Little Colorado River and Bright Angel, Shinumo, Kanab, and Havasu Creeks. There may also be resident populations of bluehead suckers in Crystal and Clear Creeks, as young were found there, as well.

Flannelmouth Sucker

Flannelmouth suckers were found throughout the Colorado River in Grand Canyon (Figure 10). The largest percentage of flannelmouth suckers were found in Reaches 50 (48%) and 30 (35%). Reaches 20 and 40 contained only 14% and 8% of the flannelmouth sucker catch, respectively. While mean CPUE of this species was higher in Reach 50 than any other reach (P=0.0001), no differences were found in mainchannel catches (P=0.7957). Flannelmouth suckers are known to spawn in the Paria and Little Colorado Rivers and Bright Angel, Shinumo, Kanab, and Havasu Creeks. However, to date, few larvae have been found in the Paria River, while juveniles have only been found downstream from RM 44.27, possibly the result of mainstem spawning in the warm springs near RM 30.

Humpback Chub

Reach 30 contained 96% of all of the humpback chub caught (Figure 11). Mean CPUE was higher in Reach 30 than in all other reaches in both backwaters and the mainchannel ($P \leq 0.0124$). However, juvenile humpback chub were captured in all reaches (2% in Reaches 20 and 40 and <1% in Reach 50) and in the mouths of all major tributaries. We caught humpback chub, including young-of-the-year (YOY), sporadically throughout the river from RM 44 - 204 and Bio/West has found several aggregations of adult humpback chub throughout the canyon (Valdez and Ryel 1995). Humpback chub YOY as small as 22 mm were caught at RM 44.27L (Reach 20) in 1993 and 1994 and age 1 chub were caught there in 1994. This backwater is over 27 km, and several large rapids, upstream from the Little Colorado River. It is unlikely that humpback chub this small could have moved upstream to this site from the LCR. Small humpback chub were also captured at RM's 168.75, 192.42, 193.85, 203.80, and 204.00 (Reach 50), including two 14 mm and one 18 mm fish. It is also unlikely that fish this small were spawned in the LCR, drifted downstream over 200 km in the cold water of the mainstem Colorado River and survived. These captures provide strong evidence of spawning, with some success, outside of the LCR.

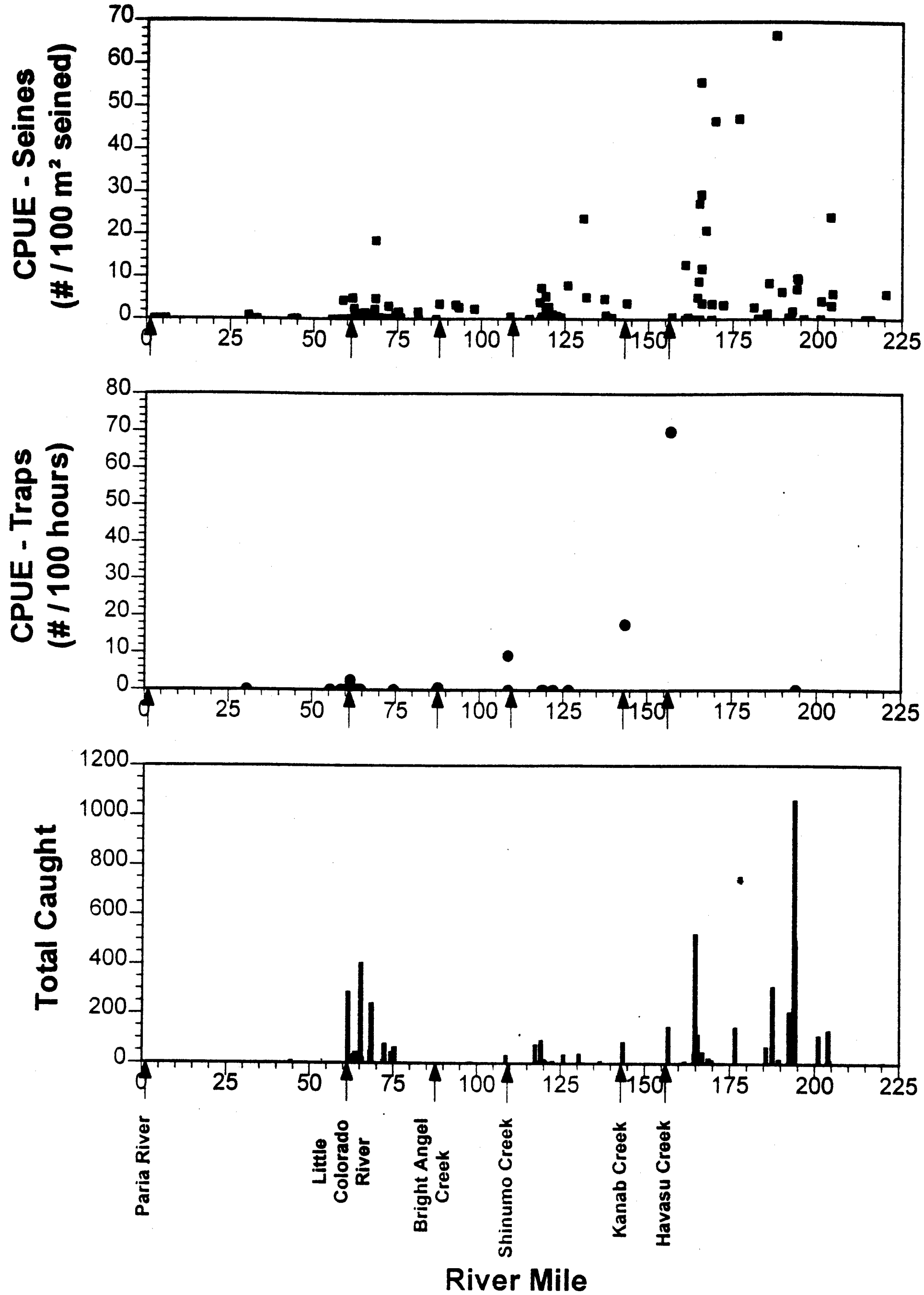

Fig. 9. CPUE of bluehead sucker in seines (top) and traps (middle) and total number caught (bottom) at each river mile during AGFD sampling trips, Colorado River, Grand Canyon, 1991-94.

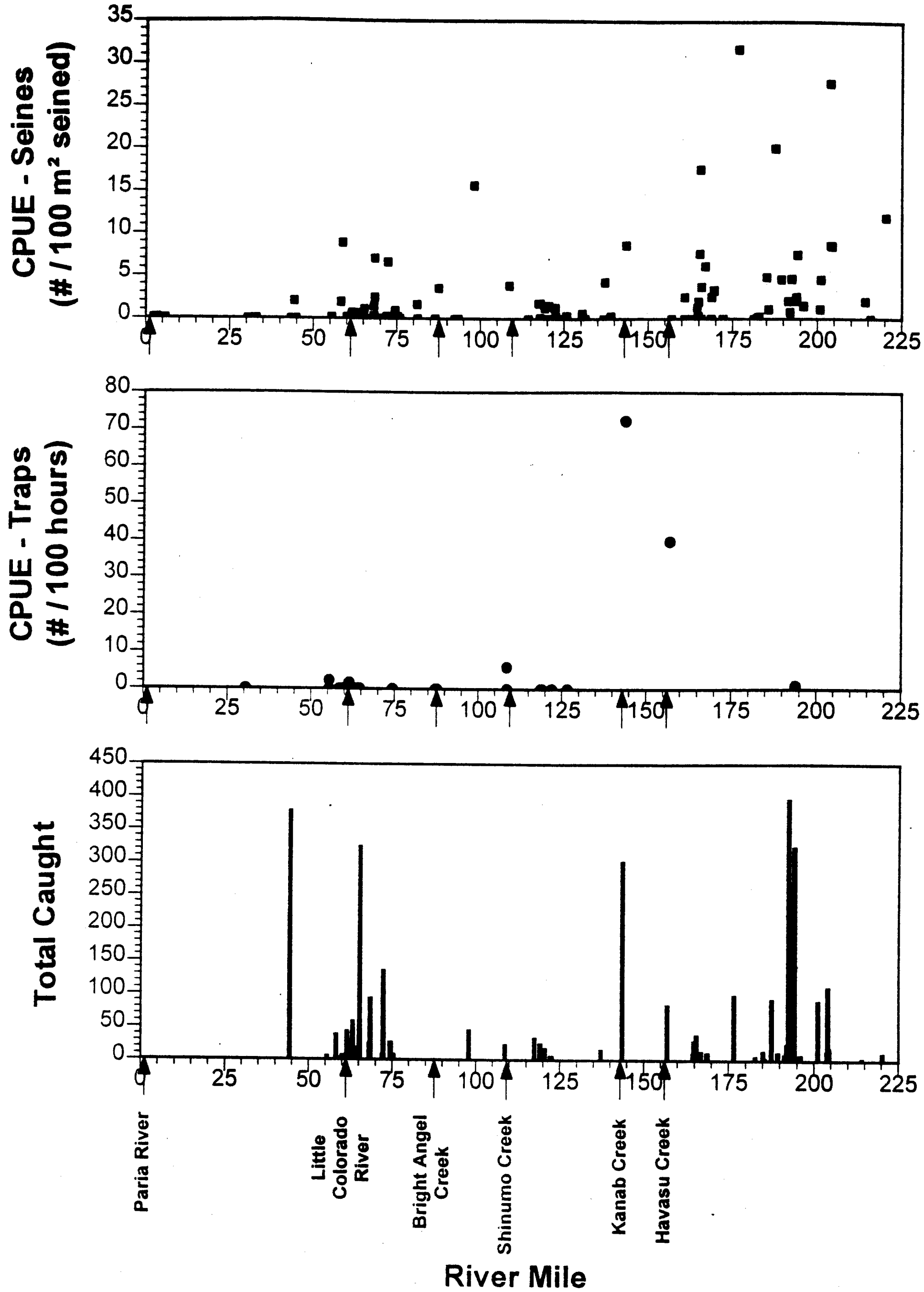

Fig. 10. CPUE of flannelmouth sucker in seines (top) and traps (middle) and total number caught (bottom) at each river mile during AGFD sampling trips, Colorado River, Grand Canyon, 1991-94.

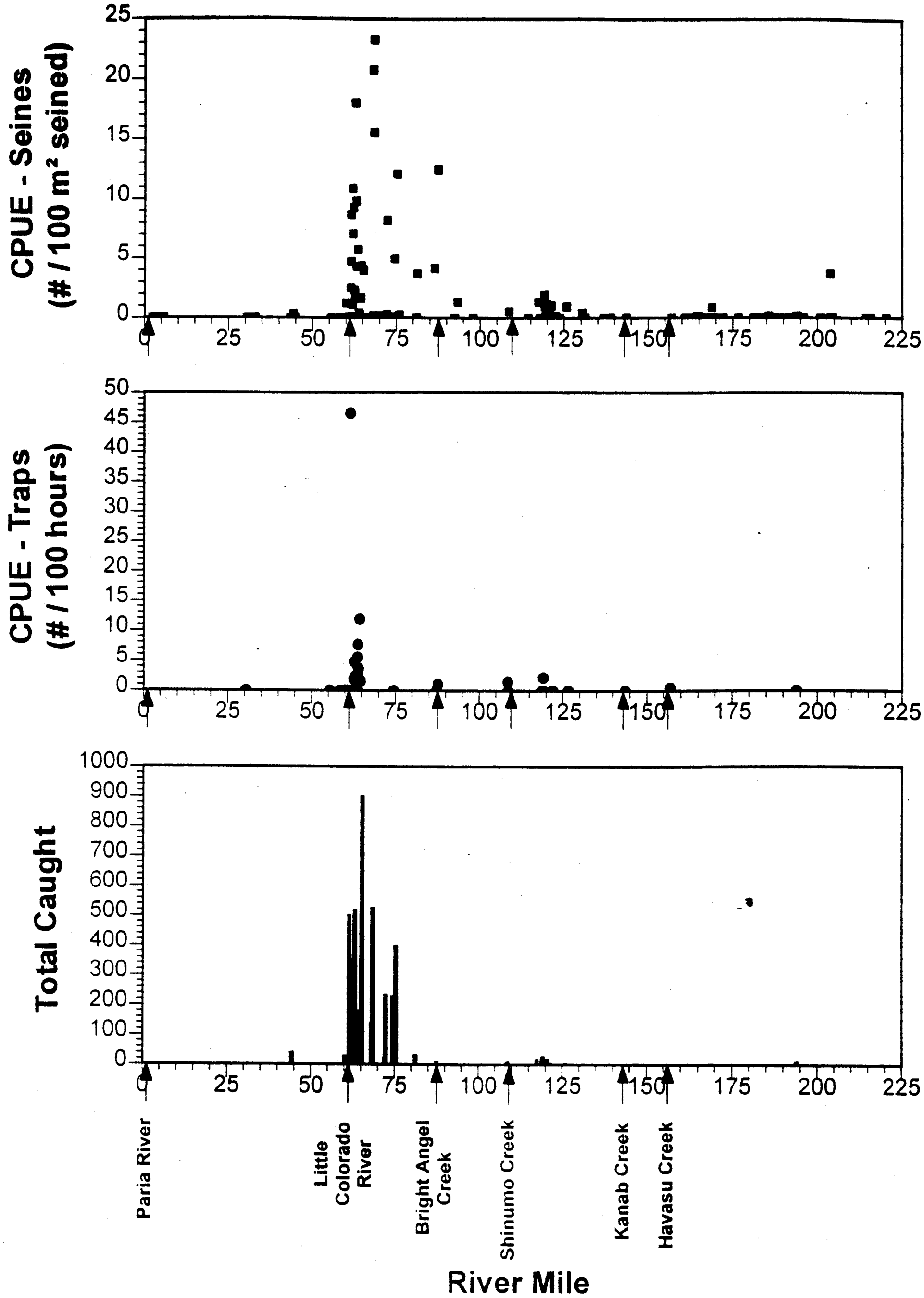

Fig. 11. CPUE of humpback chub in seines (top) and traps (middle) and total number caught (bottom) at each river mile during AGFD sampling trips, Colorado River, Grand Canyon, 1991-94.

Speckled Dace

Speckled dace were commonly collected throughout the river with the highest percentage (54%) being caught in Reach 50 (Figure 12). Reach 30 contained 23% of the captured speckled dace and Reaches 20 and 40 each contained 11%. Mean backwater CPUE for speckled dace was higher in Reach 50 than any other reach and higher in Reach 20 than Reach 40. In the mainchannel, mean CPUE was higher in Reach 50 than in Reaches 20 or 30. Dace spawn in all tributaries and possibly in warm areas of the mainstem (possibly including backwaters).

Fathead Minnow

Fathead minnows were most commonly caught in backwaters, where they are known to spawn, particularly near the LCR with 68% being captured in Reach 30 (Figure 13). Reach 50 contained 20%, Reach 40, 9%, and Reach 20, 4% (mostly from near the LCR). Although more fathead minnows were caught in Reach 30, mean backwater CPUE was higher in Reach 50 than any other reach and Reach 30 was higher than Reach 20 (P=0.0001). Mean CPUE for fathead minnows did not vary significantly between reaches (P=0.2499) in the mainchannel. These exotic fish were not commonly caught in tributary mouths but may inhabit upstream portions of some streams, such as the LCR and Kanab Creek.

Rainbow Trout

Rainbow trout were most abundant in Reaches 20 (60%) and 30 (29%; Figure 14). Mean backwater CPUE was higher in Reach 20 than any other reach (P=0.0002), while mean mainchannel CPUE did not significantly change (P=0.7610). Rainbow trout captured in Reaches 40 (10%) and 50 (<1%) were most commonly associated with tributaries . Of the tributaries, rainbow trout were found only in Shinumo Creek. However, they are known to spawn in the mainchannel near Lee's Ferry, where they are stocked by AGFD, and in Nankoweap, Clear, Bright Angel, Crystal, Tapeats, and Deer Creeks.

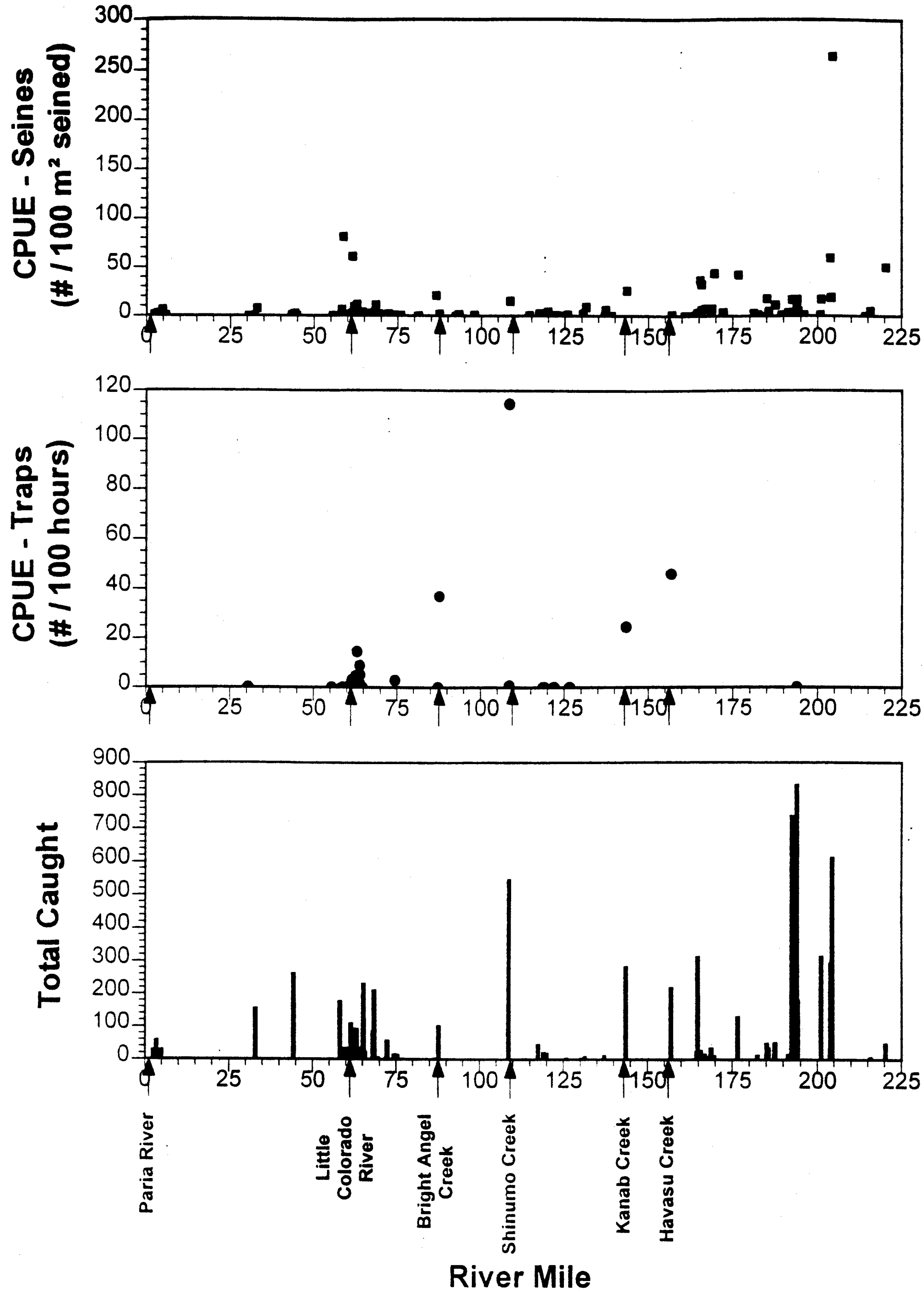

Fig. 12. CPUE of speckled dace in seines (top) and traps (middle) and total number caught (bottom) at each river mile during AGFD sampling trips, Colorado River, Grand Canyon, 1991-94.

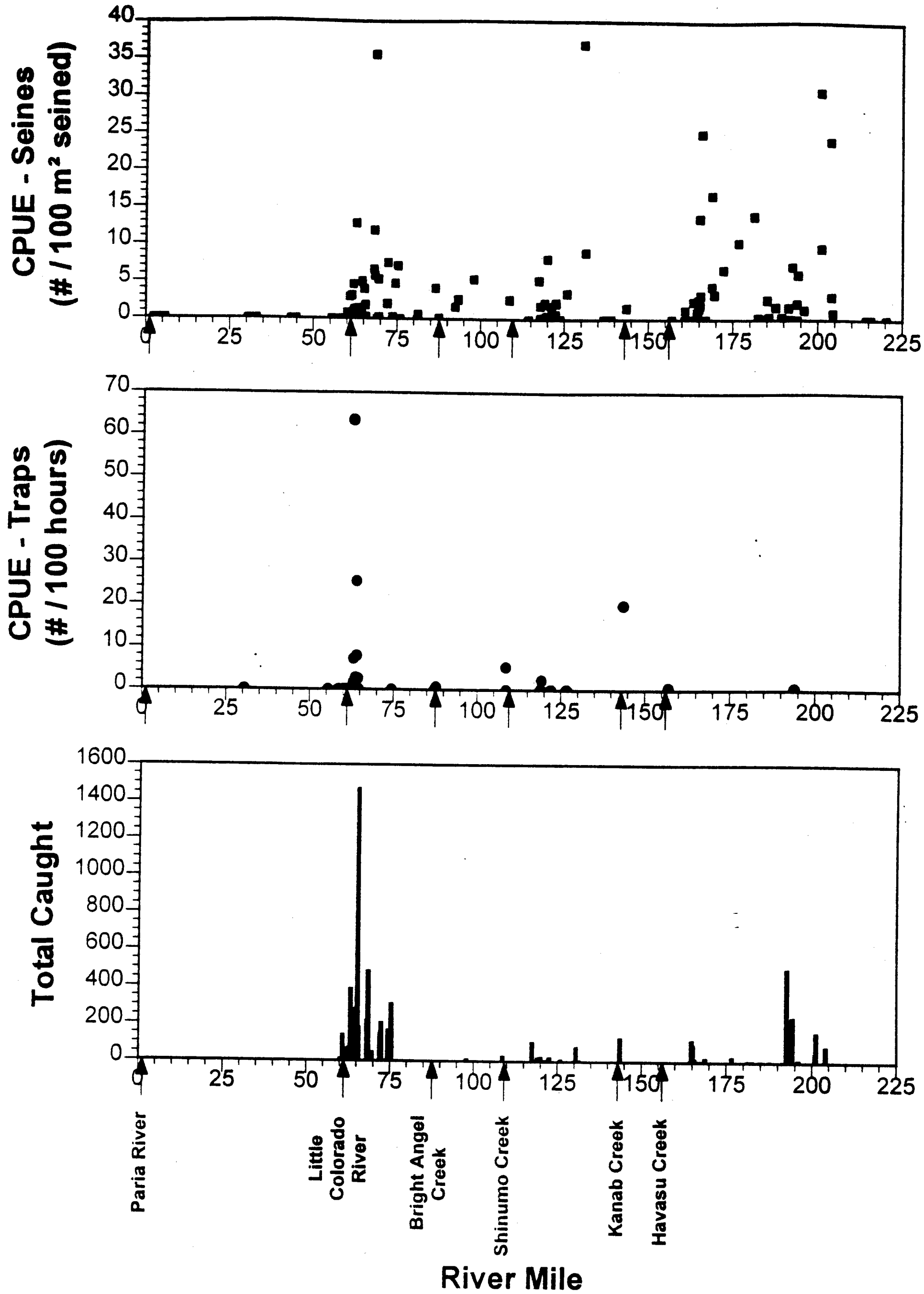

Fig. 13. CPUE of fathead minnow in seines (top) and traps (middle) and total number caught (bottom) at each river mile during AGFD sampling trips, Colorado River, Grand Canyon, 1991-94.

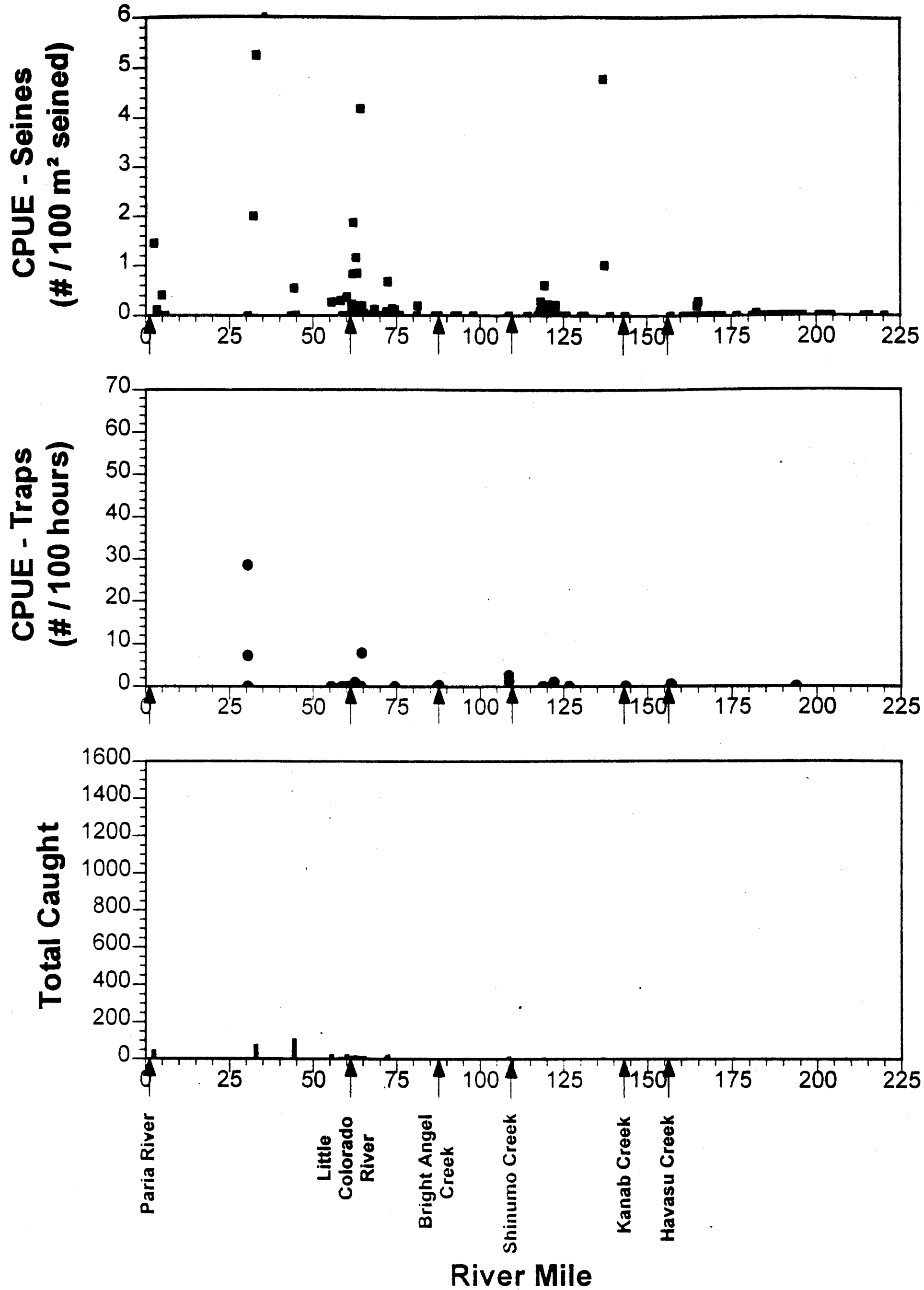

Fig. 14. CPUE of rainbow trout in seines (top) and traps (middle) and total number caught (bottom) at each river mile during AGFD sampling trips, Colorado River, Grand Canyon, 1991-94.

DISCUSSION

Native species dominated the catches in all reaches of the river and in all tributaries, except in Reach 30, where fathead minnows were the most common species collected. Rainbow trout and/or fathead minnows were also abundant in all reaches. Juveniles of all native fishes were, at least, locally and seasonally abundant in the mainstem Colorado River. Differences in the species composition of the catch among reaches is largely explained by the presence or absence of spawning areas for each species. Changes in composition of the catch among years was likely due to a combination of changes in year class strength and differences in gear selectivity.

Bluehead suckers were common below the LCR. They were the most common species found in Reach 40 and appear to spawn in large numbers in the LCR and Kanab and Havasu Creeks. These fish are also found in a disjunct population (separated from the mainstem Colorado River by a waterfall), along with speckled dace and rainbow trout, in Shinumo Creek (Allan 1993). Emigration from Shinumo Creek probably still occurs, but the waterfall prevents fish from migrating from the mainstem Colorado River to above the falls in Shinumo Creek. Prior to the closure of Glen Canyon Dam, this barrier was probably passable during spring floods, providing a large amount of spawning area to the mainstem component of these native fishes. It is also possible that other native species (e.g., humpback chub, flannelmouth sucker, razorback sucker, and Colorado squawfish) also migrated between the mainstem and Shinumo Creek to spawn, as well. A similar situation is found in Havasu Creek, where large numbers of bluehead and flannelmouth suckers spawn in the lower reach of Havasu Creek below a barrier falls. However, we have also captured juvenile bluehead suckers and speckled dace above these falls, although little sampling was conducted there. It is likely that this also represents a disjunct resident population that is a remnant from conditions before the Colorado River was regulated and the falls were not a barrier to spring spawning migrations. The percentage of the catch comprised of bluehead suckers remained low in Reach 20, probably because no spawning of this species is known or suspected to occur above the LCR. In Reach 30, the percentage of bluehead suckers in the catch was also fairly constant. However, in Reaches 40 and 50, the proportion of the catch comprised of bluehead suckers increased over the four years of this study. This is an indication that this species is reproducing and recruiting into the population.

Flannelmouth suckers were found below RM 44. We believe that juvenile fish found above the LCR were spawned in the warm springs near RM 30. It is also possible that some were spawned in the mainstem Colorado River above Lee's Ferry or in the Paria River, where concentrations of spawning adults are known to be found in the early spring. Although flannelmouth suckers have been observed spawning there, no evidence of successful spawning has been found above Lee's Ferry. However, Weiss (1993) found larval flannelmouth suckers in the Paria River in 1992 and we also found larvae there in 1994. However, it appears that few, if any of these fish survive the cold waters of the mainstem Colorado River to recruit into the spawning population. Backwaters are present in the mainstem and are available to these fish below the Paria River. However, we have not found any larval or juvenile flannelmouth suckers in the mainstem above RM 44, which suggests poor survival of these fish in the mainstem. In the summer, the Paria River warms to temperatures too excessive for flannelmouth suckers to remain there. Weiss (1993) found that the mean size of spawning adults in the Paria River in 1992 and 1993 was 53 mm longer than the mean length of spawning adults captured in 1981, possibly indicative of low recruitment into the adult population. However, flannelmouth suckers do spawn in the LCR, Kanab Creek, and Havasu Creek and possibly

Bright Angel and Shinumo Creeks. Overall, the percentage of the catch comprised of flannelmouth suckers remained relatively constant. The presence of large numbers of larval and juvenile flannelmouth suckers in these areas, especially in the later part of the study, is encouraging evidence that they appear to be maintaining their population in, at least, the lower part of the river.

Humpback chub were found immediately below the LCR, at RM 44.27, and sporadically at locations in the lower canyon. Successful spawning of humpback chub outside of the LCR was indicated by the capture of small individuals above and far below the LCR in both 1993 and 1994. Small fish would not likely be able to reach these locations if they were spawned in the LCR. Suttkus et al. (1976) found "young or small juvenile *Gila*" at RM 44, possibly the same backwater that we found juvenile humpback chub. The probable spawning area for these fish is a series of warm springs around RM 30, which may provide sufficiently warm water for incubation and early survival of larvae not swept downstream. Valdez and Masslich (1994) found larval humpback chub in these warm springs in July 1994. Suttkus et al. (1976), Suttkus and Clemmer (1977), and Maddux et al. (1987) reported evidence of potential spawning in the vicinity of Shinumo Creek. Maddux et al. (1987) also found immature chub downstream from Havasu Creek. There are several small congregations of adult humpback chub throughout the canyon (Valdez and Ryel 1995) which may find small spawning areas in the mouths of tributaries such as Shinumo, Kanab, and Havasu Creeks. Additionally, a series of warm springs below Lava Falls is another potential humpback chub spawning area. This evidence indicates that there are existing populations of humpback chub which may be benefitted by environmental manipulations. Further reductions in daily water level fluctuations may improve backwater suitability for larval fish. Providing warmer spring and/or summer water temperatures may allow mainchannel reproduction of native species.

The changes in the percentage of humpback chub in the catch between years is probably due to both changes in gear types used and reproductive success of these fish. A large year class of humpback chub was produced in 1993. Seventy-four percent of all of the humpback chub caught during this study were captured during that year. Nearly half of the humpback chub caught during this study were captured on Trip 19 (September 1993) after a monsoonal flood in the LCR. This strong year class of humpback chub may have been due to a late winter (1993) flood in the LCR followed by a long period of base flow. This flood may have scoured out spawning areas and may have been a cue for these fish to spawn. It is also possible that the flood may have removed some exotic predators (i.e., common carp and channel catfish) and exotic potential competitors (i.e., fathead minnow). The following steady flow of clear water probably allowed the LCR to warm early and stay warm, which probably increased productivity.

Speckled dace were found throughout the river and appear to be the most common species in the Colorado River, Grand Canyon. They were also the most common species in all tributaries, except the LCR. Since speckled dace are susceptible to capture by both minnow traps and seines, changes in the capture rate of this species may have been largely due to changes in river conditions.

Fathead minnows were the most common exotic species captured. They were common in the mainchannel below the LCR and in backwaters throughout the canyon. They were also found in all tributaries, being particularly common in the warm waters of Kanab Creek. They probably spawn in all tributaries and in mainstem backwaters. Fathead minnow eggs were found on a sonde placed in a backwater at RM 60.8L at the end of May. The catch of these fish was also probably influenced by the LCR flood in February 1993. The percentage of the catch composed of fathead minnows decreased in all reaches below the LCR from 1992 to 1993. Fathead minnows are probably not well adapted to cold water floods and may be easily flushed downstream, particularly under cold temperature conditions. Additionally, fathead minnows were the only species to be commonly found in backwaters during the winter months, indicating that they prefer colder quiet water to slightly warmer moving water. The populations of these fish could be very susceptible to control by managed flooding of the mainchannel in the late winter and early spring. However, the presence of these fish in every tributary and their enormous reproductive capacity means that any reductions in their populations will probably be short-lived.

Rainbow trout were the most common exotic species above the LCR, where the river is most often clear. Below the LCR, the river is frequently more turbid and rainbow trout appeared to be associated with tributaries, such as Bright Angel Creek and Shinumo Creek, in which they spawn (Maddux et al. 1987). Rainbow trout also spawn in the mainstem near Lee's Ferry, in Nankoweap Creek (Maddux et al. 1987), and may use other areas of the mainchannel above the LCR where they can find clean gravel of the appropriate size.

In summary, larval and juvenile fishes of the Colorado River, Grand Canyon, appear to be most often associated with known or suspected spawning areas for that species. Young fish, particularly humpback chub, may rear in the LCR. However, in most tributaries, larvae and juveniles appear to drift downstream soon after hatching to nearby backwaters where they rear until they are large enough to persist in the mainchannel.

Objective 3.2. Identify the temporal and spatial distribution patterns and movements of early life stages of fishes in the Little Colorado River and other tributaries.

This section addresses fish distribution in tributaries of the Colorado River, Grand Canyon. Extensive data were not collected for the Little Colorado River, which is discussed in detail in the Little Colorado River report. This section provides information on spawning periods, environmental conditions during spawning, and residence times of larval and juvenile fishes in these tributaries.

Objective 3.2.a. **Determine the timing and duration of reproductive activity for different fish species by the evaluation of otoliths and length-frequency distributions.**

METHODS

Collections of larval fishes were made in backwater, mainchannel, and tributary mouth habitats throughout the year using a variety of gear types (minnow traps, trap nets, dip nets, and seines). Length-frequency tables and histograms (1 cm length classes) were developed for each species, by month, to provide an index of when larval fish first appeared in the catch. Also, adults were captured in hoop nets set in tributary mouths, which provided additional information used to estimate the time of spawning for each species. Time of spawning was estimated by noting the timing of adult concentrations in the tributary mouths and the appearance of small fish (< 3 cm) in the catch from tributaries and the mainstem.

Growth rates of these species in the mainstem Colorado River is sporadic and will affect our ability to estimate spawning time. The amount of time spent in the warmer, more productive waters of the tributary or a backwater versus that spent in the cold, less productive water of the mainchannel greatly affects growth (Piper et al. 1982; Lupher and Clarkson 1994). Therefore, estimates of spawning time should not be considered to be exact.

RESULTS

Examination of length-frequency plots indicated that, although fish in the 0-9 mm and 10- 19 mm length classes were captured, fish were not fully recruited to these gear types until they reached 20-29 mm in total length. Adult captures in tributaries and the appearance of larval fish in collections indicated an extended period of spring spawning for bluehead suckers, flannelmouth suckers, and humpback chub. Speckled dace and fathead minnows appeared to spawn throughout the spring and summer. Other species were not captured in numbers sufficient enough to estimate spawning periods. Appendices 7-12 show the number of fish of each species caught in each length class on each trip.

Bluehead Sucker

Adult bluehead suckers were captured in the mouths of the LCR and Shinumo, Kanab, and Havasu Creeks as they ascended those streams to spawn in March, April, and May. Bluehead suckers in length classes 0, 1, and 2 cm were captured in the LCR in July, in Shinumo Creek in September, in Kanab Creek in May and April, and in Havasu Creek in April, May, and June. However, few juvenile bluehead suckers were captured in any of the tributaries, indicating that they quickly move out into the mainstem Colorado River after hatching. Larval bluehead suckers first entered the mainstem catch in April as 1 cm fish and were captured along with age 1 juveniles (Figure 15). In May, YOY became common and their modal size class was 2 cm. Bluehead sucker YOY continued to be caught through June, July, and August. No YOY bluehead suckers were captured during September. However, bluehead suckers from the 1 cm size class were captured in October and November and may represent a fall spawning period for these fish.

Flannelmouth Sucker

Adult flannelmouth suckers were captured in the mouths of the major tributaries from March through May (and even into June 1993 in Kanab Creek). Very few YOY flannelmouth suckers were captured in tributary mouths. One, flannelmouth sucker from the 1 cm size class was caught in Kanab Creek in June 1993 and 50 were caught in April 1994. Also, one flannelmouth sucker from the 1 cm size class and one from the 2 cm size class were captured in Havasu Creek in June 1993. However, large numbers of larval and juvenile flannelmouth suckers were found in backwaters in the mainstem samples (Figure 16). These first appeared in April as fish from the 1 cm size class and were captured simultaneously with age 1 flannelmouth suckers. Young-of-the-year flannelmouth suckers dominated the catch for the remainder of the year and continued to be captured through July.

Humpback Chub

Humpback chub spawn predominantly in the LCR. We captured a few adults in the mouth of the LCR in March, April, and July (refer to the Little Colorado River report for detailed information on spawning of humpback chub in the LCR). However, we have captured large numbers of YOY humpback chub in the mainstem below the LCR (Figure 17). Young-of-the-year (2-3 cm size classes) first appeared in March. These continued to appear in small numbers in April with the 1 cm size class fish being captured. Larger numbers of YOY humpback chub appeared in samples from May and YOY's dominated the catch of humpback chub from June through November. Humpback chub appear to be recruited into the population through July. However, growth of humpback chub in cold water can be extremely slow or they may not grow at all (Lupher and Clarkson 1994). Therefore, small fish captured in July may simply be fish that hatched early but moved into the mainstem soon after hatching and grew slowly.

Evidence of humpback chub spawning outside of the LCR was also discovered. Three small humpback chub, 22-30 mm were captured in a backwater at RM 44.27 in July 1993. Small humpback chub were consistently captured at this site throughout the remainder of 1993 and to a lesser extent in 1994. Small humpback chub (14-46 mm) were also found in Reach 50. Twenty-three small chub were captured between RM 185-208 and a single fish (23 mm) at RM 168.75. Both of these sites are distant enough from the LCR that it is unlikely that they were spawned in that tributary.

Speckled Dace

Speckled dace appear to spawn from May through October, and likely do so in both the mainstem and tributaries. Speckled dace in the 1 cm length class first appeared in the mainstem catch in May. Speckled dace <3 cm continued to be captured through November (Figure 18).

Fathead Minnow

Fathead minnows appear to spawn throughout the summer in both the tributaries and the mainstem. Fathead minnows < 2 cm were first captured in April and continued to be captured through September (Figure 19). Fathead minnow eggs were found attached to a datasonde set in a backwater just upstream from the LCR in late May.

Rainbow Trout

Rainbow trout are known to spawn in Nankoweap Creek and other downstream tributaries (Bright Angel Creek, Shinumo Creek, and Tapeats Creek), and in the mainchannel in the Lee's Ferry area (Maddux et al. 1987). They probably also spawn anywhere else that they can find suitable conditions, particularly clean gravel of the appropriate size. Rainbow trout 2-3 cm long were first captured in January. Young-of-the-year rainbow trout continued to be captured through the spring and summer until September (Figure 20). Spawning adults were not captured.

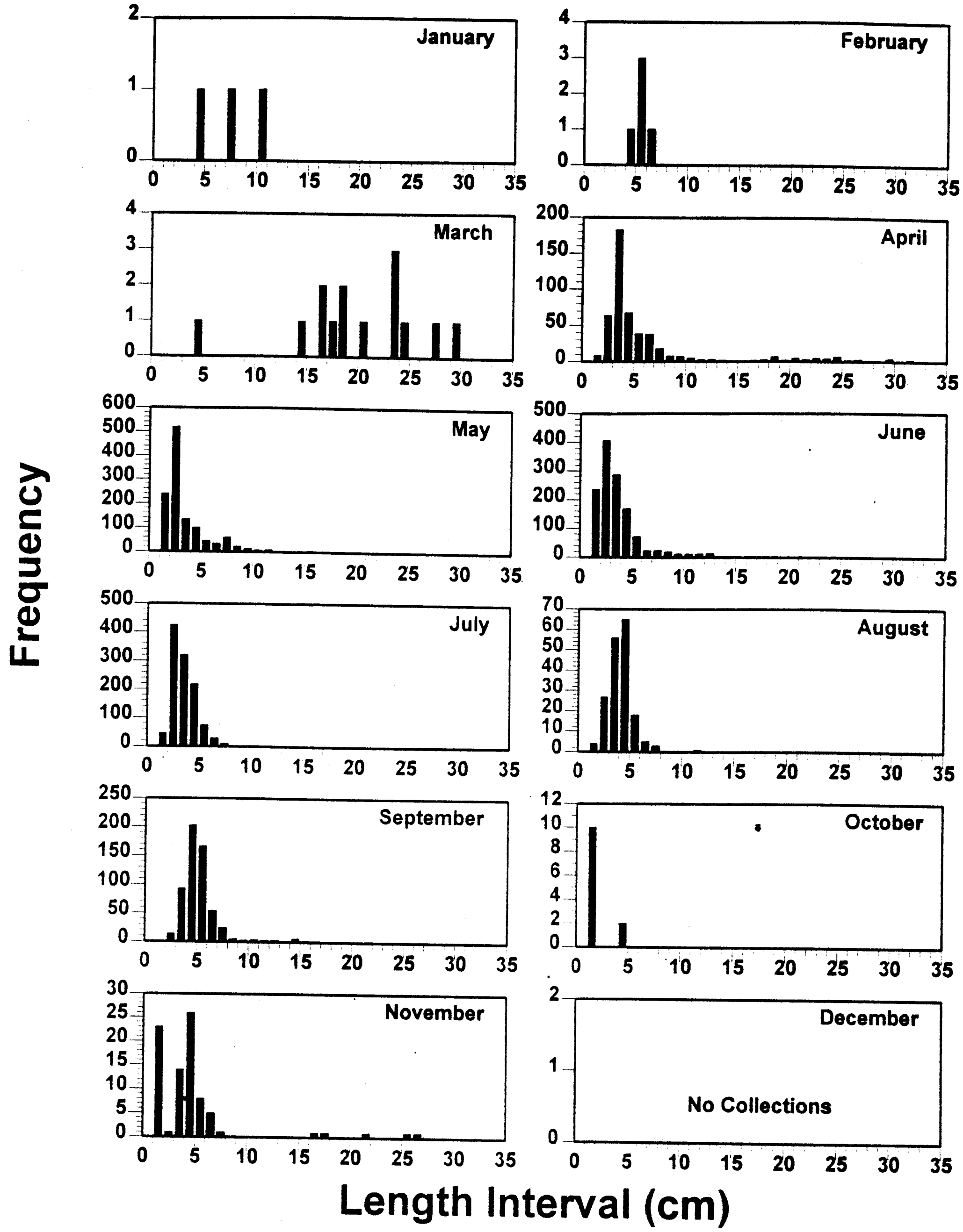

Fig. 15. Length frequency plots for bluehead suckers captured in each month in the Colorado River, Grand Canyon, 1991-94.

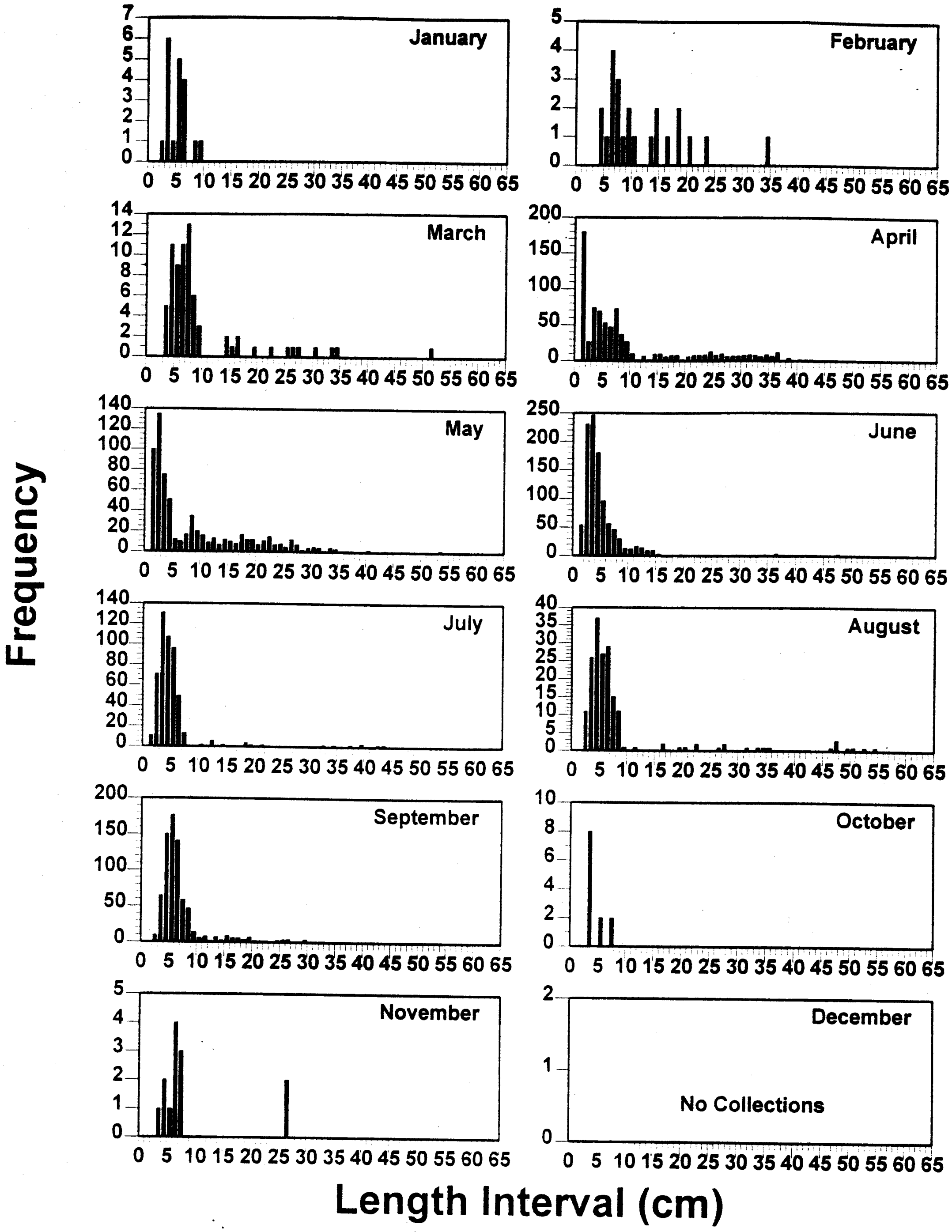

Fig. 16. Length frequency plots for flannelmouth sucker captured in each month in the Colorado River, Grand Canyon, 1991-94.

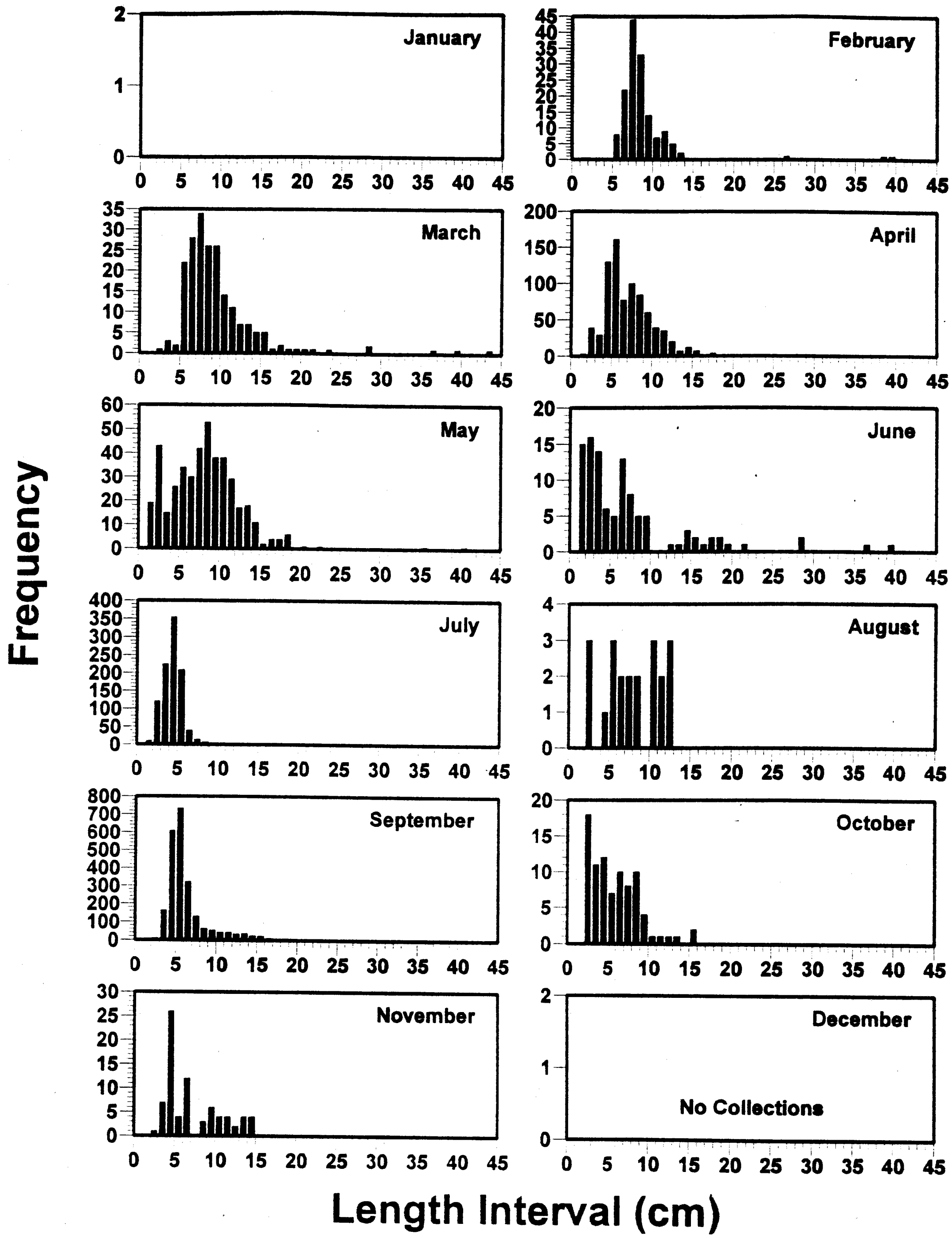

Fig. 17. Length frequency plots for humpback chub captured in each month in the Colorado River, Grand Canyon, 1991-94.

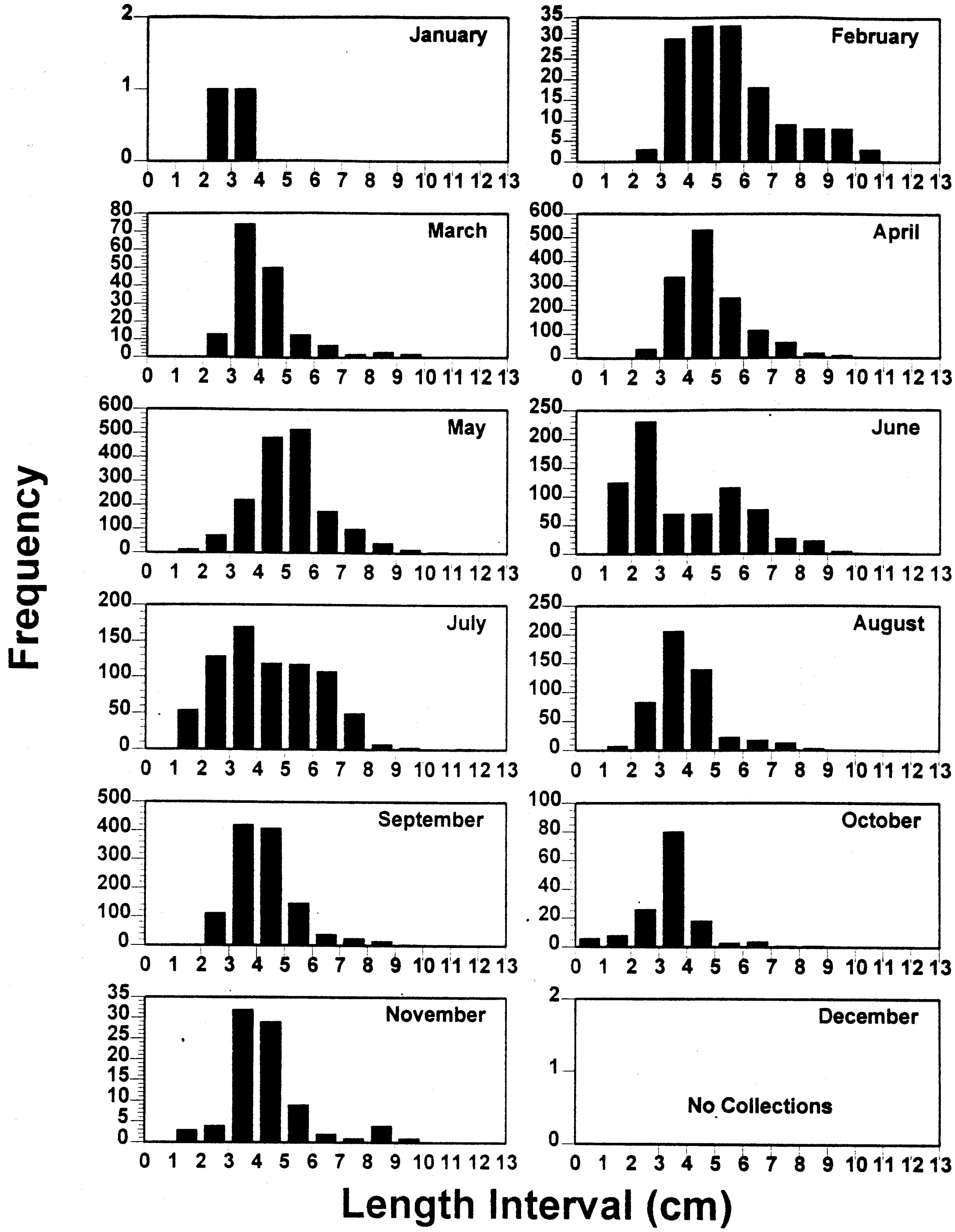

Fig. 18. Length frequency plots for speckled dace captured in each month in the Colorado River, Grand Canyon, 1991-94.

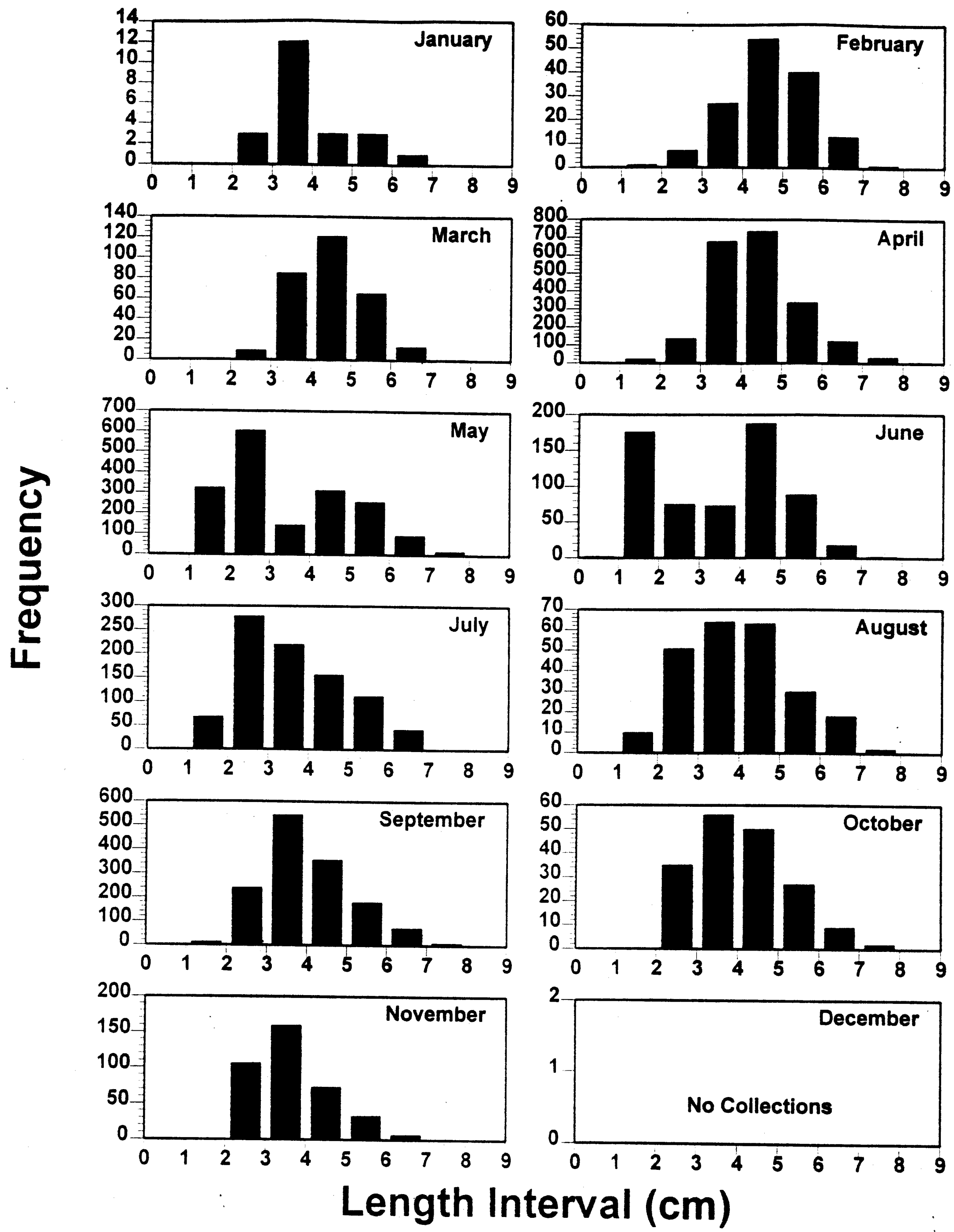

Fig. 19. Length frequency plots for fathead minnow captured in each month in the Colorado River, Grand Canyon, 1991-94.

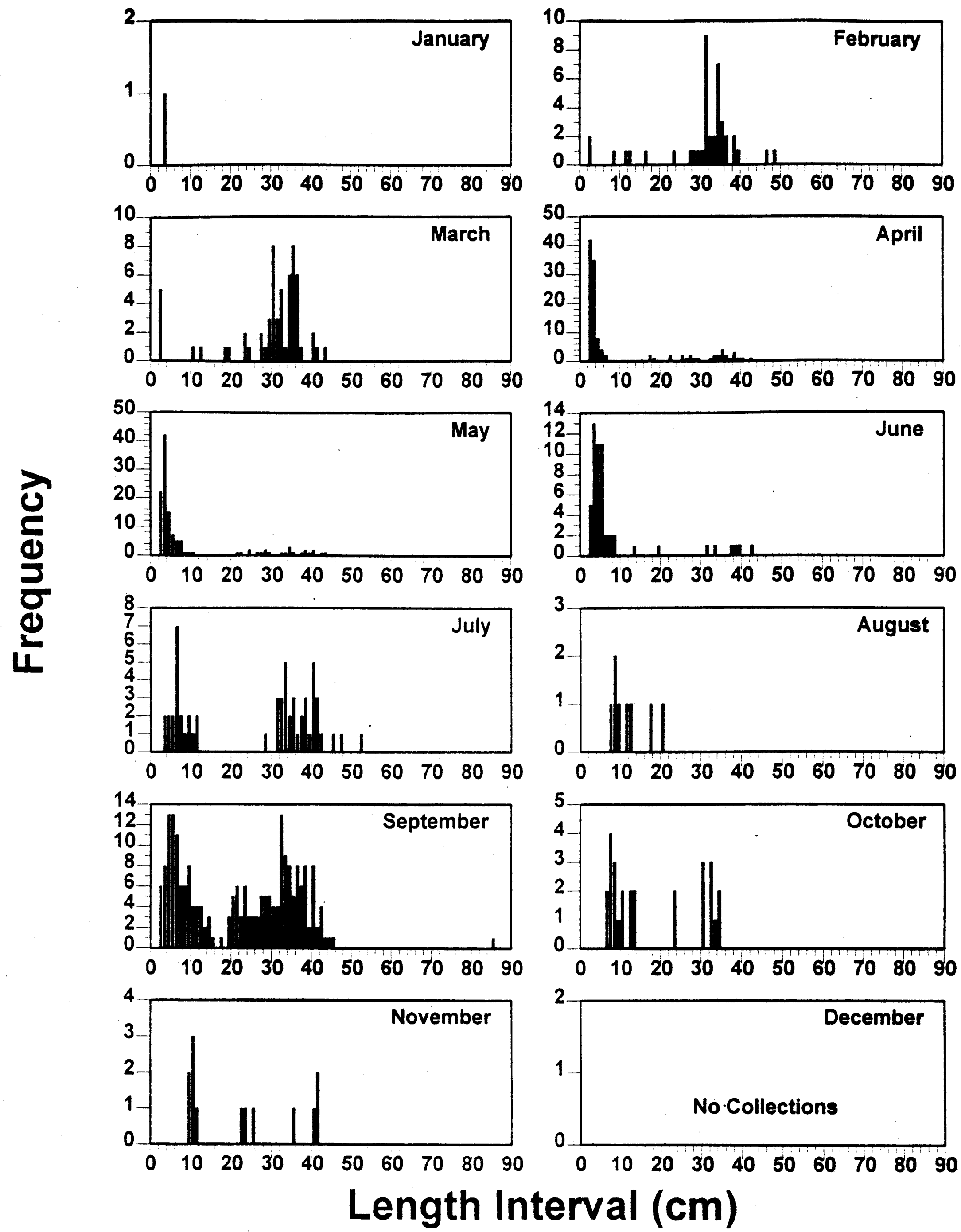

Fig. 20. Length frequency plots for rainbow trout captured in each month in the Colorado River, Grand Canyon, 1991-94.

DISCUSSION

Information from adult and larval captures indicate an extended period of spawning activity for all species. Precise determination of the time of spawning from these data was not possible, for any species, since no eggs and few newly hatched larvae were collected. Also, we did not sample extensively in the late winter and early spring and could have missed early spawning activity. Bluehead suckers, flannelmouth suckers, and humpback chub appear to spawn in the spring, from March through May in one or more of the major tributaries: Little Colorado River, Shinumo Creek, Kanab Creek, and Havasu Creek. The smaller species, speckled dace and fathead minnow, spawn later in the spring and throughout the summer. John (1963) found that spring and late summer flooding induced spawning in speckled dace. These fish likely spawn in both the tributaries and in backwaters of the mainstem Colorado River. Rainbow trout appear to have a protracted spawning period, as small YOY were found from March through September.

Bluehead suckers also appear to spawn in small tributaries, e.g., Clear Creek and Crystal Creek, and may spawn in the fall, as indicated by the collection of larvae in the 1 cm length class in October and November. One of these (13 mm) was caught in the mouth of Crystal Creek. The remainder were found in backwaters in the lower canyon, below Havasu Creek, the furthest known spawning area downstream. Crystal Creek is a very small tributary. Clear Creek is a small, perennial tributary where bluehead suckers have been observed in spring and early summer. If bluehead suckers spawn in these small streams, they may be able to use other small, seasonal tributaries for spawning, as well.

Flannelmouth suckers also spawn in the Paria River (Weiss 1993, AGFD 1994) and Bright Angel Creek (Otis 1994). Weiss found newly hatched flannelmouth sucker larvae in spring 1992. However, no flannelmouth suckers were found soon afterwards, indicating a quick dispersal from the stream. No flannelmouth sucker larvae were found by either Weiss or AGFD in 1993. We found larval flannelmouth suckers in the Paria River in 1994. Our data show very few larvae or juveniles in the tributaries but large numbers in backwaters in the mainstem Colorado River downstream from spawning tributaries. This indicates that these fish quickly leave the tributaries, possibly an adaptation to declining water quality conditions in spawning streams. The Paria River and Kanab Creek warm to excessively high temperatures (34°C in Kanab Creek in August) during the summer, making them inhospitable to fish. In Shinumo and Havasu Creeks, the presence of barrier falls a short distance from the mouth means that the fish have only a short length of stream available to them. Also, resident rainbow and brown trout, both of which are likely predators of young flannelmouth suckers (Valdez and Ryel 1995) are present in Shinumo Creek. Havasu Creek has large expanses of spawning gravel but little or no areas of slow moving water for rearing. Therefore, with the exception of the LCR, the tributaries of the Colorado River in Grand Canyon do not appear to be suitable for development of larval fish spawned from mainstem resident adults.

Our discovery of humpback chub spawning outside of the LCR in 1993 and 1994 is of great interest. The upstream site at RM 44.27 is 27.7 km and several large rapids upstream from the LCR. It is extremely unlikely that fish as small as 22 mm could travel that distance upstream through fast and turbulent water. The probable spawning area of these fish is a series of warm springs near RM 30. The backwater at RM 44.27 is the first backwater below the supposed spawning area that is reliably present. Valdez and Masslich (1994) found ripe adults in the area of the warm springs (RM

30) and on 14 July 1994 found "approximately 100 YOY humpback chub in the mouth of the spring at RM 30.7" (mean length of 24 mm). Using a growth equation from Muth (1990), Valdez and Masslich estimated the age of these fish to be approximately 36 days, making their date of hatching, approximately 8 June 1994. However, this curve was developed for fish raised at temperatures of 18-23°C and these wild humpback chub were captured in water of 16-19°C. Additionally, these wild chub were probably not receiving as much food as those in Muth's study. Therefore, it is likely that these fish are substantially older. Our captures of juvenile humpback chub at RM 44.27 show a wide range of sizes throughout the year with fish as small as 29 mm being captured in September 1993. Using this same method of assigning hatching dates, our data would indicate a protracted spawning period from June through August for fish collected at RM 44.27. This is possible, but growth in these fish is probably extremely slow and greatly variable, suggesting that the actual hatching dates may be earlier.

Small humpback chub were also collected in backwaters in Reach 50, approximately 200 km downstream from the LCR. It is possible that these fish drifted from the LCR, but they would have had to negotiate a large number of extremely turbulent rapids and avoid predation to have reached this area of the river. Again, using Muth (1990) as an estimator, these juvenile humpback chub have backcalculated hatching dates ranging from mid-April through mid-August. These dates may be possible, but probably also reflect slow and sporadic growth of these fish in the mainstem due to variable foraging success and changing water temperatures as fish move between habitats.

Estimating growth of humpback chub in Grand Canyon is a complex problem. The amount of time spent in backwaters or the LCR, where the water is warmer and food is more available greatly affects growth rates. Fish that leave the warm springs for a backwater may grow faster than those remaining in the area of the warm springs. The water temperature in the warm springs is warmer than the mainchannel but colder and probably has less available food than most backwaters. In any case, spawning of humpback chub in the warm springs probably occurs in May and June, as the water of the mainstem warms slightly with lengthening photoperiod and more direct exposure to the sun. Mean mainchannel temperatures increased from 8.44°C in March to 9.22°C in April and to 10.58°C in May, before leveling off for the remainder of the summer. This increase in temperature may have initiated spawning of humpback chub. An increase, then decrease in river discharge is also a spawning cue for humpback chub (Karp and Tyus 1990). However, weekday stream discharges in 1994 did not change substantially from March through early June.

In summary, humpback chub, bluehead sucker and flannelmouth sucker spawn in the spring and early summer with timing varying annually and with the spawning site. Humpback chub spawn in the Little Colorado River and probably in limited numbers outside of the LCR. Flannelmouth suckers spawn in the major tributaries of the Colorado River. Bluehead suckers spawn in the major tributaries and probably smaller tributaries. There is evidence of fall spawning of bluehead sucker in Crystal Creek and, possibly, other tributaries in the lower canyon. Speckled dace and fathead minnow spawn from late spring and into the early fall, probably as long as water temperatures remain sufficiently high.

Objective 3.4. Determination of the changes in environmental conditions in mainstream and tributary confluence zone native fish rearing habitats under different flow regimes.

As noted earlier, backwaters and tributary mouths are important native fish rearing areas in the Colorado River, Grand Canyon (Maddux et al. 1987; Angradi et al. 1992). This section of this report examines environmental conditions in these areas, as compared to the mainchannel, and their variation under different flow regimes.

Objective 3.4.a. **Measure water depth, temperature, pH, dissolved oxygen, specific conductance, and redox potential at each backwater, tributary mouth, and adjacent mainstream sites under a variety of controlled GCES Research flows and interim operations.**

METHODS

At each sampling site, a series of measurements were taken to characterize the habitat. The number of locations from which habitat data were recorded within each sampling site depended on the sampling protocol used. Data collected included all or some of the following: temperature (°C), turbidity (NTU), velocity (cm/s), dissolved oxygen (DO; mg/L), conductivity (µS/cm), pH, estimated stream discharge (m^3/s, cms), and flow stage. Flow stage indicated whether river discharge was ascending, descending, steady high (peak), or steady low (nadir). Temperature, DO, conductivity, and pH were measured using a Hydrolab H20. Turbidity was measured using a Mini 20 Spectrophotometer with a nephelometer attachment. Velocity was measured using a Marsh-McBirney Model 201D portable water current meter. The Little Colorado River and Bright Angel, Shinumo, Kanab, and Havasu Creeks were sampled several times throughout the year, but not necessarily on every trip. We usually sampled each tributary only once per trip, making it difficult to discern potentially important differences. Also, variation in the location of sampling within a tributary mouth may have affected results.

For both mainstem (mainchannel and backwater habitats) samples, MANOVA was used to test for differences in the habitat variables (temperature, turbidity, velocity, DO, and conductivity, between estimated discharge, flow stage, month, year, reach, and habitat. If a significant relationship was found for habitat, ANOVA was conducted to examine differences in the habitat variables between estimated discharge, flow stage, month, year, and reach in backwaters and mainchannel habitats, separately. Tributary analyses were conducted similarly: MANOVA tested significance differences in the habitat variables between tributary, month, year, estimated discharge, and flow stage. If differences were found between tributaries, separate ANOVA's were conducted to examine differences in the habitat variables in each tributary in relation to month, year, estimated discharge, and flow stage. The Ryan-Einot-Gabriel-Welch multiple F test (Day and Quinn 1989) was used to determine the source of significant differences found in ANOVA's. A regression of mainchannel water temperature vs. river mile was used to determine the rate of warming as the water flows downstream for each month. Statistical tests were considered to be significant at $\alpha=0.05$.

RESULTS

Mainstem

Mean mainstem (backwater and mainchannel) temperature, turbidity, DO, conductivity, and pH all changed significantly (P=0.0001) over the period of the study. Specific changes are discussed below.

Mainchannel temperatures warmed significantly (P=0.0004) as the water flowed downstream. The average rate of change was 1°C / 48.31 miles. This predicted rate of warming ranged from 1°C / 28.44 miles in June to 1°C / 273.07 miles in February. The regressions for January, October, and November were not significant ($P \geq 0.0937$). In January and November the regressions predicted cooling of the water.

Temperature

Mean overall temperature (°C) in the mainstem Colorado River (Figure 21) varied significantly by month (P=0.0001), year (P=0.0005), and reach (P=0.0001). Backwaters were significantly warmer than the mainchannel (P=0.0001). Mean temperature did not significantly vary with changes in estimated discharge (P=0.4150) and flow stage (P=0.1642).

In the mainchannel, temperature varied significantly with month (P=0.0001), reach (P=0.0001), year (P=0.0011), estimated discharge (P=0.0006), and flow stage (P=0.0035). Mainchannel water was warmer in August (14.67° C) than any other month. June (13.37° C), July (13.16° C), May (12.70° C), and September (12.63° C) were warmer than all months, except August. February (8.57° C) and January (8.60° C) were colder than all other months. Reach 50 (13.75° C) had significantly warmer water than the other reaches. Reach 40 (12.48° C) was warmer than Reaches 30 (10.64° C) and 20 (10.40° C), which were not significantly different. Mean mainchannel water temperature was warmer in 1991 (13.92° C) than the other three years. Mean water temperature at the time of sampling was warmer in 1994 (12.49° C) than 1992 (11.64° C) and 1993 (11.23° C) which were not different from each other. Mainchannel water was warmer under steady high or steady low flows than under descending or ascending flows.

In backwaters, mean temperature varied significantly among months (P=0.0001), reach (P=0.0001), and year (P=0.0328) but not with estimated discharge (P=0.4150) or flow stage (P=0.1642; Figure 21). Mean backwater temperature was warmer in August (16.75° C) than in all other months except May (15.56° C) and June (15.18° C). February (8.78° C) had the coldest mean water temperature in backwaters and October (11.40° C), March (11.42° C), and November (11.80°C) were colder than all other months, except February and April (12.50° C). Backwaters in Reach 50 (16.28° C) were warmer than all other reaches. Reach 40 (13.31° C) backwaters were warmer than those in Reaches 30 (12.44° C) and 20 (11.86° C), which were not different. The water in backwaters was significantly warmer in 1991 (16.67° C) than the other three years. In 1994 (14.59° C) backwaters were warmer than in 1992 (12.89° C) and 1993 (12.64° C) which were not different. The water in backwaters was warmer under steady high or steady low flows than under descending or ascending flows.

Turbidity

Mean turbidity (NTU) was not significantly different between mainchannel and backwaters (*P*=0.4966). Therefore, these data were pooled for further analyses. Mean turbidity in the mainstem Colorado River (Figure 22) varied significantly by month (*P*=0.0001), year (*P*=0.0001), and reach (*P*=0.0001). However, turbidity did not significantly vary by estimated discharge (*P*=0.0709) or flow stage (*P*=0.2162). Mean turbidity was higher in March (831 NTU) than any other month. In 1992, mean turbidity (601 NTU) was higher than in 1993 (249 NTU) and 1994 (25.4 NTU), although only 7 measurements were recorded in 1994 (no turbidity measurements were recorded in 1991). Mean turbidity in 1993 was also higher than in 1994. Reach 50 had a higher mean turbidity (342 NTU) than any other reach. Mean turbidity in Reach 20 (71.2 NTU) was lower than any other Reach. Mean turbidity in Reaches 30 (234 NTU) and 40 (174 NTU) were not different.

Dissolved Oxygen

Mean dissolved oxygen (mg/L) in the mainstem Colorado River (Figure 23) varied significantly by month (*P*=0.0004) and reach (*P*=0.0001) and mean DO in the mainchannel was significantly higher than in backwaters (*P*=0.0001). However, mean DO did not significantly vary by year (*P*=0.8241), estimated discharge (*P*=0.0853), or flow stage (*P*=0.7597).

In the mainchannel, mean DO varied significantly with month (*P*=0.0001) and reach (*P*=0.0001), but not by year (*P*=0.7475), estimated discharge (*P*=0.0777), or flow stage (*P*=0.9099). Mean DO was higher in November (11.40 mg/L) than in any other month and higher in October (10.85 mg/L) than in August (9.90 mg/L). Reaches 20 (10.87 mg/L) and 30 (10.65 mg/L) had higher mean DO levels in the mainchannel than Reaches 40 (10.37 mg/L) and 50 (10.24 mg/L).

In backwaters, mean DO also varied significantly by month (*P*=0.0001) and reach (*P*=0.0001) but not by year (*P*=0.9191), estimated discharge (*P*=0.8662), or flow stage (*P*=0.7033). In these sites, mean DO level was higher in November (10.77 mg/L) than in all other months except October (10.70 mg/L) and March (10.43 mg/L). Backwaters in Reach 20 (10.49 mg/L) had higher mean DO than all other reaches. Reach 30 (9.98 mg/L) had higher mean DO than Reach 50 (9.58 mg/L), but not higher than Reach 40 (9.84 mg/L).

Specific Conductance

Mean conductivity (μS/cm) in the mainstem Colorado River (Figure 24) varied significantly by month (*P*=0.0001), reach (*P*=0.0001), year (0.0001), estimated discharge (*P*=0.0011), and flow stage (*P*=0.0009). Mean conductivity was also significantly higher in backwaters than in the mainchannel (*P*=0.0231).

Mean conductivity in the mainchannel varied significantly between months (*P*=0.0001), reaches (*P*=0.0001), and years (*P*=0.0001), but not by estimated discharge (*P*=0.9358) or flow stage (*P*=0.3035). Mean conductivity was higher in April (1071 μS/cm) than in any other month. Mean conductivity in March (1000 μS/cm) was higher than any other month, except April. In July (786 μS/cm) mean conductivity in the mainchannel was significantly lower than any month except October (816 μS/cm) and November (826 μS/cm). Mean conductivity in Reaches 30 (958 μS/cm) and 50 (953 μS/cm) were higher than the other two reaches. Reach 20 (868 μS/cm) had lower mean conductivity in the mainchannel than all other reaches, including Reach 40 (916 μS/cm). Multiple comparisons did not reveal any differences in mean conductivity between years (probably due to variation in sample sizes between years).

Backwater mean conductivity also varied significantly with month (P=0.0001), reach (P=0.0001), and year (P=0.0001), but not estimated discharge (P=0.4195) or flow stage (P=0.7715). April (1071 µS/cm) had a higher mean conductivity than all other months. Mean conductivity in March (1000 µS/cm) was higher than all other months, except April. October (791 µS/cm) and July (797 µS/cm) had lower mean conductivities than all other months. Mean conductivity in Reach 50 (955 µS/cm) was higher than all other reaches except Reach 30 (943 µS/cm). Mean conductivity in Reach 20 (880 µS/cm) was lower than that of all other reaches. Reach 40 (917 µS/cm) was significantly different from all others, except Reach 30. Mean backwater conductivity in 1994 (872 µS/cm) was lower than 1992 (975 µS/cm) and 1993 (942 µS/cm). No specific conductance readings were taken in 1991.

pH

Mean pH in the mainstem Colorado River (Figure 25) varied significantly by month (P=0.0001) and reach (P=0.0001), and was significantly higher in backwaters than in the mainchannel (P=0.0001). Mean pH did not significantly vary by year (P=0.4451), estimated discharge (P=0.1979), or flow stage (P=0.4232).

Mean pH in the mainchannel varied significantly by month (P=0.0001), reach (P=0.0001), estimated discharge (P=0.0001), and flow stage (P=0.0418). Mean pH was lower in September (7.91) and October (8.00) than all other months. Mean pH in Reaches 50 (8.33) and 40 (8.31) were higher than in the other two reaches. Reach 30 (8.11) had a higher mean pH than Reach 20 (7.87). Multiple comparisons showed no difference in pH between flow stages at α=0.05.

Backwater mean pH also varied with month (P=0.0001), reach (P=0.0001), estimated discharge (P=0.0001) and flow stage (P=0.0040), but not year (0.9776). Mean pH in August (8.30), July (8.25), May (8.24), and June (8.21) were higher than those in October (7.95), September (8.00), and November (8.02). Reaches 40 (8.32) and 50 (8.27) had higher mean pH levels than those of the other two reaches. Mean pH in Reach 20 (8.01) was lower than in Reach 30 (8.16). Mean pH was higher under steady high flows (8.30) than under steady low flows (8.02).

Velocity

Mean water velocity (cm/s) of sampling sites in the mainstem Colorado River (Figure 26) varied significantly by year (P=0.0030) and estimated discharge (P=0.0484), and was significantly higher in the mainchannel than in backwaters (P=0.0001). Mean velocity did not significantly vary by month (P=0.4131), reach (P=0.1976), or flow stage (P=0.2092).

In the mainchannel, mean velocity of the sampling sites did not significantly change by reach, month, year, estimated discharge, or flow stage (P=0.0633). No further analyses were conducted.

In backwaters, mean velocity changed significantly with month (P=0.0091), year (P=0.0378), and estimated discharge (P=0.0430) but not by reach (P=0.3081) or flow stage (P=0.3845). Mean velocity of backwaters sampled in August (6.78 cm/s) was higher than those sampled in May (3.50 cm/s), October (3.32 cm/s), July (3.29 cm/s), and February (2.00 cm/s). Multiple comparisons did not show any differences in mean velocity between years.

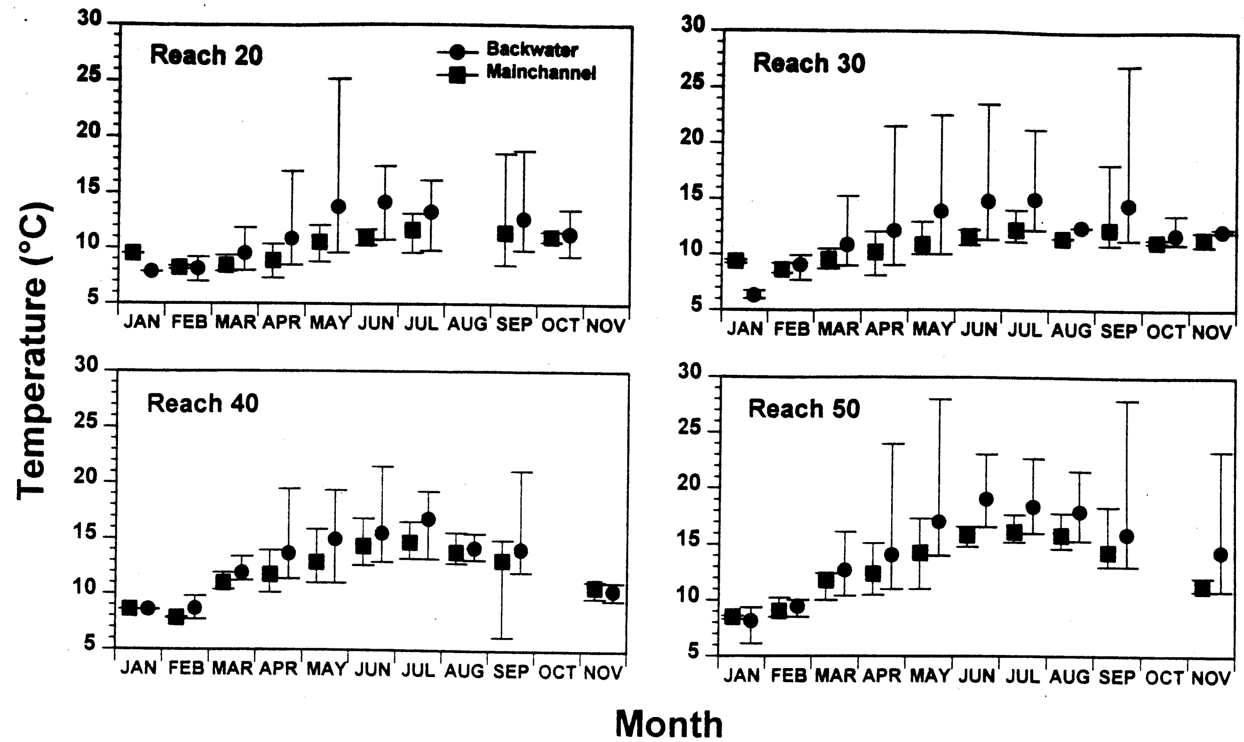

Fig. 21. Mean, minimum, and maximum temperature (° C) recorded in backwaters and mainchannel by month in Reaches 20, 30, 40, and 50 of the Colorado River, Grand Canyon, 1991-94.

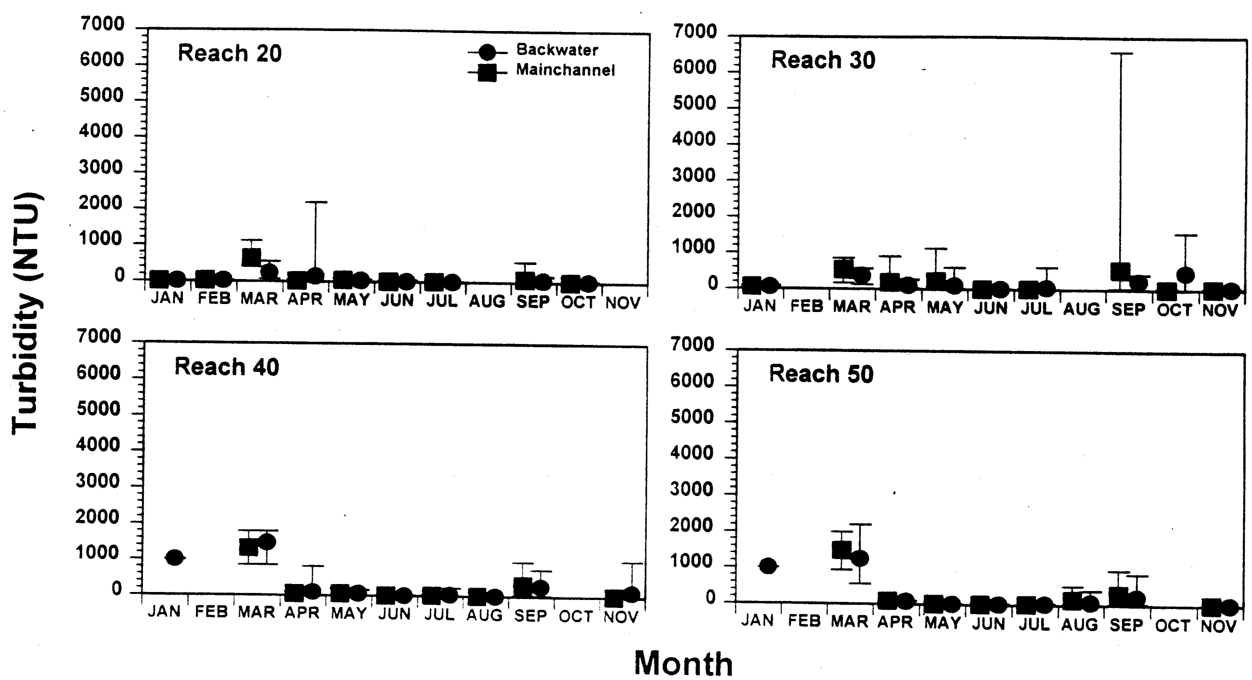

Fig. 22. Mean, minimum, and maximum turbidity (NTU) recorded in backwaters and mainchannel by month in Reaches 20, 30, 40, and 50 of the Colorado River, Grand Canyon, 1991-94.

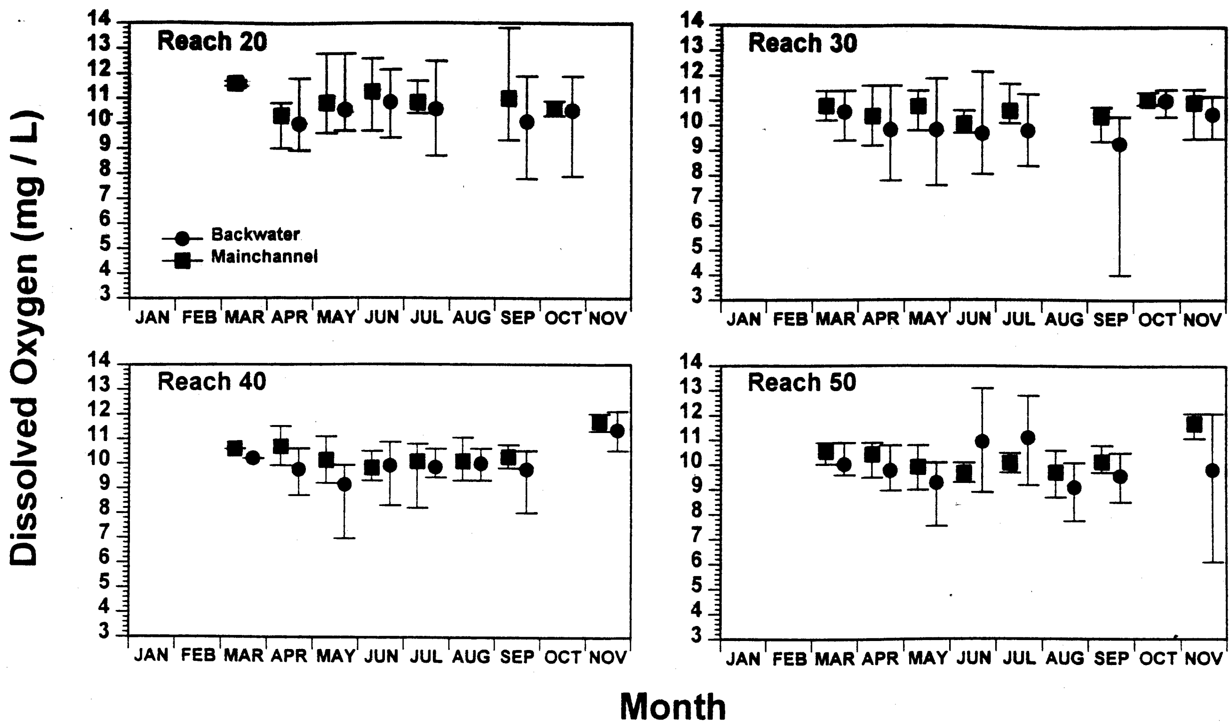

Fig. 23. Mean, minimum, and maximum dissolved oxygen (mg/L) recorded in backwaters and mainchannel by month in Reaches 20, 30, 40, and 50 of the Colorado River, Grand Canyon, 1991-94.

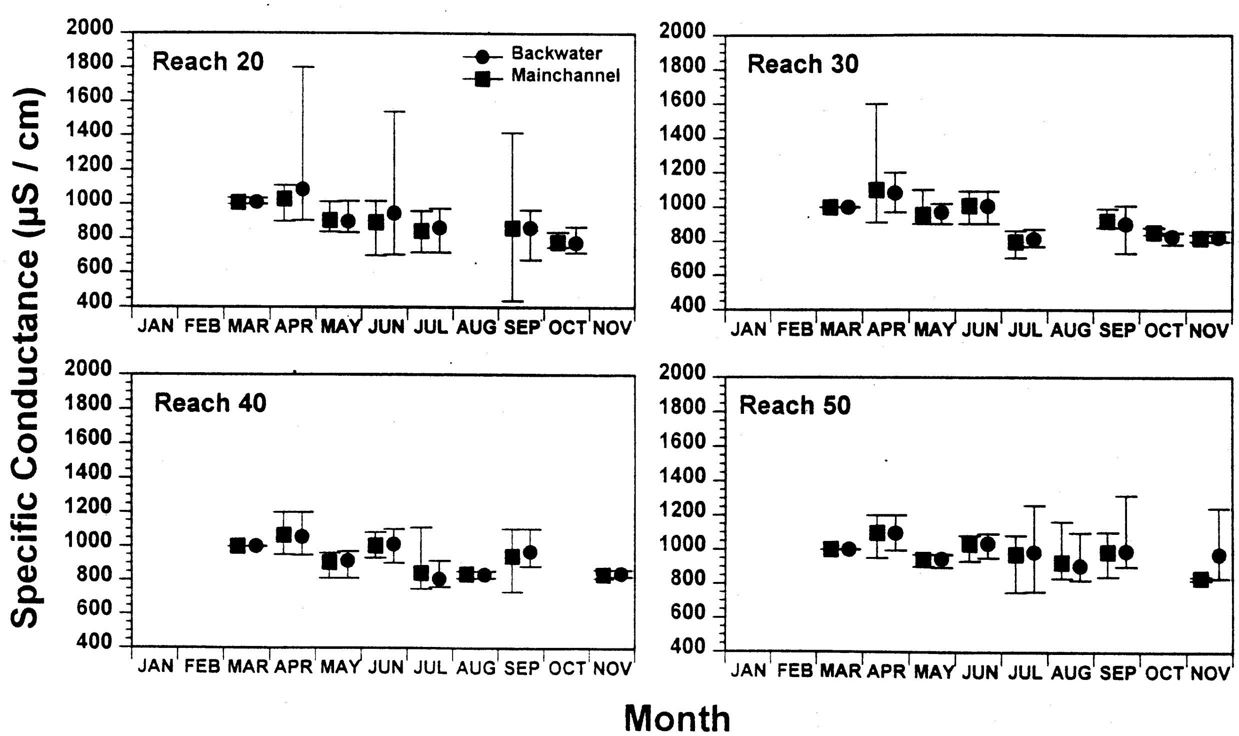

Fig. 24. Mean, minimum, and maximum specific conductance (μS / cm) recorded in backwaters and mainchannel by month in Reaches 20, 30, 40, and 50 of the Colorado River, Grand Canyon, 1991-94.

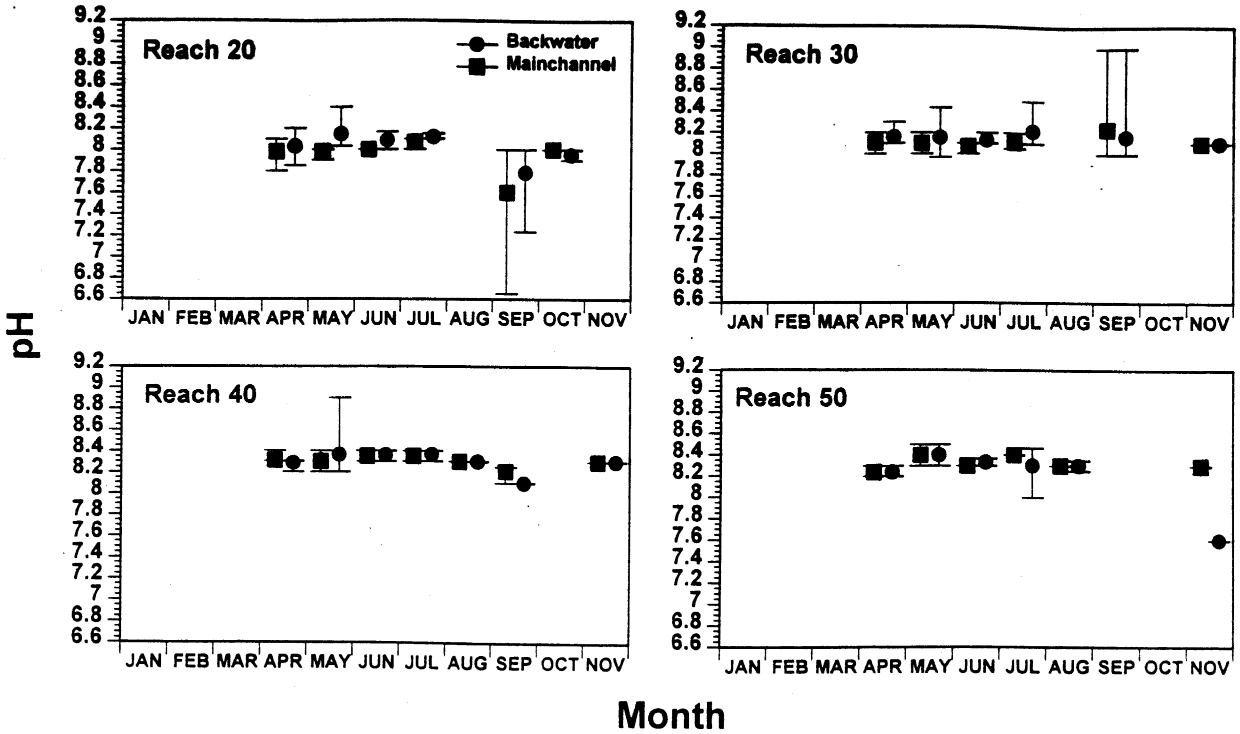

Fig. 25. Mean, minimum, and maximum pH recorded in backwaters and mainchannel by month in Reaches 20, 30, 40, and 50 of the Colorado River, Grand Canyon, 1991-94.

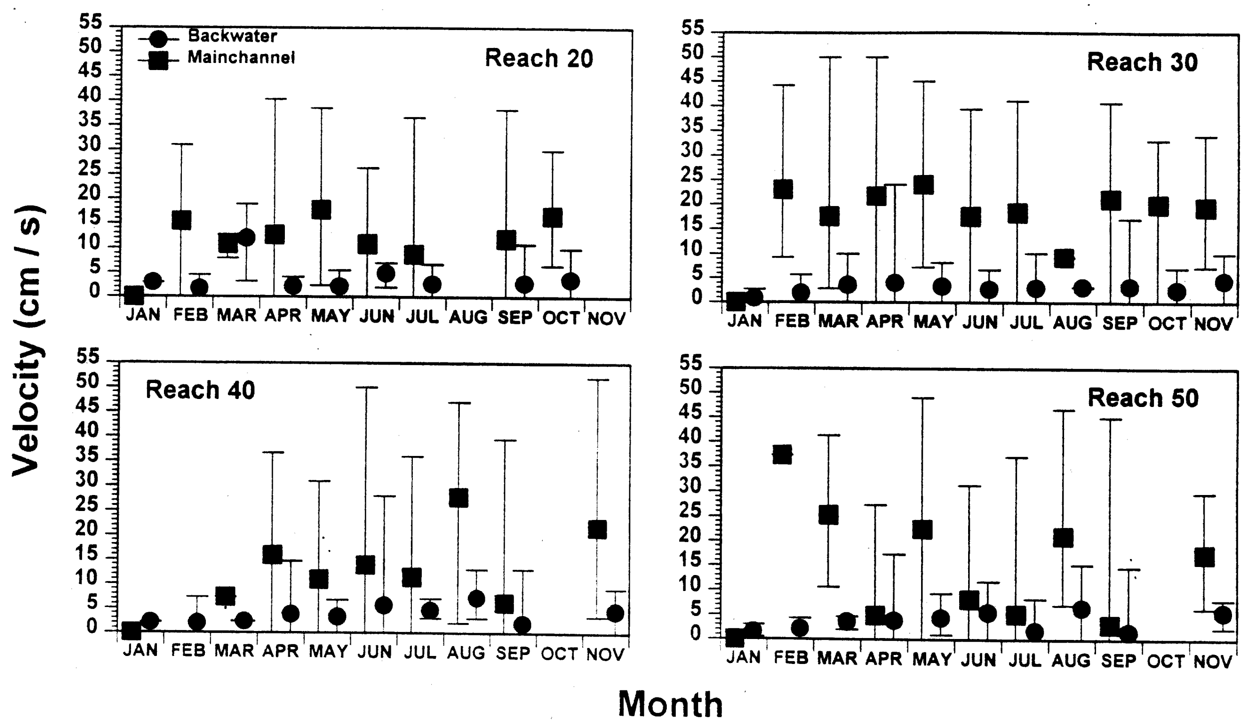

Fig. 26. Mean, minimum, and maximum velocity (cm / s) recorded in backwaters and mainchannel by month in Reaches 20, 30, 40, and 50 of the Colorado River, Grand Canyon, 1991-94.

Tributaries

In the tributaries, temperature, turbidity, dissolved oxygen, and conductivity all changed significantly over the sampling period ($P \leq 0.0198$). However, pH did not vary significantly (P=0.9931).

Temperature

Mean temperature (° C) in the tributaries (Figure 27) varied significantly by month (P=0.0001) and tributary (P=0.0064). However, mean temperature in the tributaries did not significantly vary by year (P=0.2566) or estimated discharge (P=0.6809). Mean temperature in Kanab Creek (21.72° C) was warmer than all other tributaries, except Havasu Creek (19.36° C). Mean temperatures in the other tributaries ranged from 17.72-18.13° C.

Mean temperature at time of sampling in LCR did not significantly change (P=0.3799). Mean temperature in Bright Angel Creek was significantly (P=0.0011) lower in January (6.33° C) than during all other months (14.25-19.65° C). Mean temperature at time of sampling in Bright Angel Creek did not vary between years (P=0.1930). Mean temperature in Shinumo Creek was significantly higher (P=0.0001) in August (20.46° C), July (19.37° C), and September (18.68° C) than in January (5.10° C), February (7.60° C), April (10.70° C), and March (10.73° C). Mean temperature in Shinumo Creek did not vary between years. In Kanab Creek, mean temperature in August (25.92° C) was significantly (P=0.0001) higher than all other months. Mean temperatures ranged from 16.91-20.27° C and were significantly lower in January (7.25° C), February (9.20° C), November (10.71° C), and March (12.58° C) than all other months. In 1994 mean temperature in Kanab Creek (20.83° C) was significantly (P=0.0010) higher than 1991-1993. Mean temperature in 1991 (12.92° C) was significantly lower than in 1993 (16.35° C), but not different from 1992 (15.20° C). Mean temperature in Havasu Creek was significantly higher (P=0.0001) in July (22.95° C) than in any other month. August (20.90° C) and May (20.24° C) had higher mean temperatures than all other months except July. Mean temperature in November (14.3° C) was lower than all other months. In 1994 mean temperature at time of sampling (20.74° C) was significantly higher (P=0.0001) than in 1993 (17.47° C).

Turbidity

Mean turbidity (NTU) in the tributaries (Figure 28) varied significantly by month (P=0.0001), year (P=0.0001), and tributary (P=0.0001). LCR had a higher mean turbidity (2181 NTU) than all other streams. Mean turbidity in Kanab Creek (56 NTU) was higher than all other streams (5-16 NTU), except LCR.

Mean turbidity at time of sampling in LCR varied significantly by month (P=0.0001) but not with year (P=0.0957). Mean turbidities for all months were significantly different: September (6600.0 NTU), March (3399.3 NTU), April (1106.7 NTU), and July (4.8 NTU). Mean turbidity in Bright Angel Creek (P=0.4604) and Shinumo Creek (P=0.2106) at time of sampling did not significantly change. Mean turbidity in Kanab Creek was significantly higher in March (4520 NTU) than in all other months (3-280 NTU). There were no significant differences in turbidity among years in Kanab Creek (P=0.8917). Mean turbidity at time of sampling in Havasu Creek was significantly higher (P=0.0474) in November (18 NTU) than in June (2 NTU). Mean turbidity in Havasu Creek did not significantly vary between years (P=0.2639).

Dissolved Oxygen

Mean dissolved oxygen (mg/L) in the tributaries (Figure 29) varied significantly by year (*P*=0.0034) and tributary (*P*=0.0050). However, mean DO did not vary by month (*P*=0.0970). Mean DO was lower in LCR (7.00 mg/L) than any other tributary (8.30-9.47 mg/L).

Mean DO in LCR was significantly higher (*P*=0.0202) in 1993 (9.34 mg/L) than in 1994 (4.53 mg/L), although only one measurement was recorded for 1994. Mean DO in the LCR did not vary by month (*P*=0.1495). Mean DO at time of sampling in Bright Angel Creek (*P*=0.7682) and Shinumo Creek (*P*=0.0755) did not significantly change among months. Mean DO in Kanab Creek at time of sampling was significantly higher (*P*=0.0019) in September (9.03 mg/L) and April (8.84 mg/L) than in June (7.20 mg/L) and August (7.60 mg/L). Multiple comparisons of mean DO in Kanab Creek showed no significant variation among years ($P \geq 0.05$). Mean DO at time of sampling was significantly higher (*P*=0.0002) in November than any other month. Mean DO in July (8.10 mg/L) was significantly lower than any other month except April (8.60 mg/L). Mean DO in Havasu Creek did not significantly vary between years (*P*=0.0870).

Specific Conductance

Mean conductivity (µS/cm) in the tributaries (Figure 30) varied significantly with month (*P*=0.0001), year (*P*=0.0001), and tributary (*P*=0.0001). Mean conductivity was higher in LCR (2920 µS/cm) than all other tributaries. Kanab Creek (1213 µS/cm) had the second highest and Havasu Creek (670 µS/cm) had the third highest mean conductivity. Shinumo (350 µS/cm) and Bright Angel (303 µS/cm) Creeks were the lowest and not significantly different.

Mean conductivity at time of sampling in LCR (*P*=0.0604), Bright Angel Creek (*P*=0.6554) and Shinumo Creek (*P*=0.2475) did not significantly change. Mean conductivity in Kanab Creek was significantly higher (*P*=0.0001) in April (1728 µS/cm) than in all other months (960-1199 µS/cm). Mean conductivity was also significantly higher (*P*=0.0003) in 1993 (1404 µS/cm) than in 1994 (1061 µS/cm) or 1992 (1000 µS/cm), which were not significantly different. In Havasu Creek, mean conductivity was significantly higher (*P*=0.0007) in April (720 µS/cm) than in all other months (610-630 µS/cm) except June (710 µS/cm) and May (699 µS/cm). There was no significant difference in conductivity in Havasu Creek between years (*P*=0.3091).

pH

The MANOVA for pH in the tributaries (Figure 31) showed no significant (*P*=0.9931) differences. Therefore, no further analyses were conducted.

Velocity

Mean velocity of the sampling sites in the tributaries (Figure 32) varied by year (*P*=0.0043) and tributary (*P*=0.0224), but not with month (*P*=0.3601). Velocity at sampling sites in Bright Angel Creek (32.0 cm/s) were higher than those in Kanab Creek (6.8 cm/s). Mean velocities in the other tributaries ranged from 16.2-24.0 cm/s.

No significant differences were found in mean velocity at sampling sites in LCR (*P*=0.7700), Bright Angel Creek (*P*=0.1232), Shinumo Creek (*P*=0.4315), or Havasu Creek (*P*=0.3720). Mean velocity at sampling sites in Kanab Creek was significantly higher (*P*=0.0001) in September (55 cm/s) than in all other months (4.3-7.2 cm/s). Mean velocity did not significantly vary among years in Kanab Creek (P=0.6532).

DISCUSSION

Since the closure of Glen Canyon Dam, conditions in the Colorado River in Grand Canyon have dramatically changed. Specifically, changes in water temperature and turbidity have great potential for impacting native fishes. Due to hypolimnial releases from Glen Canyon Dam, water temperatures in the Colorado River, Grand Canyon, have become constantly cold with little seasonal fluctuation. Summer temperatures at Lee's Ferry are now an average of 11° C colder than pre-dam conditions (Stanford and Ward 1991). Backwaters and tributary mouths offer some refuge from these cold temperatures. However, fluctuating flows, that are a normal part of dam operations, moderate backwater warming by flushing and/or inundating these habitats (Kennedy 1979). Mainstem water temperatures did warm as the water traveled downstream from Lee's Ferry to Diamond Creek. We found that water temperature changed as much as 1° C per 28.44 miles traveled downstream, in June. This means that by the time the river reaches Diamond Creek in June, mainchannel temperatures are only approximately 17.5° C, and still have not reached the preferred temperature (21.0-24.4° C) for juvenile (80-120 mm) humpback chub (Bulkley et al. 1982). No mainstem (including backwaters) monthly mean temperature reached these preferred temperatures. The only mean temperatures reaching this level were in Havasu Creek (July) and Kanab Creek (August). Kanab Creek in August reached as high as 34° C, too warm for any native fish in the Grand Canyon.

The timing of the seasonal temperature cycle has also changed. Pre-dam high temperatures coincided with low flows in July and August. Now, flows are highest during the later summer months due to increased demands for electricity. High flows of cold water do not warm as quickly, keeping mainstem water temperature cold throughout the canyon, even during July and August when air temperature can exceed 50° C. Conversely, backwaters warm in a more seasonal manner. However, since they are affected by mainchannel temperatures they rarely reach preferred temperatures for humpback chub, especially in the upstream reaches where humpback chubs are most commonly found. Our findings were similar to that of Maddux et al. (1987), who demonstrated that backwater habitats are benefitted by decreasing fluctuation of discharges. Decreased exchange between mainchannel and backwaters allows for an increase in the warming of the backwater (Kennedy 1979). Hoffnagle *(in review)* found that both the mainchannel and backwaters warmed significantly under a steady flow regime as compared to a fluctuating flow regime. Appendix 13 provides further discussion of the effects of steady vs. fluctuating flows on temperature and water quality of backwaters.

Turbidity in the Colorado River, Grand Canyon, is now mostly dependent upon input of sediments from the Paria and Little Colorado Rivers (Cole and Kubly 1976; Andrews 1991). Maddux et al. (1987) found turbidity levels to increase with distance downstream from the dam when either the Paria or Little Colorado Rivers were discharging above base flow. Yard et al. (1993) reported increased light attenuation in the Colorado River with distance downstream from the dam.

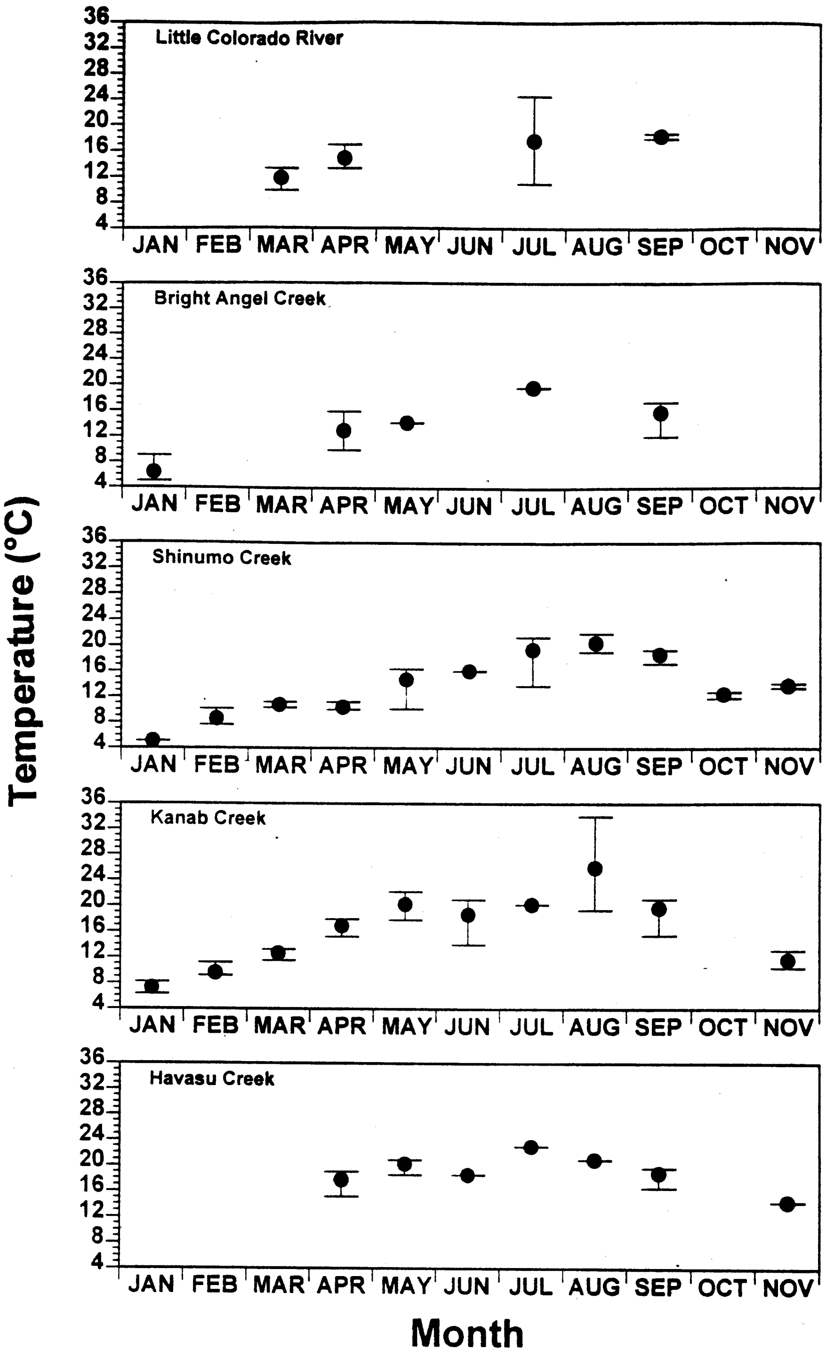

Fig. 27. Mean, minimum, and maximum temperature (° C), by month, recorded during sampling in the mouths of Little Colorado River, Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek, Grand Canyon, 1991-94.

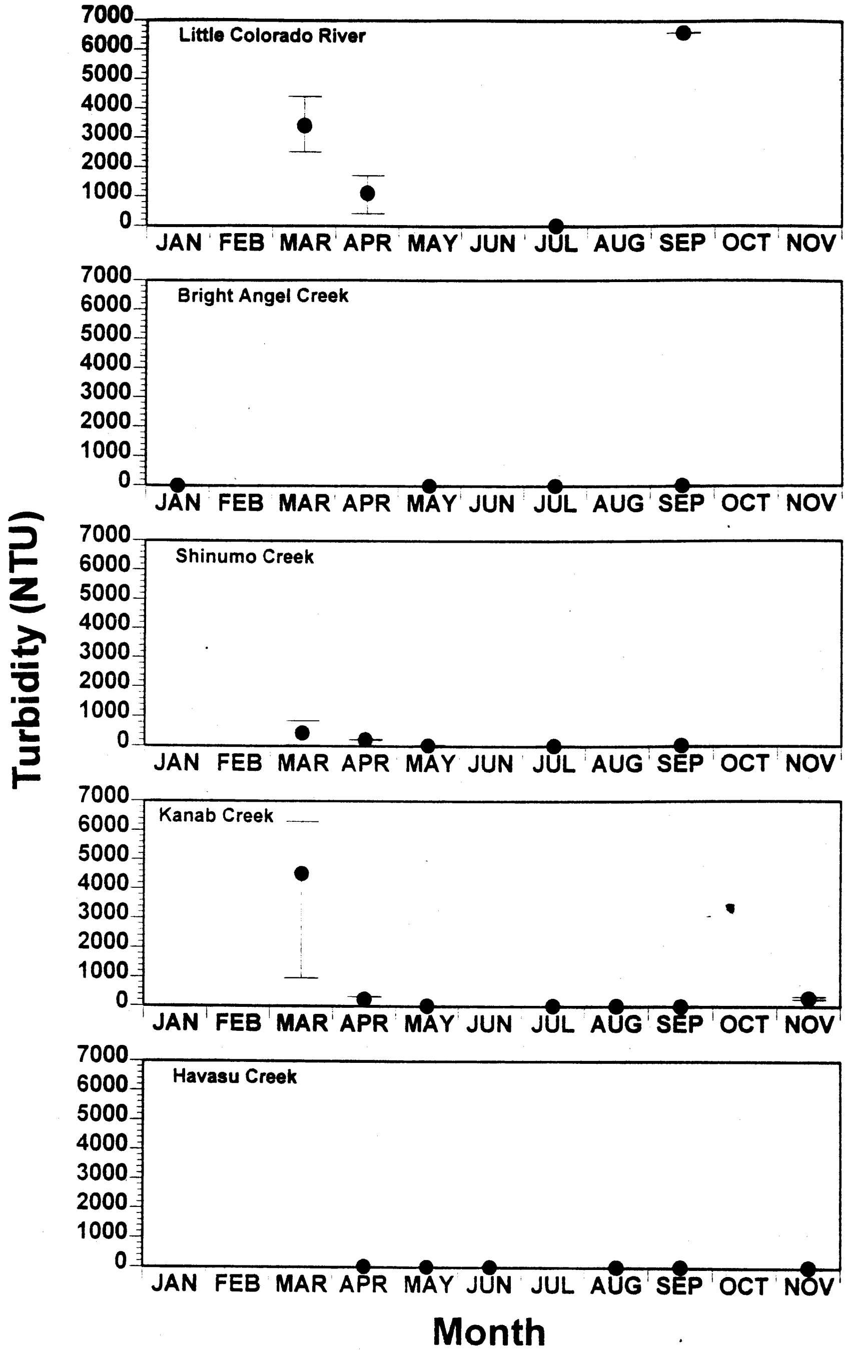

Fig. 28. Mean, minimum, and maximum turbidity (NTU), by month, recorded during sampling in the mouths of Little Colorado River, Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek, Grand Canyon, 1991-94.

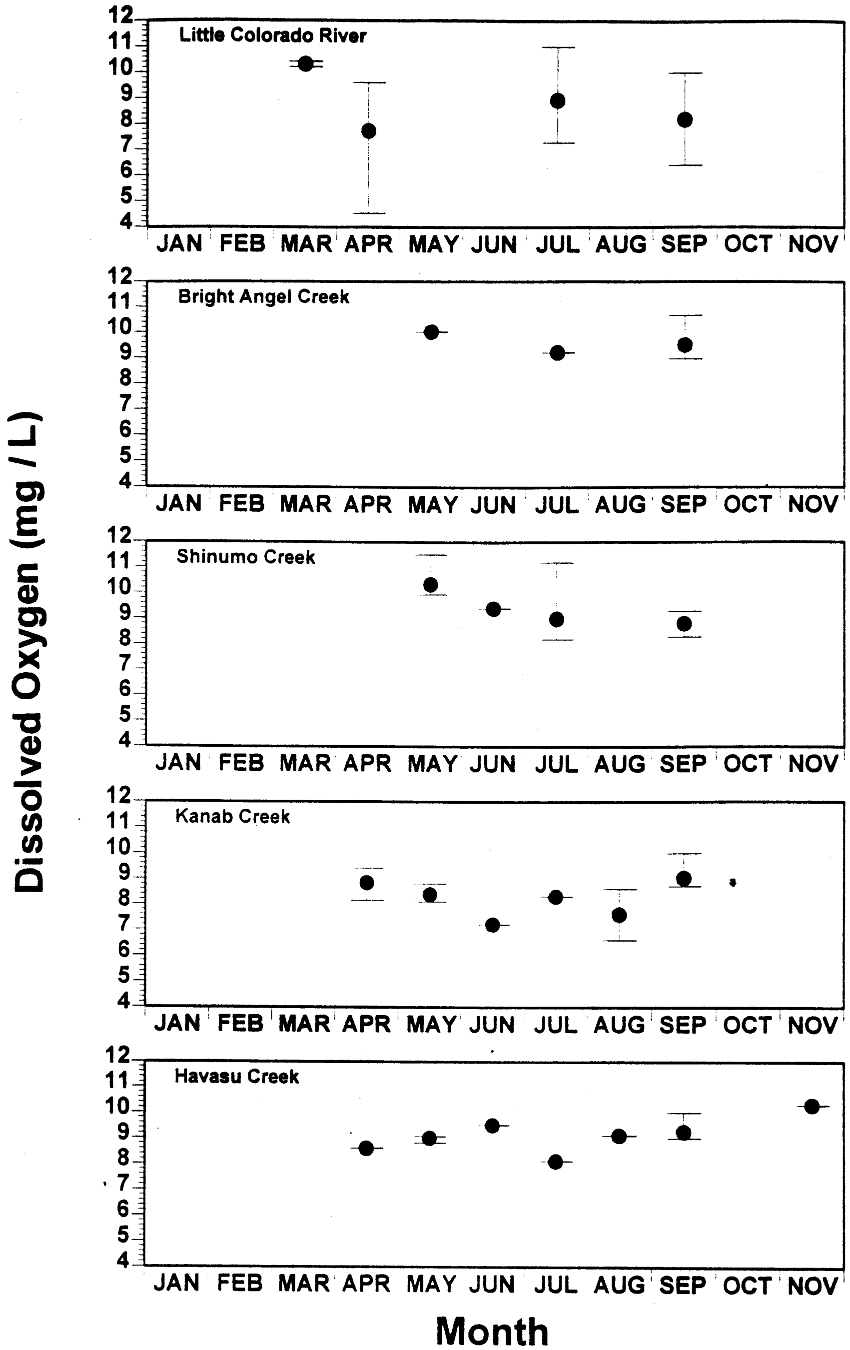

Fig. 29. Mean, minimum, and maximum dissolved oxygen (mg/L), by month, recorded during sampling in the mouths of Little Colorado River, Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek, Grand Canyon, 1991-94.

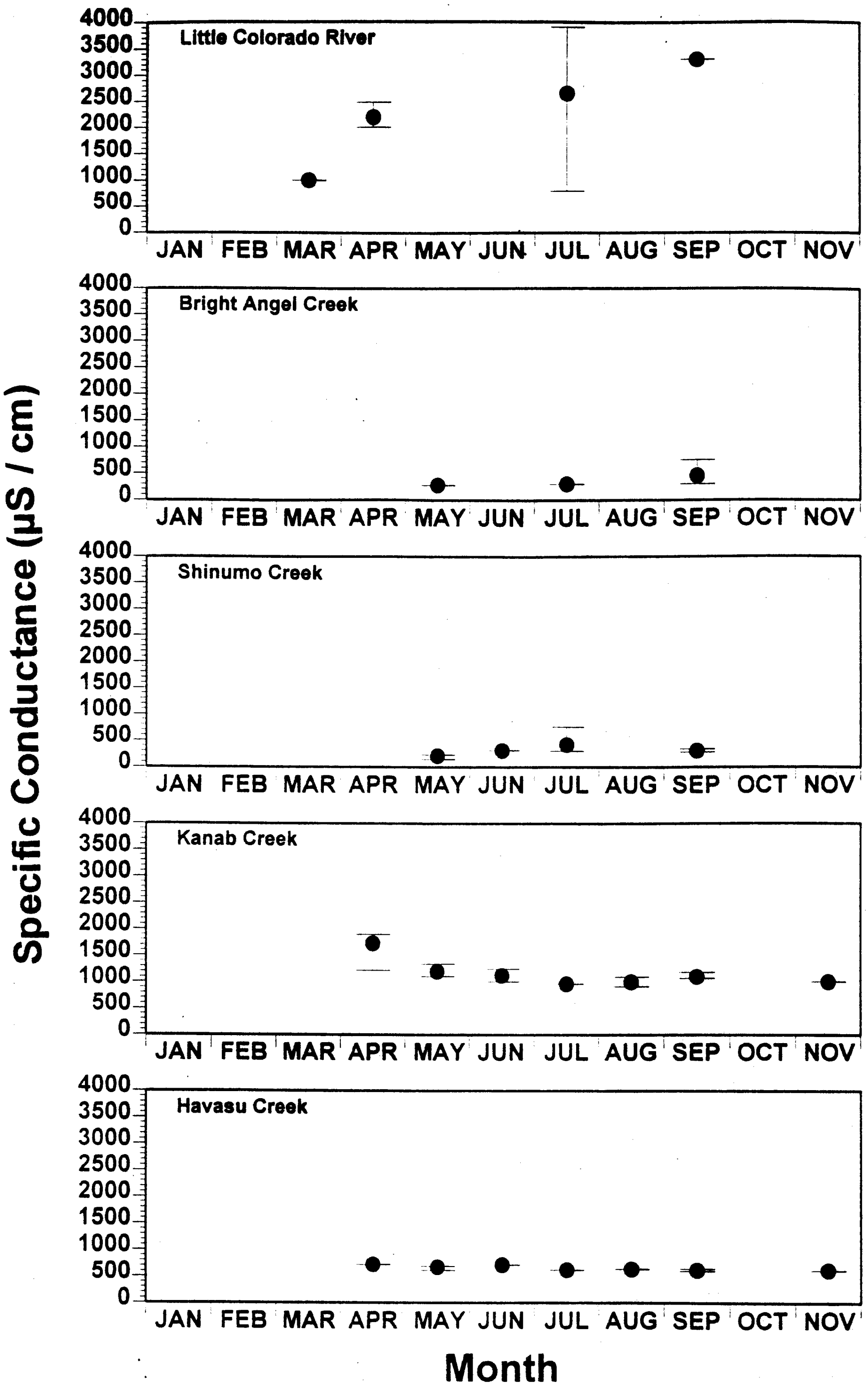

Fig. 30. Mean, minimum, and maximum specific conductance (μS / cm), by month, recorded during sampling in the mouths of Little Colorado River, Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek, Grand Canyon, 1991-94.

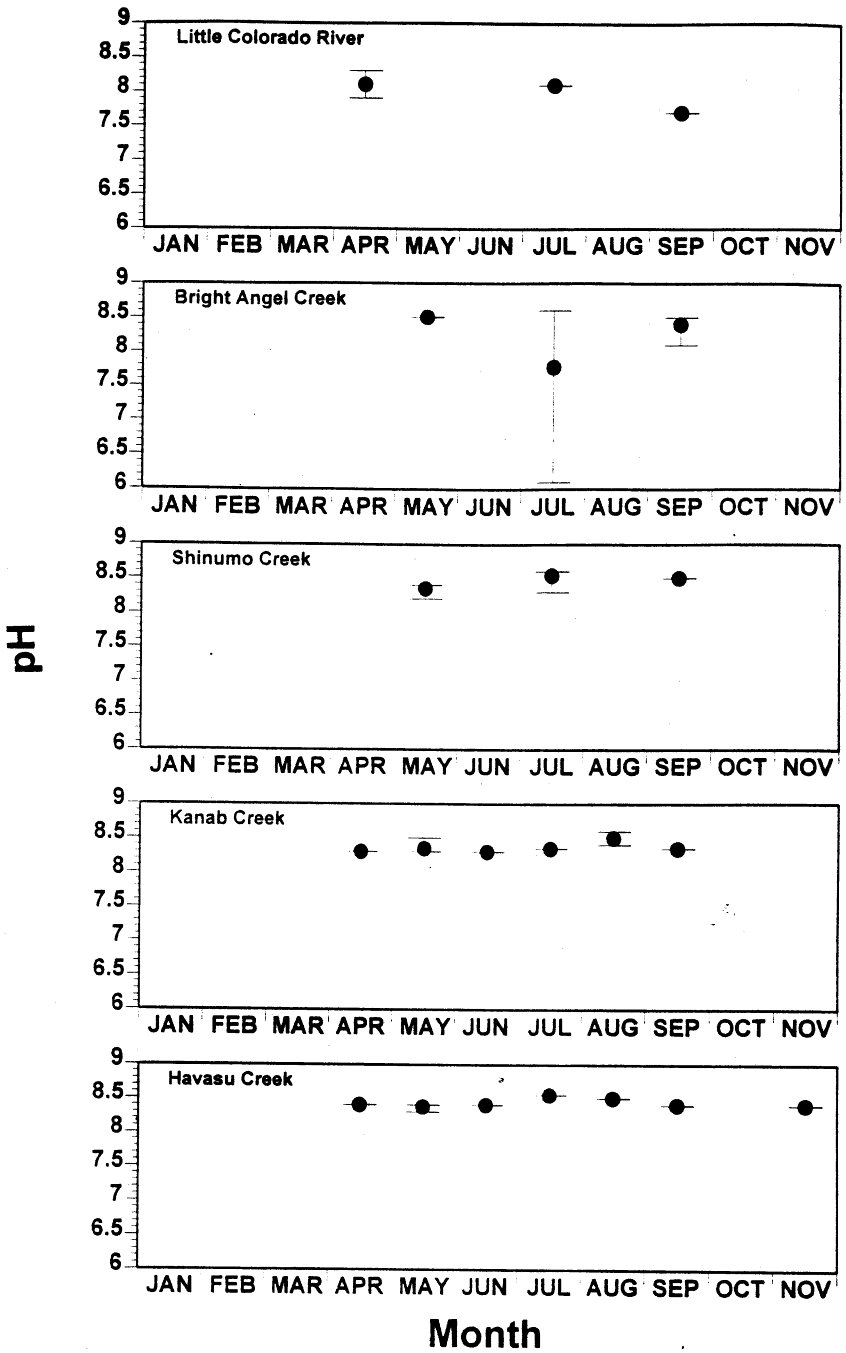

Fig. 31. Mean, minimum, and maximum pH , by month, recorded during sampling in the mouths of Little Colorado River, Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek, Grand Canyon, 1991-94.

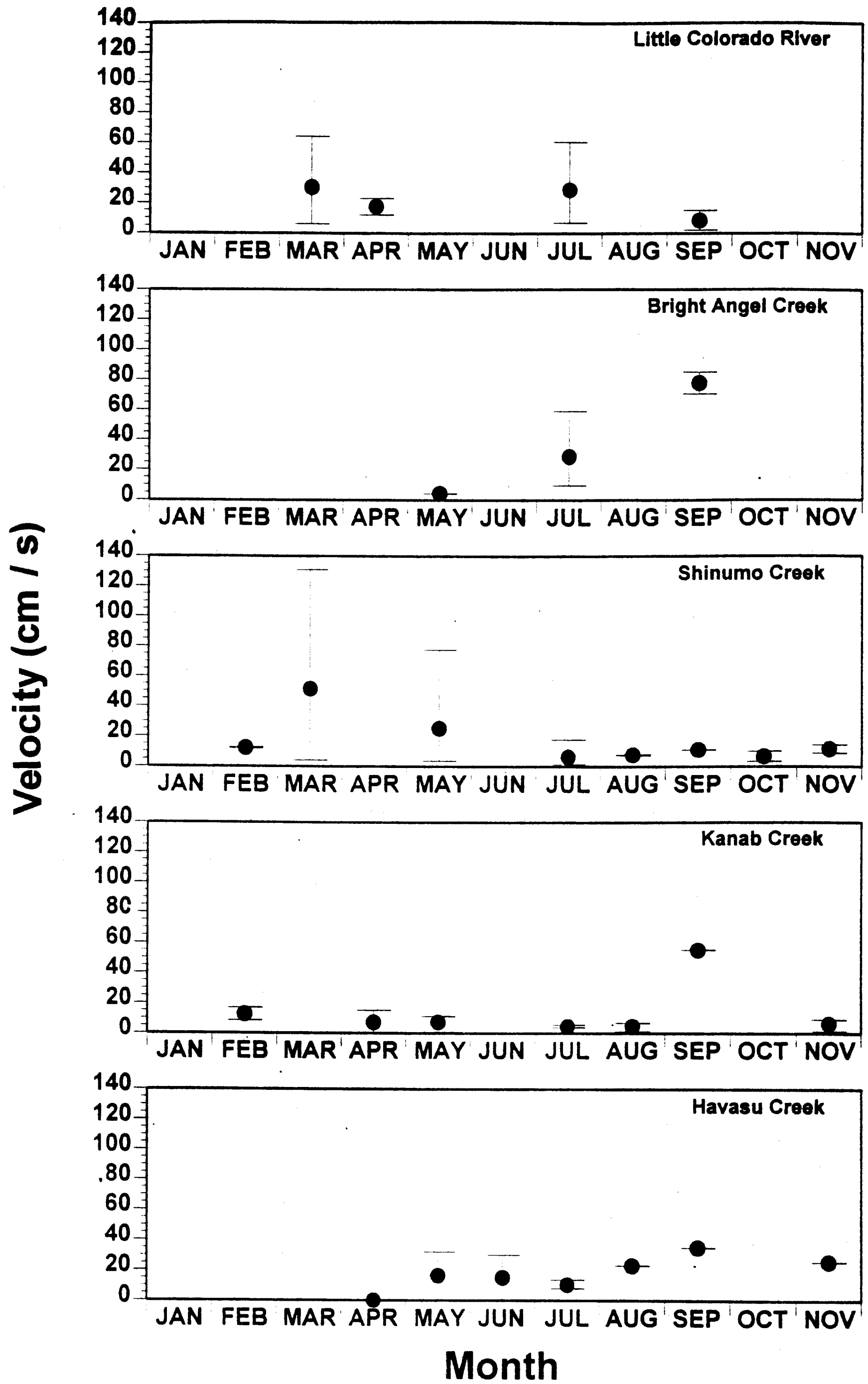

Fig. 32. Mean, minimum, and maximum velocity (cm/s), by month, recorded during sampling in the mouths of Little Colorado River, Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek, Grand Canyon, 1991-94.

They reported that the most common light scattering component was suspended sediment particles. Our data generally agree, showing that turbidity was lowest in Reach 20, Reaches 30 and 40 had intermediate levels of turbidity, and Reach 50 had the highest mean turbidity. We also found turbidity to be highest during March, when snowmelt runoff is most predictably entering the mainstem from the Paria and Little Colorado Rivers and other tributaries.

Low turbidity appears to strongly affect fish behavior. Data from this study (see Objective 3.6) show that speckled dace and juvenile humpback chub and flannelmouth sucker are more likely to use near shore areas under conditions of high turbidity. Valdez and Ryel (1995) found similar results with adult humpback chub and flannelmouth sucker. High turbidity is probably used as cover by these fish as it reduces the probability of being seen by a potential predator (Miner and Stein 1996).

Dissolved oxygen was found to be higher in the mainchannel than in backwaters. However, backwater dissolved oxygen levels were never so low as to be limiting for fish. This agrees with the findings of Grabowski and Hiebert (1989) in the Green River, Utah. Mean DO was also found to be lower in downstream reaches, but was still >10 mg/L. Considering the amount of turbulence found in the Grand Canyon, it is not surprising that dissolved oxygen levels remained high throughout.

Conductivity, in both the mainchannel and backwaters, was highest during periods of high tributary flow. It is likely that tributary inputs increase conductivity in the Colorado River. All tributaries, except Havasu Creek, had higher mean conductivities than the mainstem. Mainchannel conductivity was highest in Reaches 30 and 50, both of which contain major tributaries in their upper portions. None of these conductivity levels are likely to have affected the native fish species. Pimentel and Bulkley (1983) found that humpback chub avoided total dissolved solids (TDS) concentrations >5100 mg/L. Our recorded conductivity levels, ranging from 230-4350 μS/cm are equivalent to 147-2784 mg/L total dissolved solids (TDS = 0.64 × Conductivity), well below those avoided by humpback chubs, but also often below that preferred (1563-3906 NTU) by these fish.

The levels of pH found in this study were relatively constant. Mean pH ranged from 7.60-8.55 and was not extreme in any reach or in any month. Most fresh waters have a pH of 6.7-8.2 (Piper et al. 1982). Most fish have a wide tolerance of pH (Hynes 1970) and, in general, fish grow best in waters with pH between 6.5-9.0 (Boyd 1979; Piper et al. 1982). Therefore, it is unlikely that pH is limiting fish or invertebrate populations.

Overall, cold temperature is probably the greatest environmental factor limiting larval and juvenile native fish growth and survival in the Grand Canyon. Turbidity is another potential limiting factor due to its use as cover by native fishes. Dissolved oxygen, conductivity, and pH were all within acceptable levels for fish growth and are unlikely to be limiting.

***Objective 3.4.c.* Collect sediment cores from the tributary mouths, backwaters, and mainchannel and analyze for constituents of environmental importance.**

Backwaters are important rearing habitats for native fishes throughout the Colorado River, Grand Canyon, Arizona (Kubly 1990). The fate of these backwaters is largely dependant on sediment input and movement (Rubin et al. 1990; Schmidt 1990; Schmidt and Graf 1990). The major source of sediment input comes from the Paria and Little Colorado Rivers (Andrews 1991). Sediment type can affect the species composition and number of benthic invertebrates within a backwater, thus affecting the quality of backwater habitat for larval, juvenile, and adult fishes. Sediment samples were collected to characterize sediment composition of backwaters, their associated mainchannel beachfaces, and tributaries of the Colorado River, Grand Canyon.

METHODS

Sediment core samples were collected from 1991-94. Sediment cores were collected from backwaters, their associated mainchannel beachfaces, and several tributary mouths. Sampling sites were representative of four reaches in the Grand Canyon, from Lees Ferry (RM 0) to Diamond Creek (RM 225). When conditions allowed, individual backwaters were sampled repeatedly throughout the project. Sediments were separated into organic and inorganic matter within two size classes. Inorganic particles > 63 µm and < 1 mm were described as sand and inorganic particles < 63 µm were described as silt (Hynes 1970). Coarse particulate organic matter (CPOM) was defined as organic matter > 63 µm and < 1 mm. Fine particulate organic matter (FPOM) was defined as organic matter with a diameter < 63 µm (Cole 1983).

Sediment cores were collected using several protocols over the four years of sampling. In 1991 and 1992 (Trips 1-13), two sampling techniques were used to collect sediment cores from backwaters, their associated mainchannel beachfaces, and tributaries (Type A and Type B sampling protocols). In Type A sampling, one sediment core was collected within the backwater and one from the mainchannel beachface. In Type B sampling, sediment was sampled in several places along the long axis of the site. The number of core samples was determined by the size of the backwater and adjacent eddy.

Tributaries were sampled only in 1991 and 1992. Sediment cores were collected from Clear Creek in 1991 and Kanab and Shinumo Creeks in 1991 and 1992. The mean percentage of coarse vs. fine particles were determined for Clear Creek in 1991. The mean percentage of coarse vs. fine and inorganic vs. organic particles were determined each year for Kanab and Shinumo Creeks. Tributary samples were collected along a transect. This transect was established to best followed the changing conditions from the tributary mouth to the upper reach of the tributary affected by the mainstem under fluctuating flows (zone of fluctuation). The number of samples taken was determined by the size of the area impacted by water level fluctuations.

During 1993 and 1994, sediment core samples were collected only from backwaters. We used a modified Type A protocol which divided backwaters into three parts: foot (shallowest), center, and mouth (opening to mainchannel). Sediment samples collected in 1993 consisted of three samples taken from the backwater (one each from the foot, center, and mouth) and one sample taken from the mainchannel beachface. Sampling in 1993 was conducted quarterly (Trips 14, 17, 19, and 21). In 1994, samples were collected at all Type A backwaters with three samples taken from each backwater (one each from the foot, center, and mouth) and associated mainchannel beachface (one each from three locations along a transect perpendicular to shore).

Sediment samples (50 mL) were collected with a 60 mL plastic syringe with the tip removed. Sediment samples from Trips 1-14 were preserved in formalin, and Trips 17, 19, 21, and 22-25 were preserved in 95% ethanol. In the lab, the preservative was replaced with a 5% Calgon (sodium metaphosphate) solution to prevent clumping of particles.

Three methods were used in the lab to determine sand+CPOM (coarse) vs. silt+FPOM (fine) and inorganic (sand+silt) vs. organic (CPOM+FPOM) composition of the sediment samples. Method I determined the coarse vs. fine composition of backwaters, their associated mainchannel beachfaces, and tributaries for years 1991-1993 (Trips 1-10, 17, 19, 21). Sediment samples were placed into pre-weighed crucibles and dried at 105°C for 48 hours. The crucibles were then removed, allowed to cool, placed into a desiccator and weighed to determine the total dry weight of the sample. The sample was then sifted through a 63 μm sieve to remove fine (silt+FPOM) and smaller particles (such as clay particles). Particulate matter too large to pass through the 63 μm sieve was then transferred back into the crucible. The weight of coarse particles was determined by drying for 24 hours, cooling, desiccating, and then reweighing the sample. Fine particle weights were determined by calculating the difference between total weight and coarse weight.

Method II was used to determine the inorganic vs. organic composition of the sediment samples from Trips 3 and 11-14 from backwaters, mainchannel beachface, and tributaries. After determining the total weight of the sample, as in Method I, the sample was ashed for two hours at 500°C. After cooling, the sample was reweighed and screened using a 63 μm sieve to wash out the fine particles. The remainder of the sample was dried for 24 hours and reweighed to determine the composition of sand in the sample.

Method III was used to analyze sediment samples from backwaters and mainchannel beachfaces in 1994 (Trips 22-25). The proportions of coarse inorganic and organic particles and fine inorganic and organic particles were determined using this method. The sample was dried for 24 hours in a pre-weighed crucible. The sample was then mixed thoroughly, and half the sample was placed into another pre-weighed crucible, creating Samples A and B. As in Method II, Sample A was dried to determine total weight of the sediment sample and ashed to determine the proportions of inorganic vs. organic matter of the sediment sample. Sample B was also dried to determine total dry weight, sieved as in Method I and ashed as in Method II to determine the proportions of coarse vs. fine particles.

Sediments were characterized as coarse organic, fine organic, coarse inorganic, and fine inorganic components. Means of the variables were used to calculate percentages coarse and organic composition. These proportions were transformed using a square root arcsine transformation (Krebs 1989). Variables used in the analyses were dichotomous (coarse vs. fine and inorganic vs. organic). Therefore, only the proportions of coarse and organic particles were statistically analyzed.

Separate ANOVA and Ryan-Einot-Gabriel-Welch Multiple F tests (Day and Quinn 1989) were performed to test differences in percentage of coarse and inorganic particles between year, season, reach, habitat (backwater vs. mainstem), and their interactions. Season was broken down in the following manner: Spring=March-May, Summer=June-August, Fall= September-November, and Winter=December-February. Due to small sample sizes, the comparison of sediment composition among tributaries is presented only as a summary of mean percentages.

RESULTS

There was a significant difference ($P = 0.0001$) in the percentage of coarse particles between habitats (Table 5). Backwaters contained a lesser percentage of coarse particles (68%), compared to mainchannel beachfaces (88%). The percentage of coarse particles in all habitats also differed significantly among years ($P = 0.0001$), seasons ($P = 0.0091$), and reaches ($P = 0.0001$).

Inorganic sediment composition for samples collected from 1991-94 show an overall significant difference in the percentage of coarse particles. There was a greater percentage of coarse particles (87%) in 1991 than all other years. Samples from 1993 contained a lesser percentage of coarse particles (54%) than any other year. The percentage of coarse particles in 1992 (80%) and 1994 (75%) did not significantly differ.

Inorganic sediment composition significantly differed seasonally. There was a significantly greater percentage of coarse particles in winter (81%) than all other seasons. Spring contained the least percentage of coarse particles (75%) of all seasons. Summer and fall (77% each) did not differ in their percentage of coarse particles.

There was also a significant difference in inorganic sediment composition among reaches. Reach 30 sediments (68%) contained a significantly lesser percentage of coarse particles than the other three reaches (75-83%) which were not different from each other.

Backwaters (1.7%) contained a significantly higher percentage of organic matter ($P = 0.0001$) than did mainchannel beachfaces (1.1%; Table 6). There was also a significant difference in percentage of organic matter among years ($P = 0.0001$). There was no significant difference in percent organic composition among seasons ($P = 0.0806$) and reaches ($P = 0.0937$).

The organic matter content in sediments in 1992 was significantly higher (2.4%) than in 1994 (1.2%) and 1991 (0.5%). The percentage of organic matter in the sediments in 1993 (2.2%) were significantly greater than in 1991 but did not differ from 1994.

Sediments were composed primarily of coarse particles for Clear Creek in 1991 and for Shinumo and Kanab Creeks in 1991 and 1992 (Table 7). Shinumo and Kanab Creeks both had low percentages of organic particles within their sediments in 1991 and 1992.

Table 5. Mean percentage of coarse vs. fine particles for each habitat, year, season, and reach in sediment samples collected in the Colorado River, during AGFD sampling, 1991-94.

	N	Percent Coarse	Percent Fine	Standard Error
Habitat				
Backwater	532	67.5	32.5	1.27
Mainchannel	439	88.1	11.9	0.76
Year				
1991	212	86.8	13.2	1.18
1992	201	80.3	24.9	1.92
1993	141	53.7	46.3	3.00
1994	417	75.1	19.7	1.01
Season				
Winter	68	81.6	18.4	2.72
Spring	389	75.3	24.7	1.40
Summer	243	77.1	22.9	1.58
Fall	271	77.4	22.6	1.60
Reach				
20	187	75.4	24.6	2.20
30	256	68.4	31.6	1.90
40	230	83.6	16.4	1.24
50	298	79.7	20.3	1.30

Table 6. Mean percentage of inorganic vs. organic particles for habitat, year, season, and reach in sediment samples collected in the Colorado River, Grand Canyon, during AGFD sampling, 1991-94.

	N	Percent Inorganic	Percent Organic	Standard Error
<u>Habitat</u>				
Backwater	279	98.3	1.7	0.09
Mainchannel	266	98.9	1.1	1.18
<u>Year</u>				
1991	19	99.5	0.5	0.17
1992	90	97.6	2.4	0.48
1993	33	97.8	2.2	0.34
1994	403	98.8	1.2	0.07
<u>Season</u>				
Winter	33	97.8	2.2	0.34
Spring	190	98.7	1.3	0.13
Summer	149	98.8	1.2	0.09
Fall	173	98.4	1.6	0.26
<u>Reach</u>				
20	137	98.5	1.5	0.14
30	151	98.7	1.3	0.12
40	166	98.5	1.5	0.28
50	91	98.6	1.4	0.12

Table 7. Number of samples and mean and standard error of the percentages of coarse and fine particles in sediment samples from Clear, Shinumo, and Kanab Creeks, collected in each year during AGFD sampling in the Colorado River, Grand Canyon, 1991-92.

Site	Year	N	Mean	Standard Error
Clear Creek				
	1991			
% Coarse		3	79.9	5.65
% Fine		3	20.1	5.65
Shinumo Creek				
	1991			
% Coarse		10	95.7	1.01
% Fine		10	4.3	1.01
	1992			
% Coarse		1	62.8	-
% Fine		1	37.2	-
% Inorganic		2	97.1	0.22
% Organic		2	2.9	0.22
Kanab Creek				
	1991			
% Coarse		11	89.4	3.49
% Fine		11	10.6	3.49
% Inorganic		3	99.3	0.13
% Organic		3	0.7	0.13
	1992			
% Coarse		5	60.9	12.45
% Fine		5	39.1	12.45
% Inorganic		2	98.6	0.19
% Organic		2	1.4	0.19

DISCUSSION

Analyses of sediment samples show that backwaters contained a significantly lower percentage of coarse particles and a significantly higher percentage of organic matter than mainchannel beachfaces in the Colorado River, Grand Canyon. The manner in which sediment is deposited in Grand Canyon may provide insight as to why these differences in sediment composition exist. Backwaters are found throughout Grand Canyon in recirculation zones generally found in association with debris fans. Slower velocities in recirculation zones cause deposition of suspended sediments and organic particles from the mainchannel. Larger sediment particles (sand) are deposited first, creating a reattachment bar. Smaller particles such as silt, clay, and fine organic particles are then deposited in the primary-eddy return channel when the water level drops and velocity decreases. This eddy return channel becomes the backwater when water levels drop sufficiently so that no current is flowing through them (see Figure 3 in Schmidt and Graf 1990).

Sediment composition differed between years and may be attributed to tributary sediment input and changes in discharge from Glen Canyon Dam. Sediments in 1991 contained a larger percentage of coarse particles than 1992, 1993, or 1994. The interim flow period was not initiated until August 1991. Prior to this date, minimum and maximum discharge and ramping rates were greater. Higher flows and more varied discharges probably resulted in less stable substrates and a greater likelihood that fine particles will be transported downstream. Varied discharges can also result in increased sand erosion from riverbanks, further increasing the percentage of coarse particles in the river sediments.

In 1993, the sediments were comprised largely of fine particles, more so than the other years sampled. This difference in sediment composition may be explained by flooding in the Little Colorado River in January and February of that year. These floods deposited large amounts of sediments downstream from the LCR, creating many backwaters in which fine sediments were deposited. These backwaters were also deep and bordered by high sand bars, reducing the flushing effect and potential for inundation by fluctuating flows.

Sediments collected in winter months contained the largest percentage of coarse particles. Winter months may contain more coarse particulate matter because there is probably a reduced amount of fine particles entering the system from tributaries. Larger amounts of fine particles in the sediments in the spring may be attributed to tributary flooding during this period.

Variation in sediment composition among the four reaches can best be explained by the general morphology of the canyon and the effect that tributaries have on the different reaches. Schmidt and Graf (1990) described various reaches of Grand Canyon as either wide or narrow. Different amounts and types of deposits are associated with wide or narrow sections of the canyon, with finer sediments generally being deposited in the wider areas (Schmidt 1990) where currents are slower and less turbulent. Reach 40, which contained the greatest percentage of coarse particles in its sediments, is a narrow part of the Grand Canyon and contains few low velocity areas for suspended sediment to be deposited (Schmidt and Graf 1990).

The primary sediment load to the Grand Canyon comes from the Paria and the Little Colorado Rivers (Andrews 1991). Reach 30 contained the lowest percentage of coarse particles (highest percentage of fine particles) within its sediments. Reach 30 is located directly below the LCR and receives a large amount of fine particles from that tributary. Sediments from the Paria and Little Colorado Rivers are not all deposited in Reaches 20 and 30, however. Much of this sediment is transported downstream. Due to its narrowness and turbulence, little of these suspended sediments are deposited in Reach 40. However, much of them are also deposited in Reach 50 which contains many wide areas.

Sediment composition in tributaries varied widely, probably in relation to recent flooding events in either the tributary or mainchannel. Tributary mouths are similar to backwaters in that they are generally low velocity areas where fine sediments can precipitate. Indeed, tributary mouths contained similar percentages of fine and organic particles to those found in backwaters. Backwaters contained a mean percentage of 33% fine and 1.7% organic particles while tributary mouths contained a mean of 22% fine and 1.7% organic particles.

In conclusion, backwaters contained finer sediments with more organic matter than mainchannel beachfaces. Tributary mouths contained similar sediments to backwaters. Wide reaches generally contained finer sediments than narrow reaches. Annual and seasonal changes in sediments were largely related to periods of high discharge from the Paria and Little Colorado Rivers.

***Objective 3.4.d.* Map and identify each area of study.**

Backwaters of the Colorado River in the Grand Canyon are continually altered. Some backwaters change rapidly, whereas others are slower to change. Mapping enabled us to examine changes in backwaters between trips, reaches, seasons, years, and estimated discharges. Changes are due to siltation or scouring of return-current channels, sloughing of associated sandbars, and other effects of river flows. Backwaters can be characterized in terms of size, depth, or water volume, and these parameters can then be compared with fish abundance. This portion of the study examines the changes in these backwater parameters over time.

METHODS

Plane table maps were drawn of each Type A sampling site and some Opportunistic sites. These maps show perimeter at the water surface of the backwater, contour lines for 25 cm, 50 cm, 100 cm, and 150 cm depths, significant features surrounding the site (tapeats ledges, boulders, trees, etc.), location of nets, and area of habitats within the backwaters such as substrates and vegetation. Each map was oriented to true north and a measured baseline was drawn for scale. Maximum depth, study number, location (river mile and side), date, time, and estimated discharge were recorded on each map. Reference benchmarks were placed at backwaters and vertical distance from benchmark to water level was measured and recorded.

Maps were analyzed by scanning them into the Map and Image Processing System (MIPS) software. The maps were calibrated using a measured baseline, enabling us to measure total perimeter, surface area, area of each contour interval, and net length, which were then used to calculate volume.

Maximum depth (cm), total surface area (m^2), total volume (m^3), perimeter (m), and percentages of sediment classes (silt, sand, gravel, pebble, cobble, and boulder) were tested by MANOVA

(α=0.05) for the main effects of reach, season, year, and estimated discharge (flow). Data were transformed by either a log transformation (maximum depth, surface area, total volume, and perimeter) or arcsin transformation (sediment data) before statistical analysis to adjust for non-normality. Univariate ANOVA multiple comparison procedures (Ryan-Einot-Gabriel-Welch multiple F-test, Day and Quinn 1989) were used to show differences in means found to be significant by the MANOVA.

RESULTS

A total of 352 maps were drawn of backwaters during 1991-94. Due to some missing values in the data set, only data from 284 backwaters were used in the analyses. The results of the MANOVA showed that overall effects of reach (P=0.0152) and year (P=0.0094) were significant for maximum depth, surface area, total volume, and perimeter (Table 8).

Maximum depth was significantly associated with reach (P=0.0001) and year (P=0.0224). There were no significant interactions between main effects. Multiple comparison tests showed that mean depth of backwaters in Reaches 20 and 40 did not differ significantly, but was significantly deeper than mean depth of backwaters in Reaches 30 and 50 (Table 9). Backwaters in Reaches 30 and 50 did not differ significantly in depth. Backwaters were significantly shallower in 1992 than in 1993 and 1994, which were not significantly different from each other.

Surface area was significantly associated with reach (P=0.0001) and year (P=0.0071). There were no significant interactions between main effects. Mean surface area of backwaters in Reaches 20 and 30 did not differ significantly, but were significantly larger in surface area than backwaters in Reaches 40 and 50 which did not differ significantly (Table 9). Mean surface area was greatest during 1993 than all other years while surface area did not differ in 1991, 1992, and 1994.

Total volume was significantly associated with reach (P=0.0001) and year (P=0.0010). There were no significant interactions between main effects. Mean total volume of backwaters in Reaches 20 and 30 did not differ significantly, but these backwaters had significantly greater water volume than backwaters in Reaches 40 and 50 which did not differ significantly (Table 9). Mean total volume was significantly greater during 1993 than during 1992 and 1994, but did not significantly differ from 1991. Mean total volume did not differ significantly among years during 1991, 1992, and 1994.

Backwater perimeter length was significantly associated with reach (P=0.0001) and year (P=0.0093). There were no significant interactions between main effects. Mean perimeter length of backwaters in Reaches 20 and 30 did not differ significantly, but these backwaters had significantly greater perimeter length than backwaters in Reaches 40 and 50 which did not differ significantly (Table 9). Mean perimeter length was significantly greater during 1993 than during 1992 and 1994, but did not significantly differ from 1991. Mean perimeter length did not differ significantly among years during 1991, 1992, and 1994.

The percentages of backwater area covered by silt, sand, and boulder significantly varied by year and reach ($P \leq 0.0106$) while the areas of pebble and cobble did not vary ($P \geq 0.6065$).

Although the MANOVA for gravel was significant (P=0.0021), individual ANOVA's for year and reach were not significant ($P \geq 0.0636$). There were no significant interactions between main effects.

The mean percentage of silt was significantly lower in 1991 than in 1992, 1993, and 1994, which did not differ from each other (Table 10). Silt covered a significantly greater percentage of the bottom in Reach 30 than any other reach.

Table 8. Multivariate analysis of variance (MANOVA) for reach, season, estimated discharge (flow), year, reach*season, reach*flow, reach*year, season*flow, season*year, and flow*year for backwaters in the Colorado River, Grand Canyon, during AGFD sampling, 1991-94. MD=maximum depth. SA=surface area. TV=total volume. PE=perimeter.

Source	Wilk's Lambda	Approx. F	df	$P>F$	Univariate Significance
Reach	0.771	2.140	12/249	0.0152	MD,SA,TV,PE
Season	0.875	1.078	12/249	0.3792	-
Flow	0.487	0.849	88/374	0.8218	-
Year	0.809	2.629	8/188	0.0094	SA,TV,PE
Reach*Season	0.741	0.818	36/354	0.7642	-
Reach*Flow	0.276	1.159	124/376	0.1483	-
Reach*Year	0.747	1.197	24/329	0.2417	-
Season*Flow	0.400	1.107	88/374	0.2581	-
Season*Year	0.750	1.420	20/313	0.1105	-
Flow*Year	0.499	1.000	72/372	0.4835	-

Table 9. Mean and sample size for maximum depth, surface area, total volume, and perimeter of backwaters in the Colorado River, Grand Canyon, for reach and year from plane table maps drawn during AGFD sampling, 1991-94. There is a significant difference between means with different letters.

	Maximum Depth (cm)		Surface Area (m^2)		Total Volume (m^3)		Perimeter (m)	
Variable	Mean	N	Mean	N	Mean	N	Mean	N
Reach								
20	123.9 [a]	42	408.64 [a]	55	141.31 [a]	55	115.69 [a]	55
30	81.0 [b]	68	341.11 [a]	80	97.15 [a]	80	111.51 [a]	80
40	112.4 [a]	55	138.16 [b]	66	52.00 [b]	66	64.10 [b]	66
50	75.6 [b]	56	165.20 [b]	83	44.29 [b]	83	78.86 [b]	83
Year								
1991	-	0	246.91 [a]	30	102.32 [ab]	30	92.21 [ab]	30
1992	79.9 [a]	52	194.29 [a]	70	55.85 [b]	70	79.09 [b]	70
1993	103.1 [a]	87	307.60 [b]	102	97.87 [a]	102	105.57 [a]	102
1994	97.3 [a]	82	246.50 [a]	82	69.41 [b]	82	85.25 [b]	82

Table 10. Sample size and mean percentage of each sediment class in backwaters in the Colorado River, Grand Canyon, for reach and year from plane table maps drawn during AGFD sampling, 1991-94. There is a significant difference between means with different letters.

		Sediment Class					
Variable	N	Silt	Sand	Gravel	Pebble	Cobble	Boulder
Reach							
20	60	52.8 [a]	39.5 [bc]	0.0 [a]	0.0 [a]	0.0 [a]	7.7 [a]
30	81	73.1 [b]	25.9 [c]	0.1 [a]	0.0 [a]	0.0 [a]	0.9 [b]
40	73	41.3 [a]	51.9 [ab]	2.1 [a]	0.0 [a]	0.2 [a]	4.5 [ab]
50	128	42.3 [a]	54.3 [a]	0.0 [a]	0.1 [a]	0.3 [a]	3.0 [b]
Year							
1991	75	26.8 [b]	66.6 [a]	0.1 [a]	0.1 [a]	0.3 [a]	6.2 [ab]
1992	94	61.0 [a]	34.9 [c]	1.7 [a]	0.0 [a]	0.2 [a]	2.1 [b]
1993	102	50.7 [a]	48.1 [b]	0.0 [a]	0.0 [a]	0.0 [a]	1.3 [b]
1994	71	64.8 [a]	28.5 [c]	0.0 [a]	0.0 [a]	0.1 [a]	6.5 [a]

The mean percentage of sand varied inversely from that of silt both by year and reach (Table 10). The percentage of sand was significantly higher in 1991 than all other years. In 1993, the percentage of sand was significantly higher than in 1992 or 1994, which did not differ from each other. The percentage of area covered by sand in Reach 50 was similar to that in Reach 40, but significantly higher than in Reaches 20 or 30. Reach 40 was significantly higher than Reach 30, but not Reach 20.

The percentage of area comprised of boulders in 1994 was similar to 1991, but significantly higher than in 1992 and 1993 (Table 10). Boulders comprised a greater percentage of backwater substrates in Reach 20 than Reaches 30 or 50, but not Reach 40.

DISCUSSION

Backwaters are altered by silting, sloughing, scouring, and other effects from river flows. Silting and sloughing make backwaters shallower which decrease maximum depth and total volume. Scouring, on the other hand, makes backwaters deeper, increasing total volume. In addition to main-current erosion, Budhu (1991) found that ground water seepage, tractive force, and wave-induced erosion contribute to the erosion of sandbars. Failure of a sandbar, an instantaneous loss in volume of sand, may cause a reduction in backwater size. Daily flow fluctuations may decrease backwater size or destroy backwaters by eroding the sandbars and causing sand to slough into the backwater. Sandbars may also erode due to wind or recreational activities.

Although the backwaters studied went through some changes over the study period, both increases and decreases were observed in the measured variables, with few consistent trends. Comparisons were difficult to make due to continually changing conditions: discharge was estimated in the field, size and shape of backwaters changed according to stage based on daily fluctuating flows, and flood flows scoured and reshaped existing backwaters and created new backwaters.

There were significant differences in the characteristics of backwaters among reaches. Mean maximum depth in Reaches 20 and 40 was greater than in Reaches 30 and 50. The river corridor is relatively narrow in Reaches 20 and 40 with faster moving water. This may result in greater scouring of backwaters, thus possibly increasing mean maximum depth in these reaches. Reach 20 has relatively low sediment input, limited to that of the Paria River. The mean annual sediment discharge from the Paria River between 1947 and 1976 was 3.02 million tons/year (Andrews 1991). The LCR deposits a large volume of sediment into the Colorado River. During the post-1941 period, an average of 12.3 million tons of sediment per year were deposited in the Colorado River from the Paria and Little Colorado Rivers combined (Andrews 1991). Reaches 30 and 50, below the LCR confluence, are comparatively wider with shallower runs and slower moving water which aid in deposition of sediments.

Fluctuating flows and floods are the primary causes of physical alterations of backwaters. This study examined a sample of backwaters during fluctuating flows, and reports both positive and negative relationships between fluctuating flows and backwater size. It is difficult to determine why the effect of flow varies among backwaters. It would seem that as flow increased, so would water level which would increase the maximum depth, surface area, and total volume of backwaters.

Silting and sloughing of sediment may help explain negative relationships. Another explanation is that with increased flow, water may inundate part or all of the reattachment bar associated with a backwater. As flow increases toward inundation there will be a point when maximum depth, surface area, and total volume will begin to decrease. Carothers and Dolan (1982) suggested that flows of 40,000 cfs would inundate portions of humpback chub habitat. Flows of far less than this will inundate backwaters today. Also, active erosion and aggradation processes (Cluer and Dexter 1994) may cause sandbars to shift in elevation. This shift in sandbar elevation may account for the inundation or exposure of sandbars according to river stage.

Differences in backwater morphometry between years can be explained more simply. In 1993, many backwaters were formed by a series of flood events of the Little Colorado River (LCR) during January and February, 1993 (Figure 3). These flood waters were laden with sediment which provided materiel for sandbar formation and large amounts of silt and sand were deposited downstream from the LCR. The increases in number of backwaters, maximum depth, surface area, total volume, and perimeter length in 1993 can be attributed to new backwaters being formed and existing backwaters being reformed by the 1993 LCR floods. After the 1993 floods deposited sediment and reshaped backwaters, the sediments in the Grand Canyon system quickly eroded (Beus et al. 1994). This may account for the decreases in backwater numbers, maximum depth, surface area, total volume, and perimeter length.

The dominant substrates in backwaters were silt and sand. Changes in the composition of these substrates occurred among years and reaches. Two possibilities may account for the change in backwater substrate composition: deposition or erosion of silt and sand. Sand was the primary component in 1991 and 1993 and is probably the result of high fluctuations in flow during much of 1991 and the LCR floods in early 1993. Silt dominated the backwater substrates during 1992 and 1994, which probably represents a low amount of disturbance of these sites. Also, silt was the primary substrate class in the upper two reaches, probably due to its proximity to the two largest sources of sediments in the river: the Paria and Little Colorado Rivers.

In conclusion, backwaters are extremely dynamic in their nature. Large alterations of backwaters can be caused by scouring, sloughing and eroding of sand bars, and siltation. Floods, which both scour and deposit new sediments, have the most dramatic effect on backwaters. The size of a backwater is also greatly dependent upon the stage of the hydrograph at the time of sampling.

Objective 3.5. Determine invertebrate standing crops and their relative contributions to diets of young native fishes in tributary, backwater and mainchannel habitats.

Benthic and planktonic invertebrates provide an important food source for juvenile fish in the Colorado River, Grand Canyon. However, fluctuating water levels (Kennedy 1979) and cold temperatures (Ward 1976) in rivers below hydroelectric dams limit invertebrate production. Under peaking power dam operations (prior to August 1991), fluctuations in water depth caused cycles of inundation and/or desiccation of backwater habitats within the study area. The institution of interim flows caused backwater habitats to become more stable, with most experiencing less severe daily flushing, which provides better refugia for larval and juvenile fishes and aquatic invertebrates. This section examines benthic invertebrate and zooplankton densities in backwaters and associated mainchannel beachfaces in the Colorado River, Grand Canyon, from 1991-94. The primary objectives of this portion of the study were to describe the benthic and planktonic community and compare the relative abundance of these items in the diet of native and non-native fishes.

METHODS

During the four years of Phase II studies, invertebrate samples (benthos and zooplankton) were collected from different habitats in the study area. The sampling protocol was adapted to various fish collection techniques used during the course of the study. Here, we describe generally sampling schedules and protocols used to sample zooplankton and benthic invertebrate densities and collect fishes for examination of diet. Specific methods concerning gear types, preservation of samples, and laboratory and statistical methods are described in detail in later sections.

From March 1991 through September 1992, zooplankton was sampled in conjunction with Type A and Type B sampling protocols (See Sampling Area & Protocols). From October 1992 to November 1993, a quarterly sampling protocol was adopted. In 1994, efforts were made at collecting data from various microhabitats within backwaters as part of the Type A protocols. Procedures for invertebrate sampling are described in detail below.

In Type A samples collected prior to October 1992, two benthos and two zooplankton samples were taken from each study location. One was collected from the backwater and one from the mainchannel beachface. Occasionally, an additional sample was taken from the eddy at the mouth of the backwater (backwater eddy). Representative locations within the habitat, usually near the center, were sampled. In Type B backwater samples, benthos and zooplankton were collected along a transect that followed the fluctuation of the water, usually from the foot of the backwater, through the backwater mouth and into the eddy. Tributary samples were also taken as part of Type B sampling. These samples were taken in a transect along the tributary including habitat influenced by mainstem water (tributary mouth) and habitat upstream from the tributary mouth (tributary stream).

Quarterly sample collections were taken from three sites within the backwater: mouth (opening of the backwater), center (middle third of the backwater) and foot (back third of the backwater). In addition to sampling the backwater, one site was sampled in the mainchannel, usually the mainchannel beachface. In each of these sites, one zooplankton and three benthos samples were collected for a total of four zooplankton samples and 12 benthos samples per study location. All backwater samples were taken from the center of the deepest channel. Mainchannel beachface samples were taken offshore at a depth of about 1 meter. One backwater was typically sampled from each of the four reaches during the February-March, May, July and October-November trips of 1993.

In 1994, we continued to collect three samples from the backwater, but two more sample sites were added to the mainchannel beachface habitat to balance the study design: a total of three zooplankton and three benthos samples in each of the backwater and mainchannel beachface per study location. Also in 1994, we divided the Colorado River, Grand Canyon into subreaches based upon the shoreline topography, hydrology and the distribution of native fishes within the study area (Table 11). A minimum of two study locations per subreach were sampled in conjunction with Type A sampling. These subreaches were designated to be used in the dietary study discussed below. All analyses of benthos and zooplankton used the four reaches standard to this study.

Diet was examined only in 1994. Fish were collected only in conjunction with zooplankton and benthos sampling. This will enable us in the future to compare gastrointestinal tract contents with prey availability in the environment. Five fish were collected of each species < 30 mm in total length and five fish of each species > 30 mm in total length in each of eight subreaches. All fish were collected by seining in backwater habitats.

Table 11. Subreaches and their boundaries used for benthic invertebrate, zooplankton, and diet sampling in 1994.

	Beginning of Reach		End of Reach	
Reach	Location	River	Location	River
CR1	Lee's Ferry	0	Shinumo Wash	29.3
CR2	Shinumo Wash	29.3	Little Colorado River	61.5
CR3	Little Colorado River	61.5	Lava Chuar Rapid	65.5
CR4	Lava Chuar Rapid	65.5	Hance Rapid	76.7
CR5	Hance Rapid	76.7	Elves Chasm	116.5
CR6	Elves Chasm	116.5	Forster Rapid	122.8
CR7	Forster Rapid	122.8	Hell's Hollow	182.5
CR8	Hell's Hollow	182.5	Diamond Creek	225.6

***Objective 3.5.a.* Determine the exchange of zooplankton, drift organisms and particulate organic matter between backwaters and mainchannel and tributary mouths.**

While these data would be of interest in understanding the dynamics of the mainstem aquatic community, collection of these data would have taken intensive sampling at a number of sites. Due to the size of the study area and the nature river system, this was not logistically feasible. Data concerning differences in invertebrate densities between backwaters and mainchannel beachfaces are discussed in this section, but we were unable to determine exchange rates, specifically.

***Objective 3.5.b.* Determine changes in the zooplankton community of backwaters during the GCES Research and Interim flows.**

In unregulated rivers, zooplankton are found primarily in the lower reaches (Vannote et al. 1980). However, in regulated river systems, zooplankton abundance, species composition, and longitudinal distribution are primarily determined by the zooplankton community in the reservoir located immediately upstream from the dam and by dam operations (Petts 1984). Therefore, the two factors that are important in regulating the zooplankton in the Colorado River in Grand Canyon are, 1) the distribution and abundance of zooplankton in Lake Powell, and 2) the characteristics of the Glen Canyon Dam discharge regime.

Glen Canyon Dam is a hypolimnial release dam with penstock intakes at a depth of 70 m when Lake Powell is at full pool. Water can also be released from jet tube intakes (100 m depth) and surface withdrawal spillways. Because lentic zooplankton species generally occur throughout these depth ranges and have depth preferences depending on species, growth stage, season, time of day, etc. (Hutchinson 1967), the discharge from Lake Powell affects the species composition and number of zooplankton found in the Colorado River.

Studies of zooplankton in the Colorado River, Grand Canyon, from Lee's Ferry to Diamond Creek, are few. Cole and Kubly (1976) identified zooplankton species in the mainchannel and tributaries, but did not report densities. They concluded that most of the zooplankton in the mainchannel Colorado River originated in Lake Powell or the tributaries, primarily Elves Chasm and Tapeats and Diamond Creeks. Maddux et al. (1987) reported zooplankton densities ranging from 5 - 758/m^3 from collections taken from December 1984 to November 1985. Total densities calculated from Haury (1981) ranged from 0.36 - 232 /m^3. Haury (1986, 1988) reported total densities of 300 - 10,000 /m^3. Haury (1981, 1986, 1988) found copepods to be the most numerous taxa and found no direct relationship between zooplankton densities and river mile. He speculated that reproduction of copepods was occurring, based on the presence of females with eggs, males with spermatophores, and nauplii in samples collected throughout the length of the river. Kubly (1990) reported densities from mainchannel and backwater collections from 1987 - 1989. He found densities ranging from approximately 80 - 20,000 /m^3 in the backwaters and approximately 100 - 900 /m^3 in the mainchannel (densities presented are approximations taken from Figure 12; Kubly 1990). No statistical comparisons based on habitat differences have been reported.

All previous studies occurred prior to interim flows. However, Haury (1981, 1986, 1988) recognized the potential importance of refuge habitats (e.g., stable backwaters) in providing habitat for zooplankton reproduction and growth at stable or low fluctuating flows. The primary objectives

of this section were to examine differences in zooplankton densities, species composition, and population structure by year, season, reach (distance downstream from Glen Canyon Dam) and habitat; and ultimately food resource availability. This should provide important information pertaining to the prey base available for young-of-year and juvenile native fishes. (Objective 3.5.d).

METHODS

Zooplankton samples were collected by filtering 30L (March 1991 - September 1992) or 50L (October 1992 - September 1994) of water through an 80 µm plankton net (#40 Wisconsin "bucket" net). Samples were collected from near the water surface in the middle of each transect using a 10 L bucket. Samples were preserved in 5% formalin (prior to 1993) or 75% ethanol (after 1992) and labeled with study number, habitat code and site number.

In the laboratory, samples were condensed to a volume of 50 mL. Five 1 mL subsamples were then examined using a Sedgwick-Rafter counting cell (Wetzel and Likens 1991). All organisms were counted and identified to Class, except for rotifers, which were identified to Phylum. The mean number of organisms in each subsample was used to determine the mean total number of organisms and mean number of each taxa per liter. Densities (individuals/m^3) were then calculated for each sample. Density estimates for each sample were then pooled by habitat (backwater or mainchannel beachface) for further analysis.

Zooplankton density estimates were tested for normality using the Shapiro-Wilks test and the F-max test for homogeneity of error variance. Non-parametric statistics were applied to our data due to lack of homogeneity of error variance. A Kruskal-Wallis test was used to test for significant differences in total zooplankton and individual species density by year, reach, and season. The Mann-Whitney *U* test was used to test for significant differences by habitat. Significance for these tests was set at $\alpha = 0.05$. Multiple comparisons were made using multiple Mann-Whitney *U* tests. A Sequential Bonferroni test was conducted to determine a critical α for multiple comparisons.

RESULTS

Copepod nauplii and adults were the most common zooplankton found in 1991, 1992, and 1994 followed by rotifers (Table 12). Cladocerans were the most abundant zooplankton in 1993 followed by copepod adults. A large number of protozoans were also observed in the samples, primarily *Volvox* sp. and dinoflagellates. Due to the limitations of our equipment (80 µm plankton net), a quantitative sampling of protozoans could not be accomplished and were omitted from the estimates of total densities and subsequent analyses. Several non-planktonic taxa were also found in our samples; these were also excluded from our analyses (Table 13).

Zooplankton density estimates varied significantly by year (P=0.0001), season (P=0.0021), and reach (P=0.0001). Several species of zooplankton also showed significant differences by year, season, reach, and habitat (Table 14). Seasonal changes in species density were observed during 1991 - 1994 (Figure 33). Zooplankton density estimates in backwaters were significantly higher than those from mainchannel beachfaces (P=0.0273).

Table 12. Mean and standard deviation of densities (number/m^3) of zooplankton collected in backwater and mainchannel habitats of the Colorado River, Grand Canyon, 1991-94.

	Backwater		Mainchannel	
Taxa	Mean	Standard Deviation	Mean	Standard Deviation
1991: Total	5,054.7	6,084.59	3,284.4	3,759.55
Cladocera	427.9	1,889.90	342.2	1,025.17
Copepoda-adults	1,383.1	1,854.34	1,000.0	1,146.87
Copepoda-nauplii	1,970.2	3,521.33	1,315.6	1,968.90
Ostracoda-nauplii	69.7	197.09	75.6	229.72
Rotifera	1,204.0	2,510.55	551.1	1,295.05
1992: Total	2,435.7	3,323.67	2,190.5	3,524.50
Cladocera	48.1	200.04	38.1	143.03
Copepoda-adults	807.0	1,412.29	769.1	1,742.04
Copepoda-nauplii	1,227.9	1,791.41	975.3	1,274.42
Ostracoda-nauplii	162.8	615.58	199.3	1,307.77
Rotifera	189.9	363.64	208.8	331.88
1993: Total	6,754.2	15,312.20	3,166.7	3,142.31
Cladocera	2,266.7	11,800.35	244.4	325.80
Copepoda-adults	1,350.0	1,939.29	955.6	1,115.78
Copepoda-nauplii	895.8	2,250.67	544.4	1,090.72
Ostracoda-nauplii	1,316.7	1,937.24	800.0	1,236.69
Rotifera	925.0	1,499.86	622.2	979.53
1994: Total	2,588.3	3,960.26	1,855.7	1,368.75
Cladocera	158.7	272.63	111.3	180.74
Copepoda-adults	478.9	920.17	266.0	296.23
Copepoda-nauplii	1,439.5	2,514.29	1,083.0	971.78
Ostracoda-nauplii	165.0	572.05	72.6	171.44
Rotifera	346.2	845.11	322.6	501.80

Mean zooplankton densities in 1993 and 1991 were significantly higher than in 1992 and 1994. Mean zooplankton densities in the spring and fall were significantly higher than in the summer and winter. For all four years of the study, mean zooplankton densities were highest in Reach 20 and decreased significantly with distance downstream from Lee's Ferry (Figure 34).

DISCUSSION

Copepod nauplii and adults were the zooplankton taxa that occurred most frequently in three out of the four years of this study. This agrees with findings by Haury (1981, 1986, 1988) who found that copepods were the most abundant species in the Colorado River, Grand Canyon. Copepod nauplii and adults were also the most abundant zooplankton species found at penstock depths from Lake Powell and from Lees Ferry (~ 24 km below Glen Canyon Dam) from April 1993 - January 1995) (AGFD, unpublished data).

In 1991 and 1993, high flows were seen during January and February as a result of high precipitation and snow melt. In 1993, high flows occurred again in August and September as a result of monsoonal precipitation combined with high dam discharge rates in response to increase summer power demands. These events probably contributed to the significantly higher mean densities of total zooplankton seen in those years versus 1992 and 1994. The mean density of cladocerans was also significantly higher in 1991 and 1993 than in other years of this study.

Cladocerans are generally found in the epilimnion (Wetzel 1983). However, with increased discharge rates causing a temporary mixing of layers (epilimnion, metalimnion, and hypolimnion) near the dam, cladocerans were probably brought down to penstock depths; thus contributing to the significantly higher numbers seen in 1991 and 1993.

In all four years of this study, the mean total zooplankton density in the spring and fall was significantly higher than that of the summer and winter. In the spring, there is an increase in reproduction of zooplankton. Numbers of copepod and ostracod nauplii were significantly higher in the spring than in any other season. In the fall of 1992, 1993, and 1994, there were significantly higher numbers of cladocerans than in any other season (Fig. 33). The lowered surface elevation of Lake Powell during this time of year in conjunction with fall turnover probably caused cladocerans located in the epilimnion to be relocated to depths closer to the penstock intakes.

Zooplankton densities were significantly higher in upstream reaches and significantly decreased with distance downstream from Glen Canyon Dam. This is explained by the Serial Discontinuity Concept. This concept states that zooplankton and benthic invertebrate densities are highest immediately below a dam and decrease with distance downstream, followed by a gradual increase in the next reservoir downstream (Ward and Stanford 1983). Mean total zooplankton densities in all four years of this study were significantly higher in the upstream reaches and decreased significantly with distance downstream from Glen Canyon Dam. These data contradict findings by Haury (1986) who saw no significant decrease in zooplankton density with distance downstream from Glen Canyon Dam.

Table 13. Mean and standard deviation of densities (number/m^3) of Protista and non-planktonic taxa collected in backwater and mainchannel habitats of the Colorado River, Grand Canyon, 1991-94.

Year/Taxa	Backwater		Mainchannel	
		Standard		Standard
1991				
Hydracarina	54.7	149.04	66.7	197.58
Chlorohydra sp.	14.9	69.46	22.2	83.71
Insecta	174.1	507.05	102.2	273.85
Nematoda	213.9	558.68	177.8	459.58
Tardigrada	29.9	112.09	26.7	91.04
Protozoa	1,985.1	3,907.79	2,217.8	5,256.63
Unknown	64.7	218.96	35.6	160.45
1992				
Hydracarina	83.7	245.04	241.8	539.93
Chlorohydra sp.	2.3	21.57	3.7	34.94
Insecta	165.1	488.59	98.9	207.84
Nematoda	233.3	880.51	972.2	8,872.61
Tardigrada	147.3	652.00	130.0	335.92
Protozoa	49.6	151.05	34.4	1,119.82
Unknown	143.4	489.21	190.5	612.91
1993				
Hydracarina	29.2	82.41	55.6	114.90
Chlorohydra sp.	4.2	28.87	11.1	47.14
Insecta	12.5	48.92	33.3	76.70
Nematoda	1,375.0	1,997.71	833.3	1,011.11
Tardigrada	0.0	0.00	0.0	0.00
Protozoa	529.2	1,220.04	922.2	1,409.45
Unknown	12.5	64.00	0.0	0.00
1994				
Hydracarina	28.7	86.38	26.4	80.64
Chlorohydra sp.	0.9	13.39	3.8	27.28
Insecta	202.7	448.61	121.7	193.99
Nematoda	102.2	442.70	20.8	64.16
Tardigrada	116.6	928.06	40.6	135.10
Protozoa	547.1	988.71	537.7	979.36
Unknown	32.3	128.88	30.2	143.86

Table 14. Results of the Kruskal-Wallis (year, season, and reach) and Mann-Whitney *U* (habitat) tests for significant differences in zooplankton density by year, season, reach, and habitat collected during AGFD sampling of the Colorado River, Grand Canyon, 1991-94.

Taxa	*Year	*Season	*Reach	**Habitat
Total	*P*=0.0001	*P*=0.0021	*P*=0.0001	*P*=0.0273
Cladocera	*P*=0.0001	*P*=0.0045	*P*=0.0001	*P*=0.2791
Copepoda-adults	*P*=0.0001	*P*=0.4300	*P*=0.0001	*P*=0.0269
Copepoda-nauplii	*P*=0.0001	*P*=0.0023	*P*=0.0001	*P*=0.4043
Ostracoda-nauplii	*P*=0.0001	*P*=0.0001	*P*=0.0035	*P*=0.1630
Rotifera	*P*=0.0001	*P*=0.8394	*P*=0.0001	*P*=0.5725

Lastly, we found that backwaters had significantly higher densities of zooplankton than mainchannel beachfaces. Backwaters may provide refugia for zooplankton because they are a more stable habitat. Backwater also may retain nutrients which benefit both phytoplankton and zooplankton. Backwaters are also likely areas for zooplankton reproduction. No conclusive evidence of backwater reproduction has been found in this or in previous studies, but female copepods with egg sacs and males with spermatophores were collected in backwater samples. Whether these gravid copepods are resident within the backwaters or originated in Lake Powell is uncertain. However, densities of neither copepod nor ostracod nauplii were higher in backwaters than the mainchannel.

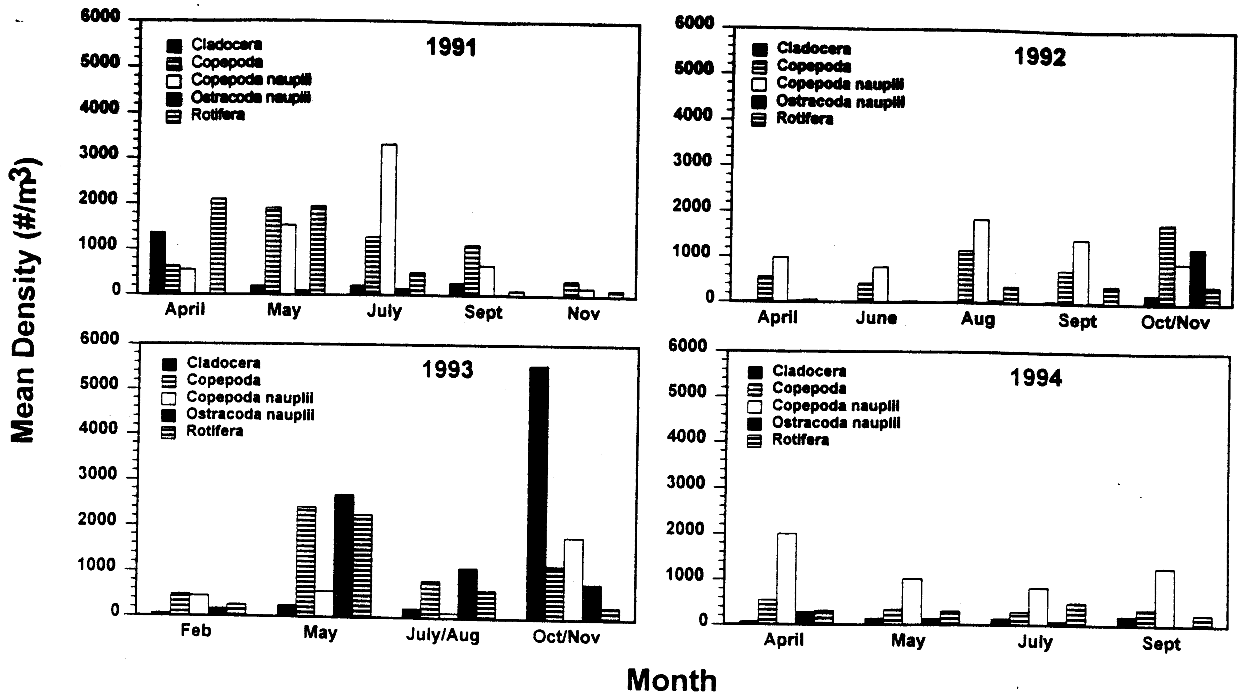

Fig. 33. Mean density (#/m^3) by month of zooplankton species collected during AGFD sampling of the Colorado River, Grand Canyon, 1991-94.

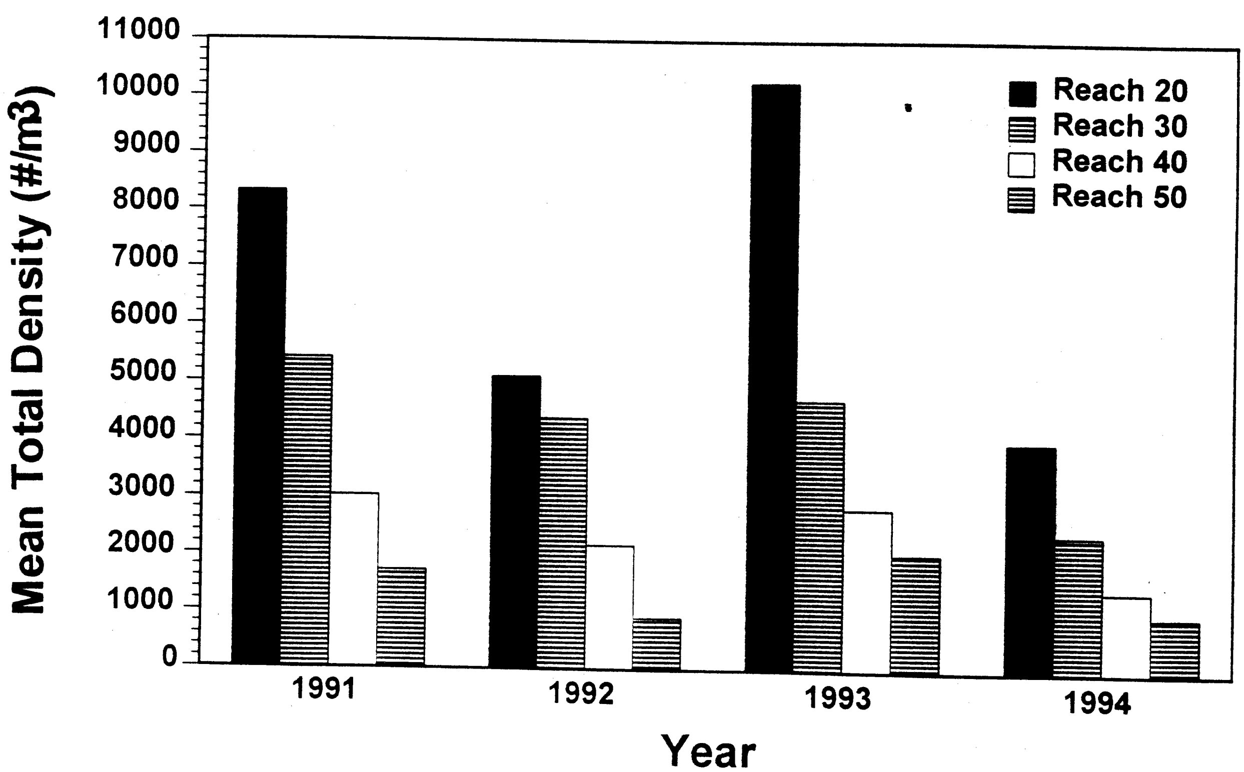

Fig. 34. Mean total density (#/m^3) by reach of zooplankton collected during AGFD sampling of the Colorado River, Grand Canyon, 1991-94.

***Objective 3.5.c.* Sample benthic invertebrates in rearing habitats both within and outside of the fluctuating flow regime impact areas.**

Benthic invertebrates provide an important food source for juvenile fish in the Colorado River, Grand Canyon. However, fluctuating water levels (Kennedy 1979) and cold temperatures (Ward 1976) limit invertebrate production in rivers below hydroelectric dams. Backwaters provide a better habitat for benthic invertebrates than mainchannel beachfaces because they are warmer, have lower velocities, more stable sediments, and allow for the accumulation of detritus. Cole and Kubly (1976) suggested that benthic invertebrate species diversity is higher in backwaters than in the mainchannel. This objective examines benthic invertebrate densities in backwaters and associated mainchannel beachfaces in the Colorado River, Grand Canyon, from 1991-94. We were interested in examining differences in benthic invertebrate densities by year, season, reach, and habitat.

METHODS

Benthic invertebrates were collected using a 15 x 15 cm (0.0232 m^2) Petite Ponar dredge. The contents of the dredge were washed through a 12 L littoral bucket with a 30-mesh (600 μm mesh) bottom. Organisms were preserved in 5% formalin or 70% ethanol.

In the laboratory, benthic organisms were identified and counted to determine total benthic invertebrate and individual species densities (number/m^2) by year, season, reach, and habitat. Invertebrates were identified to Class, except insects, which were identified to Order and dipterans which were identified to Family.

Benthic invertebrate density estimates were tested for normality using the Shapiro-Wilks test and the F-max test for homogeneity of error variance. Non-parametric statistics were applied to our data due to lack of homogeneity of error variance. Kruskal-Wallis test was used to test for significant differences in total benthic invertebrate and individual species density by year, reach, and season. The Mann-Whitney U test was used to test for significant differences by habitat. Significance for these tests was set at $\alpha = 0.05$. Multiple comparisons were made using multiple Mann-Whitney U tests. A Sequential Bonferroni test was conducted to determine a critical α for multiple comparisons.

RESULTS

Oligochaetes, nematodes, chironomid larvae, and dipteran larvae were the most common benthic invertebrates found in the Colorado River, Grand Canyon during 1991-94 (Table 15). Ostracods were also common from 1992-94.

Total benthic invertebrate density varied significantly by year, season, and reach (P=0.0001). Several species of benthic invertebrates showed significant differences by year, season, and reach (Table 16; Figure 35). Total benthic invertebrate density was significantly higher in backwaters than mainchannel beachfaces (P=0.0001).

Mean total benthic invertebrate densities in backwaters were significantly higher in 1993 and 1994 than in 1992 or 1991 (Figure 36). Mean benthic invertebrate densities in the spring were

significantly higher than those of summer, fall, or winter. Mean benthic invertebrate densities were highest in Reach 20 and decreased significantly with distance downstream from Lees Ferry.

DISCUSSION

Oligochaetes, nematodes, chironomid, and dipteran larvae, and ostracods were collected more frequently than other benthic invertebrates. No previous studies have quantified the backwater benthic invertebrate community of the Colorado River, Grand Canyon. However, the major taxa present during this study have been documented in past studies (Cole and Kubly, 1976; Carothers and Minckley, 1981).

In early 1993, the Little Colorado River flooded due to high amounts of precipitation and snow melt. The high velocities of the Little Colorado River may have caused benthic invertebrates to be flushed out into the mainstem Colorado River. Increases in total benthic invertebrate densities during 1993 may be a result of these higher velocities as well as increased nutrient loads.

Significantly higher densities of total benthic invertebrates were found in 1994 than in 1991 and 1992. After the flood in the Little Colorado River in 1993, there was an increase in the number of backwaters in the Colorado River in 1994. The increased volume and velocity of water in the Colorado River during 1993 caused large amounts of sediment to be deposited along the margins of the Colorado River forming numerous backwaters. These backwaters provide refugia for benthic invertebrates. An increase in stable habitat should increase benthic invertebrate growth and reproduction, thus accounting for the higher numbers in 1994.

Highest benthic invertebrate densities were found in the spring and summer months for all four years, largely attributed to dipterans (mainly larvae & pupae). Chironomidae and Ceratopogonidae larvae and pupae are emerging during this time of the year, resulting in high numbers (Merritt and Cummins 1984). After mid-summer we saw a sharp decrease in the numbers of dipteran larvae and pupae. The adult stage of these dipterans is terrestrial. Water temperatures during late spring and early summer are at their highest. Increase power demands during the summer cause an increase in the cold water releases from Glen Canyon Dam, thus decreasing the reproductive potential of the dipterans.

For all four years of the study, benthic invertebrate densities were significantly higher in Reach 20 and decreased significantly with distance downstream from Glen Canyon Dam. This may best be explained by 1) the Serial Discontinuity Concept (Ward and Stanford 1983) and 2) productivity. Ward and Stanford (1983) found that benthic invertebrate densities are generally highest immediately below a dam and decrease with distance downstream. Also, water clarity in Reach 20 is the highest of any reach in the Colorado River, Grand Canyon. The low amounts of suspended sediments in this reach allow for an increase in light penetration, which in turn increases primary and secondary productivity. Reach 20 also has lower densities of fish than the other reaches. Kennedy (1979) found an inverse relationship between invertebrate standing crop and fish abundance in backwaters in the lower Colorado River.

Lastly, backwaters of the Colorado River, Grand Canyon, had significantly higher densities of benthic invertebrates than did the mainchannel beachfaces. Mainchannel beachfaces were depauperate of benthic invertebrates, compared to densities of the backwater. Due to increased stability of backwater sediments compared to those of mainchannel beachfaces, this is not surprising. Backwaters appear to provide refugia for the benthic invertebrates because they are usually warmer and have lower velocities and more stable substrates which allow for the accumulation of detritus. Hoffknecht (1981) found that lower velocities and the deposition of detritus in backwater habitats have contributed to increased numbers of benthic invertebrates in backwaters over mainchannel habitats in the Colorado River, Grand Canyon.

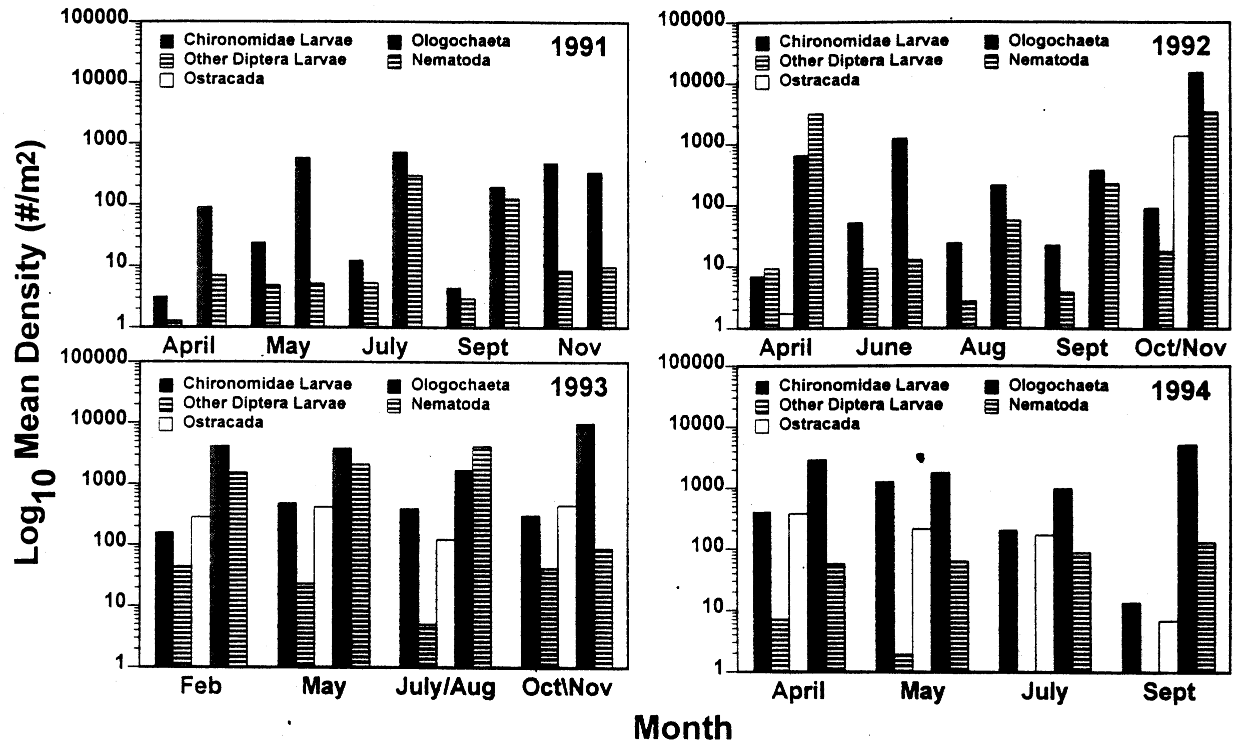

Fig. 35. Log_{10} mean density (#/m^2) by month of backwater benthic invertebrates collected during AGFD sampling of the Colorado River, Grand Canyon, 1991-94.

Table 15. Mean and standard deviation of densities (number/m^2) of benthic invertebrate species collected in backwater and mainchannel habitats during AGFD sampling of the Colorado River, Grand Canyon, 1991 - 1994.

	Backwater		Mainchannel	
Year/Taxa	Mean	Standard Deviation	Mean	Standard Deviation
1991				
Amphipoda	4.88	1.86	4.72	1.84
Aphididae	0	0	0	0
Chironomidae - larvae	21.08	9.26	6.57	2.89
Collembola	0.2	0.2	0	0
Diptera - adults	5.52	2.02	1.36	0.64
Ephemeroptera	0.2	0.2	0	0
Formicidae	1.12	0.84	0	0
Gastropoda	2.35	1.1	1.7	1.1
Hemiptera	0	0	0	0
Homoptera	0	0	0	0
Hymenoptera	0.2	0.2	0	0
Nematoda	210.99	139.77	14.09	12.12
Odonata	0	0	0	0
Oligochaeta	524.46	250.72	154.94	130.8
Ostracoda	0	0	0	0
Pelecypoda	0	0	0	0
Plecoptera	0	0	0	0
Simuliidae	3.46	1.48	0.24	0.24
Thysanoptera	0	0	0	0
Trichoptera	0.2	0.2	0	0
Total	774.66	360.05	183.61	136.09
1992				
Amphipoda	4.46	1.96	1.32	0.96
Aphididae	0	0	0	0
Chironomidae - larvae	55.34	12.02	9.85	4.99
Collembola	0	0	0	0
Diptera - adults	13.67	4.93	5.7	3.59
Ephemeroptera	0.07	0.07	0	0
Formicidae	0	0.28	0.2	0.2
Gastropoda	4.39	2.4	0.07	0.07

Table 15 continued.

Year/Taxa	Backwater Mean	Backwater Standard Deviation	Mainchannel Mean	Mainchannel Standard Deviation
1992 cont'd				
Hemiptera	0.47	0.29	0.07	0.07
Homoptera	0.2	0.2	0	0
Nematoda	2,230.3	1,801.81	16.21	8.7
Odonata	0.27	0.27	0	0
Oligochaeta	2,549.85	1,010.95	37.5	12.61
Ostracoda	127.38	89.64	1.58	0.92
Pelecypoda	0	0	0	0
Plecoptera	0	0	0	0
Simuliidae	0.2	0.2	0.4	0.28
Thysanoptera	0.4	0.4	0	0
Trichoptera	0	0	0.4	0.28
Total	4,989.06	2,247.72	73.35	19.65
1993				
Amphipoda	8.72	3.41	0	0
Aphididae	0.68	0.68	0	0
Chironomidae - larvae	469.78	129.14	2.24	1.26
Collembola	0	0	0	0
Diptera - adults	38.38	11.2	3.14	2.7
Ephemeroptera	1.88	1.36	0	0
Formicidae	0.17	0.17	0	0
Gastropoda	2.22	1.44	0.45	0.45
Hemiptera	0	0	0	0
Homoptera	0	0	0	0
Hymenoptera	0	0	0	0
Nematoda	2,489.82	967.18	4.94	2.24
Odonata	0	0	0	0
Oligochaeta	7,510.35	2,890.91	41.31	24.36
Ostracada	463.19	173.16	0.45	0.45
Pelecypoda	1.03	1.03	0	0
Plecoptera	0	0	0	0
Simuliidae	1.88	1.07	0.45	0.45
Thysanoptera	0	0	0	0
Trichoptera	0	0	0	0
Total	10,988.56	3,328.58	52.98	26.77

Table 15 continued.

Taxa	Backwater Mean	Backwater Standard Deviation	Mainchannel Mean	Mainchannel Standard Deviation
1994				
Amphipoda	9.36	2.88	0.8	0.48
Aphididae	0	0	0	0
Chironomidae - larvae	592.53	101.15	23.95	5.64
Collembola	0	0	0	0
Diptera - adults	2.93	1.03	0.6	0.44
Ephemeroptera	0	0	0	0
Formicidae	0.98	0.64	0	0
Gastropoda	5.46	2.45	0.2	0.2
Hemiptera	0	0	0	0
Homoptera	0	0	0	0
Hymenoptera	0	0	0	0
Nematoda	111.56	29.61	3.59	1.16
Odonata	0.2	0.2	0	0
Oligochaeta	3,589.61	1,203.59	59.97	14.96
Ostracoda	249.84	93.71	3.79	2.71
Pelecypoda	7.41	4.79	1.1	0.85
Plecoptera	0	0	0	0
Simuliidae	5.66	2.29	0.2	0
Thysanoptera	0	0	0	0.2
Trichoptera	5.27	1.97	0	0
Total	4,580.80	1,239.10	0.6 94.79	0.34 20.07

Table 16. Results of the Kruskal-Wallis (year, season, and reach) and Mann-Whitney *U* (habitat) tests for significant differences in benthic invertebrate density by year, season, reach, and habitat collected during AGFD sampling of the Colorado River, Grand Canyon, 1991 - 1994.

Taxa	*Year	*Season	*Reach	**Habitat
Total	$P=0.0001$	$P=0.0001$	$P=0.0001$	$P=0.0001$
Chironomidae - larvae	$P=0.0001$	$P=0.0001$	$P=0.0001$	-
Diptera - larvae	$P=0.0001$	$P=0.0015$	$P=0.0041$	-
Ostracoda - adults	$P=0.0021$	$P=0.0601$	$P=0.0030$	-
Oligochaeta	$P=0.0001$	$P=0.0193$	$P=0.0001$	-
Nematoda	$P=0.0001$	$P=0.0668$	$P=0.0001$	-

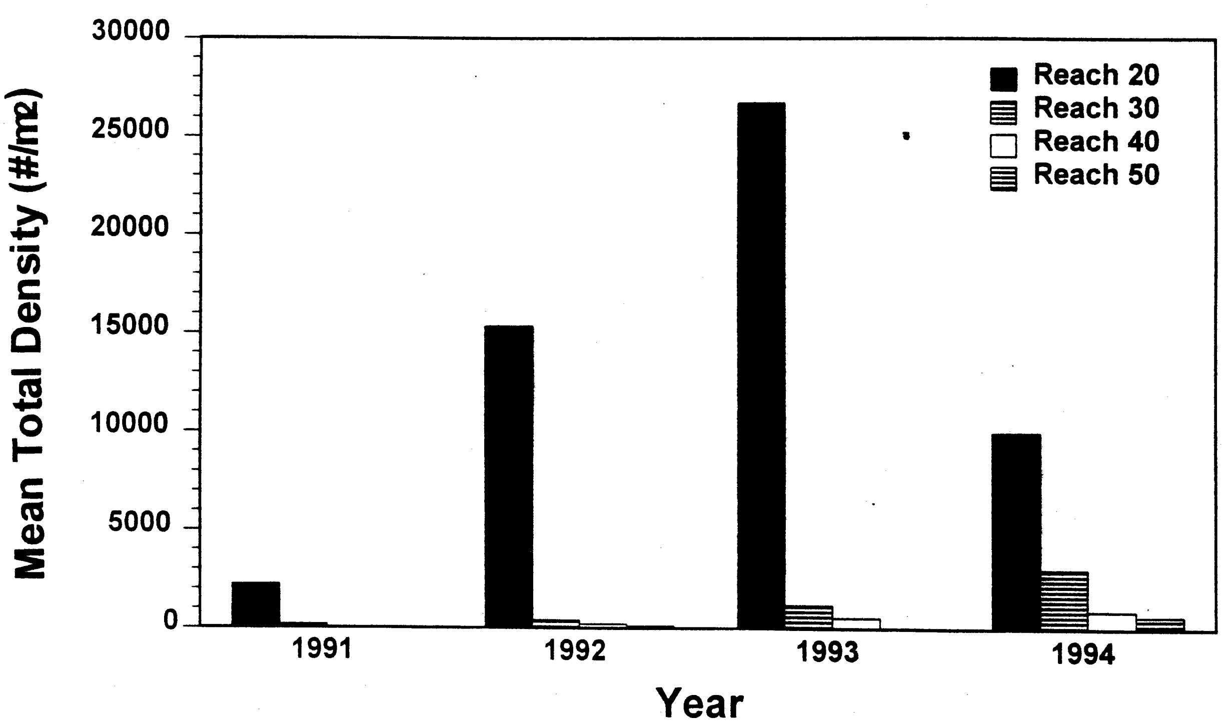

Fig. 36. Mean total density (#/m^{2}) by reach of backwater benthic invertebrates collected during AGFD sampling of the Colorado River, Grand Canyon 1991-94.

Objective 3.5.d. Sample larval to juvenile native fish from backwaters, tributary confluences, tributaries above the confluence zone and outlying mainchannel habitats for analysis of digestive tracts.

This section addresses the diet of the small fish found in backwaters of the Colorado River, Grand Canyon. The objective was to collect information concerning food habits of native and non-native fish. Also, the presence and numbers of the Asian tapeworm (*Bothriocephalus acheilognathi*) in the GI tracts was noted. This diet information will be used later to determine the relative importance of specific food items to each species, preference of specific food items, and the amount of overlap in diet between species of fish.

METHODS

A systematic sampling of fish collected in backwaters was performed in 1994, during Trips 22-25 (April - September 1994). All fish were collected in conjunction with benthic invertebrate and zooplankton samples (Type A protocol) and only from backwater habitats. Collection of these data were in a manner that the data can be used with the benthos and zooplankton data to compare dietary preferences and relative abundance by species and reach (Krebs 1989; Bowen 1983). Five fish were collected of each species < 30 mm in total length and five fish of each species > 30 mm in total length in each of eight subreaches on each trip (Table 17). Due to restrictions on their take, humpback chub were collected only from the two subreaches below the Little Colorado River, except during our March-April trip. Incidental mortalities resulted in increased sample sizes of some species in some reaches. Fish were preserved in 70% ethanol. Total length (mm), weight (g), and species of each fish was recorded along with study number, river mile, and habitat.

Diet was determined for all fish by examination of the stomach contents. Due to the size of some of the fish, the stomach was defined as the portion of the digestive tract anterior to the first loop (Greger and Deacon 1988). Stomach contents were examined by excising the stomach, opening it, and flushing with water. The stomach lining was examined for parasites and additional food items that remained attached to the stomach lining. The stomach contents were examined under a stereo dissection microscope and food items classified and enumerated according to taxa. Prey items were identified to taxa levels that were consistent with benthic and zooplankton samples. Formicids, thysanopterans, aphids, hymenopterans, and adult dipterans were combined into a terrestrial insect category. Enumeration of cestodes was difficult due to the preservative and breakage. Therefore, only presence or absence of cestodes was noted. Similarly, human food and the alga *Cladophora*, which were eaten by rainbow trout, were also difficult to enumerate and were only noted as being present or absent.

RESULTS

Gut contents were analyzed from 699 fish collected during all four sampling trips in 1994 (Table 17). Mean size of all species ranged from 29.2 - 35.2 mm TL and 0.9 - 1.2 g (Table 18), except for rainbow trout which were considerably larger (262.4 mm and 287.51 g).

At least 97% of all species contained some food in their stomach. Chironomids (larvae and/or pupae) were the most prevalent food item in all species, ranging from 17.5% prevalence in plains killifish to 62.0% in bluehead suckers (Table 19). Chironomids were also the most numerous food item found in the stomachs of all fish. In small fish (all fish other than rainbow trout) a mean of 4.9 individuals / stomach were found (Table 20). Other common items (number and/or prevalence) in the stomachs of small fish include: ceratopogonids, terrestrial insects (formicids, thysanopterans, and adult dipterans), cladocerans, copepods, simuliids, ostracods, and nematodes.

Chironomids were found in 62% of the bluehead sucker stomachs. Other prey items found in at least 5% of the stomachs included: cladocerans, terrestrial insects, and simuliids (Table 19). A mean of 14.6 chironomids/stomach were found (Table 20). Cladocerans and ceratopogonids were found with a mean of nearly one in each bluehead sucker stomach. Chironomids were found in 38.5% of the flannelmouth sucker stomachs with cladocerans, ceratopogonids, terrestrial insects, copepods, and nematodes being found in at least 5% of the samples (Table 19). A mean of 6.7 chironomids/stomach were found with ceratopogonids, copepods, and cladocerans averaging 1 - 2/stomach (Table 20).

Humpback chub had the most varied diet of all species examined, with 19 food items being found. Chironomids were found in 32.2% of the stomach samples (Table 19). Terrestrial insects, simuliids, and copepods were also prevalent. Chironomids were the most numerous food item (6.0/stomach) and a mean of at least one terrestrial insect and copepod per stomach were also found (Table 20).

In speckled dace, chironomids were found in 59.4% of the stomachs (Table 19). Simuliids, terrestrial insects, and cladocerans were also commonly found. A mean of 4.8 chironomids/stomach were found (Table 20).

Chironomids were found in 46.8% of the fathead minnows examined (Table 19). Also common were ceratopogonids, terrestrial insects, simuliids, and cladocerans. Chironomids (2.7/ stomach) were the most numerous food item in fathead minnows (Table 20).

Chironomids were found in 36.0% of the sampled plains killifish (Table 19). Ceratopogonids, nematodes, tricopterans, terrestrial insects, and amphipods were also commonly found. Chironomids were also the most numerous prey item (3.6/stomach; Table 20).

The rainbow trout were much larger than the other fish examined in this study. However, chironomids were still the most prevalent prey item, being found in 17.5% of the stomachs (Table 19). The alga *Cladophora*, amphipod (*Gammarus lacustris*), simuliids, human food (rice, beans, corn, noodles, etc.), and terrestrial insects were also prevalent. A mean of 15.3 chironomids/stomach were found in the sampled rainbow trout along with gastropods, simuliids, terrestrial insects, amphipods, oligochaetes, ostracods, and cladocerans (Table 20).

GI tract parasites were found in 10.6% of the humpback chubs, 3.7% of the speckled dace, 5.0% of the fathead minnows, and 8.0% of the plains killifish examined in 1994 (Table 19). All parasites were cestodes and tentatively identified as *Bothriocephalus acheilognathi*. No parasitic nematodes were found in this study.

Table 17. Number of fish of each species collected for examination of stomach contents in each AGFD mainstem Colorado River sampling trip in 1994, total number collected, and number containing food.

Species	Trip 22	Trip 23	Trip 24	Trip 25	Total	Number Full
Bluehead Sucker	47	160	68	17	292	290
Flannelmouth Sucker	17	76	28	18	139	139
Humpback Chub	32	47	10	27	116	116
Speckled Dace	29	71	25	27	152	152
Fathead Minnow	33	42	11	7	93	93
Plains Killifish	3	4	2	19	28	28
Rainbow Trout	11	9	2	40	62	60
Total	125	354	131	89	699	697

Table 18. Minimum, maximum, and mean length and weight of fishes examined for diet by AGFD from the Colorado River, Grand Canyon, during 1994.

Species	Length			Weight		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Bluehead Sucker	12	106	29.2	0.1	9.1	0.90
Flannelmouth Sucker	15	98	34.7	0.1	8.8	1.20
Humpback Chub	12	110	33.4	0.1	10.5	0.87
Speckled Dace	12	72	34.5	0.1	3.6	0.90
Fathead Minnow	12	77	33.7	0.1	5.4	0.85
Plains Killifish	21	57	35.2	0.2	2	0.78
Rainbow Trout	22	416	262.4	0.3	816	287.51

Table 19. Percentage of fish containing each invertebrate taxa and parasitic cestodes from bluehead sucker (BHS), flannelmouth sucker (FMS), humpback chub (HBC), speckled dace (SPD), fathead minnow (FHM), plains killifish (PKF), and rainbow trout (RBT) collected during four AGFD mainstem Colorado River, Grand Canyon, sampling trips (Trips 22-25), 1994.

	Fish Species						
Invertebrate Taxa	BHS	FMS	HBC	SPD	FHM	PKF	RBT
Acarina	0.0	1.0	1.1	0.9	0.0	4.0	0.0
Amphipoda	0.5	1.3	1.5	1.4	0.0	8.0	12.7
Bivalves	0.0	0.0	1.1	0.0	0.0	0.0	1.1
Chironomidae	62.0	38.5	32.2	59.4	46.8	36.0	17.5
Cladocerans	18.6	15.4	4.5	9.6	6.3	4.0	3.7
Cladophora	0.0	0.0	0.0	0.0	0.0	0.0	14.8
Copepoda	0.5	7.7	7.2	1.4	0.0	0.0	0.0
Coleoptera	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Ceratopogonidae	3.3	13.7	1.5	1.4	16.2	12.0	2.1
Culicidae	0.0	0.0	1.5	0.0	0.0	0.0	0.0
Insect Eggs	0.0	0.0	1.5	0.0	0.0	0.0	0.0
Human Food	0.0	0.0	0.0	0.0	0.0	0.0	9.5
Gastropods	0.0	0.0	0.0	0.0	0.0	0.0	2.6
Hydracarina	0.5	0.0	0.8	0.0	0.0	0.0	0.0
Nematoda	1.2	6.0	0.8	0.9	2.7	10.0	3.2
Nematomorpha	0.0	0.0	0.0	0.0	0.0	0.0	1.1
Oligochaeta	0.0	0.0	0.8	0.0	0.0	0.0	4.8
Ostracoda	0.7	1.0	3.0	0.0	0.0	0.0	2.6
Plecoptera	0.0	0.0	1.1	0.0	0.0	0.0	0.0
Seeds	0.0	0.0	1.5	0.0	0.0	0.0	0.0
Simuliidae	5.6	4.0	7.6	11.4	7.2	0.0	12.2
Terrestrial Insects [1]	7.2	9.0	17.8	10.0	15.3	8.0	8.5
Tricoptera	0.0	1.3	0.8	0.0	0.0	10.0	2.1
Cestodes [2]	0.0	0.0	10.6	3.7	5.4	8.0	0.0

[1] Terrestrial insects were comprised of formicids, thysanopterans, aphids, hymenopterans, and adult dipterans.

[2] Cestodes were the Asian fish tapeworm (*Bothriocephalus acheilognathi*).

Table 20. Mean number of each invertebrate taxa in GI tracts from bluehead sucker (BHS), flannelmouth sucker (FMS), humpback chub (HBC), speckled dace (SPD), fathead minnow (FHM), plains killifish (PKF), and rainbow trout (RBT) collected during four AGFD mainstem Colorado River, Grand Canyon sampling trips (Trips 22-25), 1994.

	Fish Species							
Invertebrate Taxa	BHS	FMS	HBC	SPD	FHM	PKF	RBT	TOT
Acarina	0.0	<0.1	<0.1	<0.1	0.0	<0.1	0.0	<0.1
Amphipoda	<0.1	<0.1	<0.1	<0.1	0.0	0.2	4.9	<0.1
Bivalves	0.0	0.0	<0.1	0.0	0.0	0.0	<0.1	<0.1
Chironomidae	5.7	6.7	6.0	4.8	2.7	3.6	15.3	4.9
Cladocerans	0.8	1.2	0.3	0.3	0.4	<0.1	1.4	0.5
Cladophora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	<0.1
Copepoda	<0.1	1.6	1.3	<0.1	0.0	0.0	0.0	0.5
Coleoptera	0.0	0.0	<0.1	0.0	0.0	0.0	0.0	<0.1
Ceratopogonidae	0.7	1.7	<0.1	0.6	0.6	0.4	0.1	0.7
Culicidae	0.0	0.0	0.1	0.0	0.0	0.0	0.0	<0.1
Insect Eggs	0.0	0.0	<0.1	0.0	0.0	0.0	0.0	<0.1
Gastropods	0.0	0.0	0.0	0.0	0.0	0.0	9.9	<0.1
Hydracarina	<0.1	0.0	<0.1	0.0	0.0	0.0	0.0	<0.1
Nematoda	<0.1	0.4	<0.1	<0.1	<0.1	0.1	0.2	0.1
Nematomorpha	0.0	0.0	0.0	0.0	0.0	0.0	<0.1	<0.1
Oligochaeta	0.0	0.0	<0.1	0.0	0.0	0.0	2.7	<0.1
Ostracoda	<0.1	0.2	0.4	0.0	0.0	0.0	1.9	0.1
Plecoptera	0.0	0.0	<0.1	0.0	0.0	0.0	0.0	<0.1
Seeds	0.0	0.0	<0.1	0.0	0.0	0.0	0.0	<0.1
Simuliidae	0.1	0.2	0.4	0.3	0.1	0.2	5.1	0.2
Terrestrial Insects [1]	0.2	0.4	1.4	0.3	0.6	0.4	5.0	0.6
Tricoptera	0.0	<0.1	<0.1	0.0	0.0	0.0	<0.1	<0.1

[1] Terrestrial insects were comprised of formicids, thysanopterans, aphids, hymenopterans, and adult dipterans.

DISCUSSION

The invertebrate taxa most common in the GI tracts were generally also common in the plankton and benthic invertebrate samples, with a few exceptions, indicating little selection for or against specific prey items by these fish. Chironomids were the most common prey item in both prevalence and number of individuals/stomach in all fish species examined. Chironomids ranked second in availability of all benthic invertebrates in the environment. Oligochaetes were the most common benthic invertebrates in the environment, particularly in Reach 20, but were consumed by 0.8% of the humpback chub and 4.8% of the rainbow trout. We speculate that these invertebrates are less susceptible to predation by fish than to our sampling methods. It would seem unlikely that these fish would avoid a soft-bodied prey item such as these if it were available to them. Since all other fish in this study were small (YOY or age 1), it may be that oligochaetes are found too deep in the sediments to be available to these small fish. Larger, e.g., rainbow trout, may have been able to access this food source. Ostracods, nematodes, amphipods, simuliids, and tricopterans were all consumed by most or all of the fishes sampled. Pelecypods were not consumed by any fish and gastropods were only consumed by rainbow trout. Terrestrial insects were also common food items for all species. However, it may be difficult to estimate preference or avoidance of these prey items since our benthos and zooplankton samples may have been inadequate to sample them.

Cladocerans were the most common zooplankton in the diet of all species, but ranked behind copepods, rotifers, and ostracods in the environment. Copepods, were also eaten by all native fishes, but in few numbers. Ostracods were consumed by low numbers of bluehead and flannelmouth suckers, humpback chub, and rainbow trout. Rotifers were not found in the stomachs of any fish. It appears that cladocerans are selected by these fish, rotifers are not selected, while the other zooplankton may be eaten in proportion to their presence in the environment.

However, oligochaetes were found in large numbers in benthic invertebrate samples but not in the stomach samples. Oligochaetes were eaten by humpback chub, but were common only in the GI tracts of rainbow trout.

The Asian fish tapeworm (*Bothriocephalus acheilognathi*) was recently introduced into the Little Colorado River (Brouder and Hoffnagle *in press*). This parasite is known to infect planktivorous cyprinids when the fish consume procercoid-infected copepods (Hoffman and Schubert 1984). It has been found to infect humpback chub, speckled dace, fathead minnows, and plains killifish (Heckmann et al. 1993; Clarkson et al. *in review*; Brouder and Hoffnagle *in press*). However, *B. acheilognathi* is thermophilic (Hoffman and Schubert 1984) and, thus, may not invade the cold water of the mainstem Colorado River. It is likely that all fishes found to be infected in this study were infected while residing in the Little Colorado River.

B. acheilognathi has been known to cause high mortality in fish (Hoffman and Schubert 1984). Many humpback chub captured during Trip 20 had distended stomachs. A few of these were examined in the field and found to contain large masses of intestinal tapeworms, probably sufficient to block the gastrointestinal tract of these fish. Appendix 14 provides a further discussion of the distribution and prevalence of *B. acheilognathi* in the Colorado River and tributaries in Grand Canyon.

These results provide a cursory view of the diet of these species. Since these fish were collected in conjunction with benthic invertebrate and zooplankton collections, future detailed analyses of preference for various prey items and diet overlap between species is planned.

Objective 3.6. Determine the behavioral responses of larval to juvenile native fishes to changing environmental conditions in rearing habitats.

This objective addresses the behavioral responses of juvenile fishes to environmental conditions caused by Glen Canyon Dam. Fluctuating flows have the potential to force juvenile fish out of backwaters or tributaries into the mainchannel Colorado River, where the water is usually colder and velocities greater. The use of mainstem (mainchannel beachface and backwater) habitats under different discharges and flow stages is examined.

***Objective 3.6.a.* Measurement of the associated behavioral responses by young fish to different flow regimes.**

This objective examines how larval and juvenile fishes respond to changing environmental conditions. In particular, the changes in flow stage and the changes in environmental variables that are caused by these fluctuations.

METHODS

Fish were captured in mainchannel and backwater habitats using seines in 1993 and 1994. Seines could rarely be used in tributaries due to the presence of obstructions. Therefore, tributaries were not included in these analyses. During 1991 and 1992, minnow traps were used in an attempt to answer this objective. However, extremely low catches (<1 - 13 % of the traps contained at least one fish of a particular species) made this approach infeasible. Therefore, only the seine data is presented here. During each collection period, variables were measured and recorded, including: temperature, turbidity, conductivity, pH, dissolved oxygen, velocity, depth, estimated mainchannel discharge, and stage of flow.

These analyses were restricted to fish < 150 mm TL and included juvenile humpback chub, flannelmouth suckers, bluehead suckers, rainbow trout, and juvenile and adult speckled dace and fathead minnow. Catch-per-unit-effort was calculated as number of fish caught/100 m^2 seined. Logistic regression (α=0.05) was used to analyze the data due to a large number of 0 catches (Hosmer and Lemeshow 1989). Due to inconsistencies in the data, two separate regressions were run for each native and two exotic species (fathead minnow and rainbow trout) and total catch. The first regression tested presence of fish vs. discharge, habitat, reach, and flow stage). The second regression tested presence of fish vs. the environmental variables (habitat, temperature, turbidity, dissolved oxygen, pH, conductivity, depth, and velocity). A pseudo-R^2 value (Myers 1990) was calculated by the method provided in the Stata 3.1 Reference Manual (1994). A sequential Bonferroni test was used to discern differences within effects in significant regressions (Rice 1989) with critical α = 0.05/number of comparisons.

RESULTS

Presence of small fish in the collection was significantly related to the discharge variables (P=0.0001; R^2=0.171). Fish were more likely to be caught in backwaters than along mainchannel beachfaces (P=0.0001) . We were more likely to catch fish in Reach 30 than any other reach ($P \leq 0.05$), but there was no difference in catches between the other reaches. We were also more likely to catch fish in a steady low flow stage than in a descending flow stage ($P\leq0.05$). Total catch was also significantly related to the environmental variables (P=0.0001; R^2=0.391). We were more likely to catch fish as turbidity increased (P=0.0008).

Presence of juvenile bluehead sucker in the catch was significantly related to the discharge variables (P=0.0001; R^2=0.153). Bluehead suckers were more likely to be caught in backwaters than along mainchannel beachfaces (P=0.0001). Seine hauls in Reaches 40 and 50 were more likely to contain bluehead suckers than the other two reaches, and Reach 20 was less likely to contain bluehead suckers than any other reach ($P\leq0.05$). Seine hauls conducted under steady low flow stages were more likely to collect bluehead suckers than hauls conducted under descending stages ($P\leq0.05$). The presence of bluehead suckers in a seine haul was also related to the environmental variables (P=0.0001; R^2=0.238). However, no individual environmental variable was significant ($P\geq0.1184$).

Presence of juvenile flannelmouth sucker in a seine haul was significantly related to the discharge variables (P=0.0001; R^2=0.165). Flannelmouth suckers were more likely to be collected in backwater hauls than mainchannel hauls (P=0.0001). They were also more likely to be found in collections made in Reach 50 than all other reaches ($P\leq0.05$) and during steady low or steady high flow stages than ascending or descending flow stages ($P\leq0.05$). The presence of flannelmouth suckers in a seine haul was significantly related to the environmental variables (P=0.0001; R^2=0.317) and increased with increasing temperature (P=0.0007) and turbidity (P=0.0372).

Juvenile humpback chub presence in a seine haul was significantly related to the discharge variables (P=0.0001; R^2=0.307). Humpback chub were more often caught in backwaters than along mainchannel beachfaces (P=0.0001). They were also more likely to be a component of the catch in Reach 30 than any other reach ($P\leq0.05$). There was no significant difference in likelihood of capture for humpback chubs among any flow stage. Presence of humpback chub was significantly related to the environmental variables (P=0.0001; R^2=0.296). The probability of capturing humpback chub increased as turbidity increased (P=0.0001) and dissolved oxygen decreased (P=0.0219).

The presence of speckled dace in the catch was significantly related to the discharge variables (P=0.0001; R^2=0.158). Speckled dace were more likely to be found in backwater seine hauls than from mainchannel beachfaces (P=0.0001). They were captured more frequently in Reach 50 than all other reaches ($P\leq0.05$) and during steady low flow stages than any other flow stage ($P\leq0.05$). Speckled dace presence was also related to the environmental variables (P=0.0001; R^2=0.299), being more likely to be present in the catch when temperature (P=0.0275) and turbidity (P=0.0201) increased.

Fathead minnow presence in a seine haul was significantly related to the discharge variables (P=0.0001; R^2=0.219) and were more commonly caught in backwaters than along mainchannel beachfaces (P=0.0001). Fathead minnows were less likely to be captured in Reach 20 than any other reach ($P\leq0.05$). Fathead minnow presence in a seine haul was also more likely during a steady low flow stage than during a descending stage. Presence of fathead minnows in the catch was significantly related to the environmental variables (P=0.0001; R^2=0.334). The likelihood of capturing fathead minnows increased as turbidity (P=0.0270) and conductivity (P=0.0035) increased and depth (P=0.0173) decreased.

Presence of juvenile rainbow trout in a collection was significantly related to the discharge variables (P=0.0001; R^2=0.154) and they were also more commonly collected in backwaters than along mainchannel beachfaces (P=0.0233). Rainbow trout were more likely to be found in Reach 20 than any other reach and were less likely to be found in Reach 50 than any other reach ($P \leq 0.05$). There was no difference in likelihood of capture between Reaches 30 and 40. There also was no difference in the likelihood of catching rainbow trout under any of the flow stages. Presence of rainbow trout in a seine haul was significantly related to the environmental variables (P=0.0001; R^2=0.128). The likelihood of catching rainbow trout increased with decreases in conductivity (P=0.0467).

DISCUSSION

These data show that juvenile fishes of all species are more commonly caught in backwaters than along mainchannel beachfaces. They were also more likely to be caught in Reach 30 than any other reach. Juvenile fish were more likely to be captured under a steady low flow stage in four of the six species examined, plus total catch of all species. The presence of juvenile fishes in the catch was positively affected by increases in turbidity in four of the six species examined, plus total catch of all species. Temperature (increasing), conductivity (increasing or decreasing), and dissolved oxygen (decreasing) were also related to the presence of juvenile fishes of one or more species.

The higher catches of all species of fish in backwaters as compared to mainchannel beachfaces is not surprising. Backwaters are warmer, have little or no water velocity (see Objective 3.4.a), and usually contain structure of some type (e.g., vegetation, rocks, or tree branches). In comparison, mainchannel beachfaces are largely barren expanses of sand with sometimes strong current velocities (although slower than velocities further from shore) and cooler temperatures. The lack of structure probably makes fish less likely to use these areas during daylight hours or when turbidity is low. Also, we cannot discount the possibility that water conditions and our seining methods have affected these results. Under low turbidity conditions, particularly in the mainchannel, the fish may have been able to see our seine and avoid it. In backwaters, the entire width of the backwater was covered by the seine and we moved from deep to shallow areas, making avoidance more difficult.

Catch of each species varied by reach with the total catch being highest in Reach 30. The likelihood of catching small fish of a particular species in a particular reach is probably strongly related to the presence or absence of spawning areas for that species within the reach. No known spawning areas for bluehead suckers are found above the LCR, nor are bluehead suckers of any size. Bluehead and flannelmouth suckers are both more likely to be found in the lower reaches, particularly Reach 50, which is found below Kanab and Havasu Creeks where they are known to spawn in large numbers. Although other areas are suspected, the largest spawning area for humpback chub is in the LCR, making it most likely that they will be caught in Reach 30. Speckled dace are found throughout the system, but probably prefer the warmer waters of Reach 50. Fathead minnows probably reached the Grand Canyon via the upper Little Colorado River drainage where there are warmwater reservoirs containing these fish (probably introduced for forage for game species or by bait bucket introductions). These exotics have expanded their range downstream, but have not moved far upstream in the cold, swift waters of the Colorado River and are less likely to be captured in Reach 20. Rainbow trout are stocked at Lee's Ferry and spawn in that and other areas in Reach 20 and are commonly caught there. Probably due to turbidity from the LCR, they are less common in Reach 30 and below, except near cool, clear tributaries where they can spawn.

Juvenile fishes are more frequently a part of the catch during steady low flows than they are during descending flows. Fishes in the Colorado River evolved under a regime of long-term (seasonal) fluctuations in river level, as opposed to short-term (daily) fluctuations now present in the regulated system (Minckley 1991). They leave shallow nearshore areas when water levels are dropping, probably a response to avoid stranding. We sampled many isolated backwaters in the Grand Canyon and, except for one very deep one, have found extremely few native fishes stranded in them. This indicates that fluctuating water levels do not need to desiccate or isolate a backwater to have detrimental affects on larval and juvenile native fishes.

It appears that juvenile fish were more susceptible to seining when turbidity was high. This is also expected since these fish also evolved in a muddy stream and, thus, are probably uncomfortable in shallow water when the water is clear and they are visible to potential terrestrial and/or avian predators. Under clear water conditions, they probably seek deeper water than we were able to seine effectively or areas of cover which are also difficult to effectively seine. This would have the effect of limiting our catch under clear water conditions. Again, we cannot discount the possibility that clear water also allowed the fish to see our seine better and avoid it, particularly in the mainchannel.

The presence of flannelmouth sucker and speckled dace in the catch was significantly related to increasing temperature. This can be interpreted in a number of ways. Firstly, that temperature may not have been a factor determining where other fishes, including humpback chub and bluehead sucker, were caught. This is unlikely considering that these fish evolved in a warmwater system and are now subjected to cold water. Bulkley et al. (1982) found that the preferred temperature for juvenile (80-120 mm) humpback chub was 21.0-24.4°C and it is likely that the preferred temperature for the other Colorado River native species is similar to this range. In fact, the water released by Glen Canyon Dam rarely reaches the likely preferred range for these species (see Objective 3.4.a). Secondly, since these waters are colder than the preferred temperature of these fish, it may be that they select habitats based on other factors, such as turbidity or food density. Thirdly, since all species of fish were more commonly caught in backwaters, this may indicate a preference for warmer water, since backwaters are significantly warmer than the mainchannel (see Objective 3.4.a).

Catch of both fathead minnow (positively) and rainbow trout (negatively) was shown to be related to increasing conductivity. Fathead minnows come from relatively warm, slow streams. Since conductivity was significantly higher in backwaters than in the mainchannel, this result may simply reflect a preference for backwater habitats. The negative relationship between rainbow trout presence in the catch and increasing conductivity is probably due to the increased prevalence of rainbow trout in Reach 20 which also had a significantly lower mean conductivity than all other reaches (see Objective 3.4.a).

The presence of humpback chub in the catch was found to be negatively related to increases in dissolved oxygen levels. Again, this may be related to backwater conditions, which were preferred by all species. Dissolved oxygen was significantly lower in backwaters than in the mainchannel. However, this result should not be interpreted to mean that humpback chub prefer poorly oxygenated water. The levels of dissolved oxygen recorded in this study were rarely at levels that would affect fish growth or habitat preference (Boyd 1979; Piper et al. 1982). No fish of any species were captured in the few areas where dissolved oxygen levels were extremely low.

Of interest was that the presence of any species in the catch was not significantly related to changes in velocity. Since a vast majority of the fish were captured in backwaters, which have significantly less velocity than the mainchannel, this may also simply reflect a preference for backwaters by these small fish.

These data were difficult to analyze and further analysis is clearly indicated. Further analyses of CPUE and habitat, map, benthic invertebrate and plankton data, and species associations may shed further light on a clearly complex relationship. Population estimates were completed for most backwaters sampled under the Type A protocol and these data should be analyzed with habitat, map, benthic invertebrate, and plankton data.

Previous analyses indicate that, juvenile native fish spawn in tributaries, particularly the LCR and Bright Angel, Shinumo, Kanab, and Havasu Creeks (see Objective 3.1). It appears that they spend a short amount of time there (except, possibly in the LCR) and then move (actively or passively) into the mainstem Colorado River. Once in the mainstem, they prefer backwaters, which are warmer, have low velocity and more food (benthic invertebrates). Fluctuating flows appear to be detrimental to larval and juvenile fishes, since they were less likely to be captured when water levels are decreasing, and may force fish out of backwaters and into the mainchannel. The mainchannel water is colder and less productive, which reduces food availability. There are also more are predators, such as large humpback chub, trout, channel catfish, and striped bass in the mainchannel (Valdez and Ryel 1995). All of these factors will dramatically affect the growth and survival of larval and juvenile fishes.

Objective 3.9. Determine the extent to which limnological factors, with emphasis on water chemistry and aquatic productivity, potentially limit the distribution and abundance of native fishes in the Little Colorado River and other tributaries which might serve as streams for augmentation of humpback chub in Grand Canyon.

***Objective 3.9.a.* Evaluation of water chemistry and hydrologic events as they affect distribution and abundance of fishes directly and secondarily through impacts on productivity of algae and invertebrate food resources.**

This section addresses the feasibility of introducing a new population of humpback chub into other tributaries of the Colorado River in Grand Canyon. The Little Colorado River currently contains the only regularly breeding population of humpback chubs in Grand Canyon. Creating another spawning population of humpback chub was addressed in the Glen Canyon Dam Environmental Impact Statement and is being examined to prevent a complete loss of humpback chubs in the Grand Canyon in the event of a catastrophe in the LCR. The streams in question are Bright Angel Creek, Shinumo Creek, Kanab Creek, and Havasu Creek. Humpback chub have been captured in the mouth or vicinity of each of these streams and it is possible that breeding attempts have been made there. However, no evidence of successful reproduction has been found in any tributary other than the LCR.

METHODS

Water chemistry data were collected each time fish collections were attempted in tributary streams and included temperature, turbidity, dissolved oxygen, pH, specific conductance, and redox potential. However, fish collections were not made regularly in each stream. Still, enough is known about these streams, from this and previous studies, to evaluate the likelihood of humpback chubs successfully reproducing in these streams and the feasibility of such an introduction. Parameters from the LCR were compared with those in Bright Angel, Shinumo, Kanab, and Havasu Creeks, during the same months (March, April, July, and September - months during which all tributaries were sampled), to determine which was closest to the conditions present in the LCR. Our limited data and shortage of coincident samples in LCR and other tributaries make comparisons difficult. Therefore, only qualitative and cursory comparisons have been made.

RESULTS

Habitat variables varied widely among tributaries and month of sampling in specific tributaries (see Objective 3.4.a). Table 21 lists minimum, maximum, mean, standard deviation, and number of samples collected of temperature, turbidity, dissolved oxygen, specific conductance, pH, redox potential, and stream velocity in the Little Colorado River and Bright Angel, Shinumo, Kanab, and Havasu Creeks, calculated for only the months of March, April, July, and September, 1991 - 1994.

Mean temperature during March, April, July, and September in the LCR was 15.13°C. Shinumo Creek had the closest mean temperature (14.81°C) with Havasu Creek being the furthest (20.41°C).

Mean turbidity in the LCR was 1453 NTU. Kanab Creek was closest, with a mean turbidity of 1212 NTU. Bright Angel and Havasu Creeks were the furthest, with mean turbidities of 6 NTU and 10.8 NTU, respectively.

Mean dissolved oxygen level in the LCR was 9.11 mg/L. Bright Angel Creek was the closest, with a mean of 9.20 mg/L and Kanab Creek was the furthest with a mean of 8.38 mg/L.

Mean conductivity in the LCR was 1913 µS/cm. Kanab Creek was the closest, with a mean of 1311 µS/cm. Bright Angel Creek was the furthest with a mean of 300 µS/cm.

Mean pH in the LCR was 8.10. Kanab Creek was closest, with a mean pH of 8.37 and Shinumo Creek was the furthest with a mean of 8.54.

Mean redox potential in the LCR was 353 mV. Bright Angel Creek had the closest mean (382 mV) and Kanab Creek had the furthest (439 mV).

Mean velocity at the sampling site in the LCR was 26.3 cm/s. Bright Angel Creek was the closest, with a mean of 28.5 cm/s and Kanab Creek was the furthest with a mean of 5.1 cm/s.

DISCUSSION

It appears that larval and juvenile humpback chub would be capable of surviving (at least seasonally) in all of the Colorado River, Grand Canyon, tributaries studied. None of the water quality parameters even approached extremes that would be likely to discourage humpback chub from using them for spawning or rearing. However, all of these streams have characteristics which could make creation of a successful, self-sustaining population of humpback chub difficult or unlikely.

Bright Angel Creek had the closest mean dissolved oxygen level, redox, and velocity to those in the LCR. Bright Angel Creek flows year round and does not warm excessively. However, it contains rainbow and brown trout, potential predators of all life stages of humpback chub (Valdez and Ryel 1995). Also, its turbulence may make early life difficult for larval humpback chub. Lastly, it is currently accessible to humpback chubs, but there is no evidence that they use it. Humpback chub are found in the vicinity of Bright Angel Creek, since we captured one adult in the mainchannel, just outside of the mouth, in 1994. The reason for this lack of use should be examined before any introductions are made in Bright Angel Creek.

Table 21. Minimum, maximum, mean, standard deviation, and number of samples collected of temperature, turbidity, dissolved oxygen, specific conductance, pH, redox potential, and stream velocity in the Little Colorado River and Bright Angel, Shinumo, Kanab, and Havasu Creeks during AGFD sampling in March, April, July, and September, 1991-94.

	Tributary				
Variable	Little Colorado River	Bright Angel Creek	Shinumo Creek	Kanab Creek	Havasu Creek
Temperature (°C)					
N	14	5	15	15	7
Minimum	9.8	10	10	11.5	15.1
Maximum	24.6	19.7	21.9	34	23
Mean	15.13	16.99	14.81	20.19	20.41
Standard Deviation	4.52	4.22	5.1	6.38	2.94
Turbidity (NTU)					
N	14	3	11	12	5
Minimum	4	6	2	2	3
Maximum	4,400	6	850	6,300	16
Mean	1,453.3	6	201.2	1,211.9	10.8
Std Dev	1,639.3	0	330.2	2,392.7	7.1
Dissolved Oxygen (mg/L)					
N	11	3	5	9	7
Minimum	4.53	9.2	8.2	6.6	8.1
Maximum	11	9.2	11.2	9.4	9.1
Mean	9.11	9.2	9	8.38	8.46
Std Dev	1.87	0	1.3	0.78	0.38

Table 21 continued.

	Tributary				
Variable	Little Colorado River	Bright Angel Creek	Shinumo Creek	Kanab Creek	Havasu Creek
Specific Conductance (µS/cm)					
N	13	3	5	9	7
Minimum	800	300	300	910	615
Maximum	3,900	300	760	1,900	720
Mean	1,912.7	300	416	1,310.6	662.1
Std Dev	1,055.6	0	199.2	451.3	54.4
pH					
N	3	3	5	8	7
Minimum	7.9	6.1	8.3	8.3	8.4
Maximum	8.3	8.6	8.6	8.6	8.55
Mean	8.1	7.77	8.54	8.37	8.48
Std Dev	0.2	1.44	0.13	0.1	0.08
Redox Potential (mV)					
N	1	3	4	4	3
Minimum	353	382	414	362.5	433
Maximum	353	382	455	464	433
Mean	353	382	423.9	438.6	433
Std Dev	.	0	20.8	50.8	0
Velocity (cm/s)					
N	11	3	11	12	5
Minimum	6	9	1	0	0
Maximum	64	59	131	15	23
Mean	26.3	28.5	22.8	5.1	10.8
Std Dev	20.7	26.3	38	4.1	8.4

Shinumo Creek had the most similar mean temperature to the LCR. Adult and juvenile (>49 mm) humpback chub have been captured in the mouth of Shinumo Creek. However, Shinumo Creek has the problem of a barrier falls just upstream from its mouth, providing a very limited amount of potential spawning area. It also has rainbow and brown trout which would probably prey on young humpback chub.

Kanab Creek had the most similar mean turbidity, conductivity, and pH to the LCR. Humpback chub have also been caught in the mouth of Kanab Creek, including a 34 mm juvenile. Similar to Bright Angel Creek, Kanab Creek is currently accessible to chubs, but no evidence of spawning or use upstream from the mouth has been found. Kanab Creek also contains predators. Green sunfish (*Lepomis cyanellus*) were first found in Kanab Creek in March 1995 and their numbers have been increasing. Also, striped bass have been captured in its mouth and are known from the mainstem in this vicinity (Valdez and Ryel 1995).

Havasu Creek is often thought of as the most suitable stream for introducing humpback chub, because of the belief that the water chemistries of these two streams are most similar. However, in these limited analyses, Havasu Creek was not the closest to LCR in any of the seven measured parameters. Still, it is probable that juvenile humpback chub could survive there. Havasu Creek, like Shinumo Creek, also has a problem of barrier falls a short distance upstream from the mouth, leaving only a relatively small area of fast water over gravel in which to spawn. This area may be suitable for spawning but is unsuitable for rearing. There are no low velocity areas and larval humpback chub would be quickly swept into the mainstem Colorado River where they would probably fare poorly (Lupher and Clarkson 1994). Pre-dam, it is possible or even likely that spring floods in the mainstem caused water in Havasu Creek to back up, covering the falls. This would make several kilometers of Havasu Creek (possibly excellent spawning and rearing habitat) available to chubs and to flannelmouth and bluehead suckers. However, if humpback chub did use this tributary why are they no longer there? It would seem unlikely that all of the fish would be displaced by even a major flood and there are no predators above the barrier falls. This evidence would seem to indicate that humpback chub never used Havasu Creek. Adult humpback chubs (including at least one ripe male), but no larvae or juveniles, have been captured in the mouth of Havasu Creek and may be remnants of a Havasu Creek spawning population. Havasu Creek is also the closest major tributary to the warm water predators moving upstream from Lake Mead. Indeed, striped bass have been caught near Havasu Creek (Valdez and Ryel 1995). This would be a major concern if the mainstem water is to be warmed, as proposed in the Glen Canyon Dam Biological Opinion. Determining a solution to the problem of accessibility beyond the lower falls and the reason why humpback chub are not presently in this tributary would have to be resolved before an introduction of humpback chub into Havasu Creek should be made.

Several of these streams are accessible to humpback chub but are currently not used for spawning. In Bright Angel Creek, turbulence and the presence of salmonid predators may be the reason. In Kanab Creek this may be due to extreme temperatures reached in the summer (34°C in August). In September 1993, we sampled the lowest 1 kilometer of Kanab Creek, but were able to find only 2 dead bluehead suckers and one nearly dead speckled dace. It is likely that with a large amount of algal growth and high temperatures, that Kanab Creek becomes anoxic during the night, killing most fish remaining in it. However, both bluehead and flannelmouth suckers spawn successfully in Kanab Creek, indicating that other factors may be responsible for the non-use of Kanab Creek by humpback chub. Larvae of both species of suckers drift downstream soon after hatching. Humpback chub appear to be more sedentary, a life history trait that might be unsuitable for life in Kanab Creek, given its high summer temperatures.

Flannelmouth and bluehead suckers successfully spawn in Havasu Creek below the barrier falls, but there is no evidence of humpback chub spawning there. However, if humpback chub can survive being swept into the mainstem Colorado River as larvae, then a limited spawning population may be feasible below the falls in Havasu Creek. However, data from AGFD experiments (Lupher and Clarkson 1994) indicate that humpback chub would fare poorly under these conditions. It may be that larval flannelmouth and bluehead suckers are more tolerant of cold shock (further experiments on these species are currently underway). Still, larval and juvenile humpback chub (≥14 mm) have been captured between RM 192-208, but we don't know where these fish were spawned. It is possible that these fish came from the LCR, but it seems unlikely that fish this small could have survived that journey (209 km), making a downstream spawning area seem more likely. There are warm springs below Lava Falls Rapid (RM 179.5) where chubs could, conceivably, spawn and there may be others, of which we are unaware.

Additionally, there appears to be another breeding congregation of humpback chubs in Grand Canyon. Evidence of spawning outside of the LCR was first found by AGFD in 1993. Larval humpback chub were first found at RM 44.27 throughout 1993. Valdez and Ryel (1995) reported adult chub in the area of a series of warm springs near South Canyon (RM 30), suspected to be the spawning site, since no larvae have been found above there. We also found yearling humpback chub in the spring of 1994, and continued to find more larvae and juveniles throughout that year. Bio/West, subsequently found humpback chub larvae (mean total length = 24 mm; Valdez and Masslich 1994) in the upwelling of a warm spring in 1994, providing further evidence that this is the spawning site. The size of the adult population in this area is small and was estimated to be only 52 fish (Valdez and Ryel 1995). Further investigation of this spawning area will proceed.

The evidence of spawning outside of the LCR at RM 30 and in the lower canyon may lessen the need for the introduction of a new spawning population of humpback chub in a Colorado River tributary in Grand Canyon. It also provides evidence that a reduction in the rate and magnitude of fluctuations in dam discharges improves habitat for these endangered fish. These fish were spawning in the mainchannel during Interim Flows, which feature reduced fluctuations. It may be, that spawning activity has been occurring under flow regimes with more drastic fluctuations. However, no evidence of it, in particular larval or juvenile humpback chub, have been found.

In summary, none of the tributaries of the Colorado River, Grand Canyon, appears to be immediately suitable for introduction of humpback chub and the creation of a self-sustaining population. Further investigation of these streams and, especially, the spawning requirements of humpback chub, including the possibility of imprinting (Tyus 1983, 1990), must be completed before any attempt is made at introducing these fish into a tributary.

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Appendix 1. Catalogue of samples collected on each of the 25 Colorado River mainstem trips conducted by AGFD, 1991-1994.

Trip	Dates	Sites	Type A	Type B	Type C	Angle	Oppor	Sonde	Benth	Plank	Sed	Total Map	Plane Map	Vis-cera	Fish Coll
1	28 Mar-13 Apr 1991	215	.	5	.	.	133	1	19	19	20	.	.	.	**391**
2	8-15 May 1991	436	.	15	.	.	188	9	42	41	42	8	.	.	**1,250**
3	8-20 Jul 1991	66	24	.	.	.	18	.	45	46	45	.	41	.	**468**
4	11-24 Sep 1991	137	55	.	.	1	13	.	110	110	110	.	111	20	**930**
5	3-16 Nov 1991	1,913	.	5	.	.	.	.	39	48	43	5	.	.	**345**
6	6-18 Jan 1992	64	15	.	.	2	13	.	33	22	44	.	22	.	**115**
7	19 Feb-3 Mar 1992	1,577	.	5	.	.	.	.	15	10	13	.	.	.	**636**
8	14-25 Apr 1992	99	32	.	.	1	11	.	62	63	62	.	55	.	**1,182**
9	22 May-4 Jun 1992	1,742	.	78	.	.	.	10	24	7	24	5	.	.	**1,031**
10	22 Jun-2 Jul 1992	67	26	.	.	.	14	.	50	50	50	.	25	.	**2,143**
11	6-17 Aug 1992	976	.	44	.	.	.	10	16	20	17	6	.	.	**788**
12	14-25 Sep 1992	59	26	.	.	.	11	.	49	49	49	.	26	.	**1,391**
13	25 Oct-10 Nov 1992	642	.	28	.	.	13	8	30	13	30	.	3	.	**973**
14	15-28 Feb 1993	114	9	.	.	.	89	8	45	14	45	.	10	1	**453**
15	12-26 Mar 1993	150	21	.	.	.	97	2	.	.	.	.	21	.	**932**
16	9-24 Apr 1993	123	16	.	.	.	76	6	.	.	.	.	12	3	**1,371**
17	14-29 May 1993	123	17	.	.	.	71	10	45	15	45	1	16	1	**3,124**
18	13-27 Jun 1993	69	15	.	.	.	27	2	.	.	.	.	17	.	**4,077**
19	22 Jul-5 Aug 1993	96	12	.	.	.	58	.	39	13	39	.	12	.	**4,640**
20	4-16 Sep 1993	95	11	.	.	.	68	1	.	.	.	.	10	.	**4,519**
21	26 Oct-13 Nov 1993	58	6	.	.	.	51	.	57	19	57	.	8	.	**620**
22	5 Apr-16 Apr 1994	98	18	.	5	4	48	10	108	108	108	23	23	.	**3,286**
23	17 May-2 Jun 1994	62	17	.	7	2	8	4	102	102	102	.	17	.	**4,027**
24	28 Jun-10 Jul 1994	108	19	.	2	1	18	2	114	114	114	2	21	.	**2,494**
25	13-28 Sep 1994	140	19	.	1	4	30	2	114	114	114	1	20	1	**1,236**
Total		9,229	358	180	15	15	1,055	85	1,158	997	1,173	51	470	26	**42,422**

Appendix 2. Total number of fish captured and percentage of the catch in each year for each species and total catch in Reach 20 (RM 0 - 61.5) during AGFD mainstem sampling in the Colorado River, Grand Canyon, 1991-1994.

	1991				1992				1993				1994			
	Back		Main		Back		Main		Back		Main		Back		Main	
Species	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Native Species																
Bluehead Sucker	1	0.6	0	0.0	1	0.6	0	0.0	4	0.4	0	0.0	20	3.9	0	0.0
Flannelmouth Sucker	51	29.5	0	0.0	23	14.7	1	100.0	304	28.5	9	20.5	136	26.5	0	0.0
Humpback Chub	0	0.0	0	0.0	0	0.0	0	0.0	46	4.3	8	18.2	27	5.3	0	0.0
Speckled Dace	66	38.2	1	33.3	99	63.5	0	0.0	510	47.8	9	20.5	68	13.2	1	3.8
Total Natives	118	68.2	1	33.3	123	78.8	1	100.0	864	80.9	26	59.1	251	48.8	1	3.8
Exotic Species																
Brown Trout	0	0.0	0	0.0	1	0.6	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Channel Catfish	0	0.0	0	0.0	0	0.0	0	0.0	1	0.1	0	0.0	0	0.0	0	0.0
Common Carp	1	0.6	0	0.0	0	0.0	0	0.0	1	0.1	0	0.0	0	0.0	0	0.0
Fathead Minnow	16	9.2	0	0.0	0	0.0	0	0.0	12	1.1	0	0.0	228	44.4	0	0.0
Green Sunfish	0	0.0	0	0.0	0	0.0	0	0.0	1	0.1	0	0.0	0	0.0	0	0.0
Plains Killifish	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	0.4	0	0.0
Rainbow Trout	38	22.0	2	66.7	32	20.5	0	0.0	189	17.7	18	40.9	33	6.4	25	96.2
Total Exotics	55	31.8	2	66.7	33	21.2	0	0.0	204	19.1	18	40.9	263	51.2	25	96.2
Unidentified Fish	0		0		1		0		0		0		0		0	
Yearly Total	173		3		157		1		1068		44		514		26	

Appendix 3. Total number of fish captured and percentage of the catch in each year for each species and total catch in Reach 30 (RM 61.5 - 87.8) during AGFD mainstem sampling in the Colorado River, Grand Canyon, 1991-1994.

	1991				1992				1993				1994			
	Back		Main		Back		Main		Back		Main		Back		Main	
Species	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Native Species																
Bluehead Sucker	18	5.4	10	30.3	26	2.3	2	4.4	562	9.7	59	5.5	566	10.8	42	17.1
Flannelmouth Sucker	20	6.0	1	3.0	28	2.5	2	4.4	506	8.8	37	3.5	177	3.4	2	0.8
Unidentified Suckers	13	3.9	1	3.0	0	0.0	0	0.0	569	9.9	0	0.0	3	0.1	0	0.0
Humpback Chub	152	45.6	10	30.3	93	8.3	16	35.6	2466	42.7	583	54.4	834	15.9	16	6.5
Speckled Dace	35	10.5	2	6.1	43	3.8	3	6.7	491	8.5	208	19.4	479	9.1	37	15.0
Total Natives	238	71.5	24	72.7	190	16.9	23	51.1	4,594	79.5	887	82.7	2,059	39.2	97	39.4
Exotic Species																
Brook Trout	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	0.1	0	0.0	0	0.0
Brown Trout	1	0.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Channel Catfish	0	0.0	0	0.0	0	0.0	1	2.2	3	0.1	0	0.0	0	0.0	0	0.0
Common Carp	0	0.0	0	0.0	0	0.0	0	0.0	16	0.3	0	0.0	1	0.0	0	0.0
Fathead Minnow	71	21.3	7	21.2	899	80.2	21	46.7	1,087	18.8	145	13.5	3,146	59.9	138	56.1
Plains Killifish	11	3.3	1	3.0	27	2.4	0	0.0	3	0.1	0	0.0	40	0.8	0	0.0
Rainbow Trout	12	3.6	1	3.0	5	0.4	0	0.0	73	1.3	39	3.6	3	0.1	11	4.5
Total Exotics	95	28.5	9	27.3	931	83.1	22	48.9	1,182	20.5	185	17.3	3,190	60.8	149	60.6
Unidentified Fish	2		0		2		0		1,539		0		0		0	
Yearly Total	335		33		1,123		45		7,315		1,072		5,249		246	

Appendix 4. Total number of fish captured and percentage of the catch in each year for each species and total catch in Reach 40 (RM 87.8 - 166.4) during AGFD mainstem sampling in the Colorado River, Grand Canyon, 1991-1994.

	1991				1992				1993				1994			
	Back		Main		Back		Main		Back		Main		Back		Main	
Species	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Native species																
Bluehead Sucker	11	11.0	2	33.3	100	15.6	0	0.0	203	32.2	53	32.3	919	49.4	12	29.3
Flannelmouth Sucker	10	10.0	0	0.0	88	13.7	1	2.4	120	19.0	12	7.3	95	5.1	2	4.9
Unidentified Suckers	0	0.0	0	0.0	126	19.6	0	0.0	46	7.3	0	0.0	0	0.0	0	0.0
Humpback Chub	12	12.0	3	50.0	13	2.0	1	2.4	42	6.7	5	3.0	23	1.2	1	2.4
Speckled Dace	7	7.0	0	0.0	79	12.3	2	4.8	64	10.1	28	17.1	425	22.9	10	24.4
Total Natives	40	40.0	5	83.3	406	63.2	4	9.5	475	75.3	98	59.8	1,462	78.6	25	61.0
Exotic Species																
Brown Trout	1	1.0	0	0.0	1	0.2	0	0.0	0	0.0	3	1.8	0	0.0	0	0.0
Common Carp	8	8.0	0	0.0	5	0.8	0	0.0	3	0.5	1	0.6	2	0.1	0	0.0
Fathead Minnow	21	21.0	0	0.0	208	32.4	20	47.6	143	22.7	43	26.2	382	20.5	13	31.7
Plains Killifish	2	2.0	0	0.0	2	0.3	1	2.4	1	0.2	0	0.0	2	0.1	0	0.0
Rainbow Trout	28	28.0	1	16.7	20	3.1	16	38.1	9	1.4	19	11.6	11	0.6	2	4.9
Red Shiner	0	0.0	0	0.0	0	0.0	1	2.4	0	0.0	0	0.0	0	0.0	0	0.0
Striped Bass	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	2.4
Total Exotics	60	60.0	1	16.7	236	36.8	38	90.5	156	24.7	66	40.2	397	21.4	16	39.0
Unidentified Fish	7		0		9		0		0		0		0		0	
Yearly Total	107		6		651		42		631		164		1,859		41	

Appendix 5. Total number of fish captured and percentage of the catch in each year for each species and total catch in Reach 50 (RM 166.4 - 225.6) during AGFD mainstem sampling in the Colorado River, Grand Canyon, 1991-1994.

	1991				1992				1993				1994			
	Back		Main		Back		Main		Back		Main		Back		Main	
Species	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Native Species																
Bluehead Sucker	62	3.6	7	7.4	215	7.2	4	6.1	1,282	22.2	19	14.3	630	33.3	4	12.9
Flannelmouth Sucker	133	7.8	15	15.8	590	19.7	14	21.2	841	14.5	47	35.3	422	22.3	1	3.2
Unidentified Suckers	162	9.5	2	2.1	198	6.6	0	0.0	450	7.8	0	0.0	0	0.0	0	0.0
Humpback Chub	1	0.1	0	0.0	3	0.1	0	0.0	16	0.3	0	0.0	6	0.3	0	0.0
Speckled Dace	1,061	61.9	55	57.9	793	26.4	13	19.7	2,231	38.6	58	43.6	478	25.3	21	67.7
Total Natives	1,419	82.8	79	83.2	1,799	60.0	31	47.0	4,820	83.3	124	93.2	1,536	81.3	26	83.9
Exotic Species																
Black Bullhead	1	0.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Channel Catfish	1	0.1	1	1.1	6	0.2	0	0.0	3	0.1	0	0.0	0	0.0	0	0.0
Common Carp	26	1.5	7	7.4	34	1.1	0	0.0	9	0.2	2	1.5	8	0.4	0	0.0
Fathead Minnow	252	14.7	3	3.2	1,143	38.1	33	50.0	949	16.4	7	5.3	345	18.3	1	3.2
Plains Killifish	7	0.4	0	0.0	8	0.3	0	0.0	4	0.1	0	0.0	1	0.1	0	0.0
Rainbow Trout	8	0.5	4	4.2	10	0.3	2	3.0	1	0.0	0	0.0	0	0.0	0	0.0
Striped Bass	0	0.0	1	1.1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	4	12.9
Total Exotics	295	17.2	16	16.8	1,201	40.0	35	53.0	966	16.7	9	6.8	354	18.7	5	16.1
Unidentified Fish	98		3		54		0		870		0		1		0	
Yearly Total	1,812		98		3,054		66		6,656		133		1,891		31	

Appendix 6. Number of fish caught and percentage of the catch of each species and total catch during each year of AGFD sampling in tributaries of the Colorado River, Grand Canyon, 1991-94.

Species	1991		1992		1993		1994	
	N	%	N	%	N	%	N	%
Little Colorado River								
Native Species								
Bluehead Sucker	0	0.0	0	0.0	276	30.3	9	16.4
Flannelmouth Sucker	0	0.0	0	0.0	34	3.7	4	7.3
Unidentified Suckers	0	0.0	0	0.0	0	0.0	0	0.0
Humpback Chub	0	0.0	0	0.0	451	49.6	14	25.5
Speckled Dace	0	0.0	0	0.0	119	13.1	5	9.1
Total Natives	0	0.0	0	0.0	880	96.7	32	58.2
Exotic Species								
Channel Catfish	28	96.6	1	100.0	6	0.7	0	0.0
Common Carp	0	0.0	0	0.0	11	1.2	0	0.0
Fathead Minnow	0	0.0	0	0.0	9	1.0	23	41.8
Rainbow Trout	1	3.4	0	0.0	4	0.4	0	0.0
Total Exotics	29	100.0	1	100.0	30	3.3	23	41.8
Unidentified Fish	0		0		0		0	
Yearly Total	29		1		910		55	
Bright Angel Creek								
Native Species								
Bluehead Sucker	0		0	0.0	0	0.0	1	1.0
Flannelmouth Sucker	0		0	0.0	0	0.0	0	0.0
Unidentified Suckers	0		0	0.0	0	0.0	0	0.0
Humpback Chub	0		0	0.0	0	0.0	1	1.0
Speckled Dace	0		2	20.0	0	0.0	101	96.2
Total Natives	0		2	20.0	0	0.0	103	98.1
Exotic Species								
Brown Trout	0		1	10.0	1	100.0	0	0.0
Fathead Minnow	0		0	0.0	0	0.0	2	1.9
Rainbow Trout	0		7	70.0	0	0.0	0	0.0
Total Exotics	0		8	80.0	1	100.0	2	1.9
Unidentified Fish	0		0		0		0	
Yearly Total	0		10		1		105	

Appendix 6 (continued).

Species	1991 N	1991 %	1992 N	1992 %	1993 N	1993 %	1994 N	1994 %
Shinumo Creek								
Native Species								
Bluehead Sucker	9	2.2	21	1.6	23	10.8	8	2.3
Flannelmouth Sucker	6	1.5	4	0.3	3	1.4	14	4.0
Unidentified Suckers	9	2.2	0	0.0	0	0.0	0	0.0
Humpback Chub	5	1.2	2	0.2	2	0.9	7	2.0
Speckled Dace	374	91.2	1210	93.7	168	78.9	294	83.5
Total Natives	403	98.3	1237	95.7	196	92.0	323	91.8
Exotic Species								
Brown Trout	1	0.2	0	0.0	6	2.8	1	0.3
Common Carp	1	0.2	0	0.0	0	0.0	0	0.0
Fathead Minnow	0	0.0	36	2.8	3	1.4	25	7.1
Plains Killifish	1	0.2	0	0.0	0	0.0	0	0.0
Rainbow Trout	4	1.0	19	1.5	8	3.8	3	0.9
Total Exotics	7	1.7	55	4.3	17	8.0	29	8.2
Unidentified Fish	40		0		0		0	
Yearly Total	450		1292		213		352	
Kanab Creek								
Native Species								
Bluehead Sucker	33	21.7	46	7.9	40	14.7	46	11.2
Flannelmouth Sucker	5	3.3	25	4.3	68	24.9	204	49.8
Unidentified Suckers	0	0.0	2	0.3	0	0.0	0	0.0
Humpback Chub	0	0.0	1	0.2	0	0.0	0	0.0
Speckled Dace	79	52.0	295	50.5	120	44.0	79	19.3
Total Natives	117	77.0	369	62.7	228	83.2	329	79.3
Exotic Species								
Brown Trout	0	0.0	1	0.2	0	0.0	0	0.0
Channel Catfish	0	0.0	2	0.3	0	0.0	0	0.0
Common Carp	0	0.0	0	0.0	1	0.4	4	1.0
Fathead Minnow	20	13.2	159	27.2	42	15.4	81	19.8
Plains Killifish	15	9.9	53	9.1	1	0.4	0	0.0
Rainbow Trout	0	0.0	3	0.5	0	0.0	0	0.0
Striped Bass	0	0.0	0	0.0	2	0.7	0	0.0
Total Exotics	35	23.0	218	37.3	46	16.8	85	20.7
Unidentified Fish	3		5		0		0	
Yearly Total	155		592		274		414	

Appendix 6 (continued).

Species	1991 N	1991 %	1992 N	1992 %	1993 N	1993 %	1994 N	1994 %
Havasu Creek								
Native Species								
Bluehead Sucker	0		2	40.0	132	60.8	20	8.2
Flannelmouth Sucker	0		0	0.0	49	22.6	36	14.8
Unidentified Suckers	0		0	0.0	0	0.0	0	0.0
Humpback Chub	0		2	40.0	0	0.0	1	0.4
Speckled Dace	0		0	0.0	34	15.7	186	76.2
Total Natives	0		4	80.0	215	99.1	243	99.6
Exotic Species								
Common Carp	0		1	20.0	1	0.5	0	0.0
Fathead Minnow	0		0	0.0	1	0.5	0	0.0
Rainbow Trout	0		0	0.0	0	0.0	1	0.4
Total Exotics	0		1	20.0	2	0.9	1	0.4
Unidentified Fish	0		0		0		0	
Yearly Total	0		5		217		244	

Appendix 7. Length frequency of bluehead suckers ≤ 20 cm captured during each month of AGFD sampling in the Colorado River, Grand Canyon, 1991-94.

Length Interval (cm)	1991 MAR 1	1991 MAY 2	1991 JUL 3	1991 SEP 4	1991 NOV 5	1992 JAN 6	1992 FEB 7	1992 APR 8	1992 MAY 9	1992 JUN 10	1992 AUG 11	1992 SEP 12	1992 OCT 13	1993 FEB 14	1993 MAR 15	1993 APR 16	1993 MAY 17	1993 JUN 18	1993 JUL 19	1993 SEP 20	1993 OCT 21	1994 APR 22	1994 MAY 23	1994 JUN 24	1994 SEP 25
0																	1								
1									1	2			29			3	155	210	13		4	6	83	62	
2			1	1				8	5	3			1				115	234	174	13		56	400	447	
3	1	1	5	5				41	7	16	1	4					60	83	166	53	14	141	66	394	31
4	4	7	14	22		1		14	3	43	1	6		1	1	1	39	46	145	146	28	49	50	202	29
5	3	8	24	20				10	4	30	1	8		3		5	25	15	40	122	8	21	9	53	16
6	1	4	3	8	1			15	1	14	2	2		1		3	19	2	11	37	4	19	10	26	7
7	3	3		8	1	1		6	33	13	1	1				3	22		6	9		6	3	18	7
8	1	2		2				3	6	21						1	11					3	4	1	3
9	1							4	5	14						2	10							1	3
10			1	2		1		1	3	12						4	5			1					1
11			1					1	1	12	1	1				1	7			1		1	2	1	1
12				1						14						3	3			1					1
13																2	3			1			1		
14										2					1		3		2	6		1	1		
15										2		1					4		1	1		1	1		
16													1		2	2	2		1	2			2		
17													1		1	1	2		2			2			
18															2	5	1		1			2	2		
19																1	1			1		1	2		1
20								1		1		1			1	1	1					3			

Appendix 8. Length frequency of flannelmouth sucker ≤ 20 cm captured during each month of AGFD sampling in the Colorado River, Grand Canyon, 1991-94.

Length Interval (cm)	1991 MAR APR 1	1991 MAY 2	1991 JUL 3	1991 SEP 4	1991 NOV 5	1992 JAN 6	1992 FEB MAR 7	1992 APR 8	1992 MAY JUN 9	1992 JUN JUL 10	1992 AUG 11	1992 SEP 12	1992 OCT NOV 13	1993 FEB 14	1993 MAR 15	1993 APR 16	1993 MAY 17	1993 JUN 18	1993 JUL AUG 19	1993 SEP 20	1993 OCT NOV 21	1994 APR 22	1994 MAY JUN 23	1994 JUN JUL 24	1994 SEP 25
0																									
1										3		1				129	76	48	2			51	24	12	
2				6		1		11		5	4	2				7	63	187	49	2		9	72	68	
3	1		2	34		6		60		24	2	6	1		5	2	53	111	104	21	8	11	22	160	4
4	1	1	1	29		1		50	2	59	2	19		2	11	1	31	44	83	87	2	17	17	136	16
5	5	5	1	23		5	1	20		37	4	25	1		9	2	6	37	93	121	2	26	1	47	8
6	3	4	2	42	1	4	3	25	1	11	3	23	1	1	11	5	5	24	70	63	2	14		24	13
7	6	6		13	1		2	33		6	2	7		1	13	4	11	7	26	34	4	30		33	5
8	5	12		8		1	1	21	3	14	1	8			6	3	19	2	11	21		8	1	13	10
9	2	8		1		1	1	9	2	10		5		1	3	6	10	1	1	7		10		3	1
10		4					1	4	2	14		1				3	10			5		3			
11				2				1		17	1	2					7			2		1	2	1	2
12								1		19		1				2	12					4	1	1	1
13				1						10		4		1		2	7			2					
14	1	1						4		12		1		2	2	2	9			2		3	2		
15				1				2		4		5				7	9			2		1	1		1
16			1					3		1		4		1	1	1	8		2	2		2			
17				1				3							2	2	17	1		2		3			3
18			2					3		2				2		4	11		1	3		1	1		1
19				1				2		2		2					11		1	3			1	2	1
20								2		2				1	1				1	1		1	1		1

Appendix 9. Length frequency of humpback chub ≤ 20 cm captured during each month of AGFD sampling in the Colorado River, Grand Canyon, 1991-94.

	Date and Trip Number																								
	1991					1992								1993								1994			
Length Interval	MAR	MAY	JUL	SEP	NOV	JAN	FEB	APR	MAY	JUN	AUG	SEP	OCT	FEB	MAR	APR	MAY	JUN	JUL	SEP	OCT	APR	MAY	JUN	SEP
(cm)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
0																									
1										5							1	10				3	18	10	
2	1		2	2	1					3		3	2		1		2	13	20	6	16	38	41	102	
3	2			8	1			2	1	4		2	3		3		2	7	110	135	14	25	11	118	19
4	1	2	1	16	6			4	2	2	1				2	2		4	310	578	32	123	20	44	15
5	4	3		12				3	4		3	1	1	8	22	13	14	4	141	711	10	141	14	68	11
6		1	1	25				1	3	2	2	1	8	22	28	48	18	11	8	291	14	28	5	30	5
7			4	27				6	6	2	2	2	6	44	34	89	39	6	6	91	2	5	1	3	9
8				16				2	2		2	1	9	33	26	78	47	5	6	44	4	4			1
9	1			14				2	6				2	14	26	56	35	5	1	40	8	1	1		
10				11				2	2		3	1	1	7	14	36	38		2	30	4	1		1	
11				6							2	1	1	9	11	31	28		2	35	4	4		1	
12				9					1		3		1	5	7	20	17	1	3	24	2				
13				5									1	2	7	7	18	1	1	30	4				
14		2		1											5	10	9	3	2	23	4	1			
15				2								1	2		5	6	2	2	2	19		1		1	
16										1		1			1	1	4	2	2	10					
17															2	3	4	2	1	4		1			
18															1	2	6	1	2	9					
19															1				1	2				1	
20															1	2	1			2					

Appendix 10. Length frequency of speckled dace captured during each month of AGFD sampling in the Colorado River, Grand Canyon, 1991-94.

Length Interval (cm)	Date and Trip Number																								
	1991					1992								1993								1994			
	MAR APR	MAY	JUL	SEP	NOV	JAN	FEB MAR	APR	MAY JUN	JUN JUL	AUG	SEP	OCT NOV	FEB	MAR	APR	MAY	JUN	JUL AUG	SEP	OCT NOV	APR	MAY JUN	JUN JUL	SEP
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
0													6				2								
1			2						6	11		2	11			1	6	59	12			2	4	103	
2		4	1		1	1	2	16	45	57	9	42	3	1	13	17	6	115	88	68		7	19	174	2
3	60	45			3	1	18	101	89	37	92	101	9	12	74	68	50	41	186	249	46	109	39	90	72
4	80	195		1	11		18	121	63	26	112	40	60	15	50	45	126	25	80	225	38	288	101	76	143
5	7	182	1		7		16	48	118	50	17	15	18	17	13	22	93	46	25	49	2	174	126	118	83
6	3	29			1		3	9	42	60	11	10	4	15	7	17	34	35	32	10		87	71	64	19
7	1	7						7	16	22	7	1	5	9	2	25	14	7	15	10		31	66	39	15
8		1			1		2	6	11	14	4		2	6	3	10	21	9		1	2	4	11	8	15
9		1			1		5	3	7	4		1	1	3	2	6	6	1	2	1		1	3	1	2
10							3		1							2	1						4	1	
11								2	1	2									1				3	1	
12								1																	1

Appendix 11. Length frequency of fathead minnows captured during each month of AGFD sampling in the Colorado River, Grand Canyon, 1991-94.

Length Interval (cm)	1991 MAR APR 1	1991 MAY 2	1991 JUL 3	1991 SEP 4	1991 NOV 5	1992 JAN 6	1992 FEB MAR 7	1992 APR 8	1992 MAY JUN 9	1992 JUN JUL 10	1992 AUG 11	1992 SEP 12	1992 OCT NOV 13	1993 FEB 14	1993 MAR 15	1993 APR 16	1993 MAY 17	1993 JUN 18	1993 JUL AUG 19	1993 SEP 20	1993 OCT NOV 21	1994 APR 22	1994 MAY JUN 23	1994 JUN JUL 24	1994 SEP 25
0																		2							
1				5					1	69		3		1		2		110	43	5		21	324	32	
2	3	2		32	3	3	1	21		59	6	85	22	6	9	3	3	19	81	88	116	111	600	240	35
3	43	26	2	11	6	12	2	84	1	52	50	138	65	25	85	29	20	3	48	134	144	524	96	201	261
4	44	48	2	6	9	3	6	118	9	69	63	97	90	48	121	29	70	19	3	77	24	545	187	251	176
5	29	55	5	17	7	3	2	55	20	31	27	37	35	38	65	19	68	32	4	59	18	234	115	131	66
6	11	8	2	11	2	1	3	24	13	7	15	12	8	10	13	11	36	9	3	25	6	76	38	43	23
7	2	2						3	1	1	2	1	2	1	1		4	1		1		27	11	1	8
8																2						4	3		

Appendix 12. Length frequency of rainbow trout ≤ 20 cm captured during each month of AGFD sampling in the Colorado River, Grand Canyon, 1991-94.

Length Interval (cm)	Date and Trip Number																								
	1991					1992								1993								1994			
	APR	MAY	JUL	SEP	NOV	JAN	FEB	APR	MAY	JUN	AUG	SEP	OCT	FEB	MAR	APR	MAY	JUN	JUL	SEP	OCT	APR	MAY	JUN	SEP
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
0																									
1																									
2	1	1						32	3	1				2	5	4	16	2		6		5	2	2	
3	8	7	1	1		1		15	6	5		2				11	29	8	1	5		1			
4	2	1		1				5	4	5		2					5	6	2	9		1	5		2
5	1							2	2	5		4					1	6	2	7	2	1	4		2
6	2		1						2			1					1	1	6	8	4		2		2
7			2	1					2	1	1	1	1					1	1	2	2		3		
8				2						2	1	2	1	1			1		2	2	2				1
9				1								1	3						2	5	2		1		
10				1								2	1		1				1	1			1		1
11														1					3	3	2				
12				1										1	1				1	3	2				
13				1								1						1							
14				2																1					
15												1													
16														1											1
17	1																		1						
18	1														1										1
19												1			1			1		1					
20				1								3							1	1					

Appendix 13. Changes in Water Temperature of Backwaters During Fluctuating vs. Short-Term Steady Flows in the Colorado River, Grand Canyon

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Abstract

Changes in water temperature of backwaters during fluctuating vs. short-term steady flows were compared in the Colorado River, Grand Canyon, during four days of fluctuating flow vs. three days of steady flow, 25 - 31 May 1994. Temperature gauges were deployed in four backwaters of the Colorado River in the vicinity of its confluence with the Little Colorado River. Water temperatures in both the mainchannel and backwaters displayed regular daily fluctuations under both fluctuating and steady flow regimes. Mean mainchannel temperature was warmer under steady flows. Mean, minimum, maximum, and diel range of backwater temperatures were higher under steady flows. These results indicate that steady flows will cause warming of the mainchannel Colorado River and its backwaters. Changes in dissolved oxygen and pH are also discussed. These temperature changes may both positively and negatively affect fish populations directly and indirectly through their influence on primary and secondary productivity and the potential for an increase in parasite and disease prevalence. These factors should be more closely examined before implementation of a steady flow regime or other changes that might increase water temperature in the river.

The flow of water in the Colorado River through Grand Canyon is predominantly regulated by hypolimnial discharge from Glen Canyon Dam. The closure of Glen Canyon Dam, in 1963, turned a seasonally warm, muddy river into a constantly cold and typically clear one, greatly affecting the biota of the river corridor, particularly the native fishes. Alteration of spawning and rearing habitat, blockage of migration, and introduced native species have contributed to the extirpation of four of the original eight native species (Minckley, 1991). Reproducing populations of only four native species remain: humpback chub (*Gila cypha*; listed as endangered; U. S. Fish and Wildlife Service, 1990), flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*Catostomus discobolus*), and speckled dace (*Rhinichthys osculus*). As many as 17 exotic fish species have been found in the Grand Canyon (Maddux *et al.*, 1987; Valdez and Ryel, 1995; AGFD, 1996).

Glen Canyon Dam is operated as a peaking power hydropower facility. From closure of the dam in 1963 through July 1991, discharge release patterns have fluctuated widely on a daily basis with no restrictions on ramping rates. During this period, discharge peaked in the early afternoon and could reach 893 m^3/s (31,500 cfs), while low discharge, as low as 28 m^3/s (1,000 cfs) or 85 m^3/s (3,000 cfs), depending on the time of year, occurred during the early morning. On 1 August 1991, interim operations were implemented, restricting daily flow fluctuations to a maximum discharge of 567 m^3/s (20,000 cfs), and a minimum of 227 m^3/s (8,000 cfs) from 0700h to 1500h and 142 m^3/s (5,000 cfs) at night. Ramping rates were also restricted to 71 m^3/s (2,500 cfs) per hour up and 43 m^3/s (1,500 cfs) per hour down.

Backwaters have become increasingly important as rearing areas for native fishes in the Colorado River system (Holden, 1978; Valdez and Clemmer, 1982; Carter *et al.*, 1985; Maddux *et al.*, 1987; AGFD, 1996) due to changes in habitat caused by dams, particularly decreased water temperature. Backwaters are quiet pockets of water connected to the mainchannel (but with greatly reduced or no flow) and are formed in areas of eddies where scouring occurs under higher flows. As water levels drop, a reattachment sand bar is exposed, partially isolating the eddy return channel and forming the backwater (Rubin *et al.*, 1990). Not only do backwaters provide calm, sheltered water, they are also warmer and contain greater densities of aquatic invertebrates than the mainchannel (Cole and Kubly, 1976; AGFD, 1996). However, fluctuations in dam releases cause inundation and/or dewatering of backwaters, reducing their ability to support larval and juvenile fish (Kennedy, 1979).

In an effort to improve habitat for native fish, a regimen of steady releases from Glen Canyon Dam has been proposed (U.S. Fish and Wildlife Service, 1994). Stabilized river levels would prevent the daily loss and creation of backwaters. This diel cycle forces juvenile fish to move into or out of backwaters each day. Interrupting this cycle could improve conditions for juvenile fishes. Jourdonnais and Hauer (1993) speculated that forced movement, caused by alterations in river discharge may increase predation on juvenile fish. It is likely that backwaters, under steady flow conditions, would support increased planktonic and benthic invertebrate communities as a result of increased temperature and decreased daily flushing (Kennedy, 1979). A dramatic increase in benthic invertebrate populations has been seen in backwaters sampled under reduced fluctuations (AGFD, 1996) when compared to samples collected under flow regimes designed to maximize power production (Cole and Kubly, 1976; Haury, 1986, 1988). Conversely, turbidity, which is used as cover by native fishes (Valdez and Ryel, 1995; AGFD, 1996), will likely decrease under steady flows. This would make backwaters and other nearshore areas less hospitable to larval and juvenile native fishes.

This study was conducted to examine differences in diel temperature changes in backwaters and the mainchannel during fluctuating vs. steady flows in the Colorado River, Grand Canyon. This study provides initial data concerning the effect of steady flows on larval and juvenile native fish habitat in the Colorado River, Grand Canyon.

Study Area

This study was conducted on the Colorado River, in Grand Canyon National Park, near the confluence of the Colorado and Little Colorado (LCR) Rivers (RK 99; RK = river kilometers below Lee's Ferry). The reach between Kwagunt Rapid (RK 90.1) and Lava Chuar Rapid (RK 105.4) was explored for suitable backwaters. This reach is important because all four remaining native fish species reproduce in the LCR and rear in the mainstem Colorado River in this area (AGFD, 1996).

Four backwaters, RK 94.6L, 95.9L, 97.8L, and 102.5R ('L' and 'R' denote side of river when facing downstream), were selected based on the likelihood that they would persist under both flow regimes. These backwaters varied in many physical characteristics which may affect warming and their chemical characteristics. These included: surface area, depth, mouth dimensions, amount of algae and/or aquatic vegetation, and exposure to solar radiation. Two backwaters, RK 94.6 L and RK 97.8 L, were well established, judging by the presence of aquatic, emergent, and terrestrial vegetation in and around them. The remaining two backwaters, RK 95.9L and RK 102.5 R, were bounded by clean sand bars and were probably more ephemeral.

The backwater at RK 94.6 L was long, wide, and mostly shallow (<1 m) and its size varied greatly with water elevation. The foot (terminal end) of this site remains a backwater except under high discharges ($\geq$510 m^3/s = 18,000 cfs), not seen during this study, which would inundate the site. Its mouth was wide and deep (>1 m), its location and dimensions varied greatly with varying river discharge. This backwater contained a dense mat of aquatic macrophytes, including *Potamogeton* and *Anachris* with *Equisetum* and *Typha* along its sides.

The backwater at 95.9 L was very small, narrow, and shallow. Its mouth was also shallow and narrow and the size of this backwater did not vary greatly with river elevation. This site would be inundated by flows barely exceeding those seen during this study. Due to its location, partially under an overhanging ledge, and the fact that the river there flowed north to south, this backwater received the least solar radiation of all of those studied. The only aquatic vegetation in this backwater was some *Cladophora* that had drifted in from the mainchannel.

The backwater at RK 97.8 L was wide with both deep and shallow sections. The mouth was wide, but very shallow. This site would also require flows $\geq$510 m^3/s for inundation. It was also very exposed to solar radiation and contained much aquatic vegetation, including *Potamogeton* and *Equisetum* in the shallow areas and *Cladophora* in the deeper areas.

The backwater at RK 102.5 R was wide and shallow with two arms. Its mouth was wide and deep. It was fairly well exposed to solar radiation, but contained no aquatic vegetation except some *Cladophora* that had drifted in.

Methods

Backwaters on the Colorado River, Grand Canyon, between Kwagunt Rapid and Lava Chuar Rapid were sampled during a period of approximately four days of fluctuating flows, 25 -

28 May 1994, and three days of steady flows, 29 - 31 May 1994. Fluctuating flows ranged from 221 m^3/s (7,800 cfs) to 374 m^3/s (13,200 cfs) while steady flows were approximately 233 m^3/s (8,200 cfs). Steady releases from Glen Canyon Dam began at approximately 0600h 28 May and reached the confluence of the Colorado and Little Colorado Rivers at approximately 0000h on 29 May. Sampling was completed on 31 May when fluctuations resumed with a decrease in discharge at approximately 1500h followed by an increase at approximately 2200h.

Temperature gauges were placed in the four backwaters on 24 May 1994. Mainchannel temperature and discharge data were obtained from the U.S. Geological Survey gauge on the Colorado River at RK 98.3 R, above the mouth of the LCR. All instruments were set to record at 30 minute intervals from 25 May - 1 June. Differences in diel mean, minimum, and maximum temperature (°C) between steady vs. fluctuating river discharge were tested using paired t-tests. A Sequential Bonferroni test (Rice, 1989) was used to determine the significance of differences at an overall $\alpha \leq 0.05$.

Results

Water temperatures in both the mainchannel and backwaters displayed regular diel fluctuations under both fluctuating and steady flow regimes (Figure A.1). Maximum temperatures occurred in the afternoon and minimum temperatures in the early morning hours.

In the mainchannel, mean temperature was 8.36°C under fluctuating flows but was significantly higher (P=0.0020) at 8.92°C under steady flows. Mean daily minimum temperature, maximum temperature, and diel temperature range were not significantly different in the mainchannel between flow regimes ($P \geq 0.0305$, $\alpha \geq 0.0167$).

In backwaters daily mean, minimum, and maximum temperatures, and diel temperature range were significantly warmer under steady vs. fluctuating flows ($P \leq 0.0046$). Daily mean temperature under fluctuating flows was 11.97°C and increased to 14.53°C under steady flows. Mean daily minimum temperature increased to 11.50°C, under steady flows, from 10.54°C, under fluctuating flows. Mean daily maximum backwater temperature under steady flows was 18.66°C but only 14.41°C under fluctuating flows. The mean diel temperature range was only 2.72°C under fluctuating flows but increased to 5.61°C under steady flows.

Daily mean and maximum water temperatures were significantly higher ($P \leq 0.0040$) under steady flows in the monitored backwaters at RK 94.6L, RK 97.8L, and RK 102.5L, but not significantly different at RK 95.9L (P=0.0104, $\alpha \geq 0.0100$). Daily minimum water temperature significantly increased (P=0.0060) from 10.80°C to 12.30°C in the backwater at RK 102.5R, but not at any other site ($P \geq 0.0241$, $\alpha \geq 0.0100$).

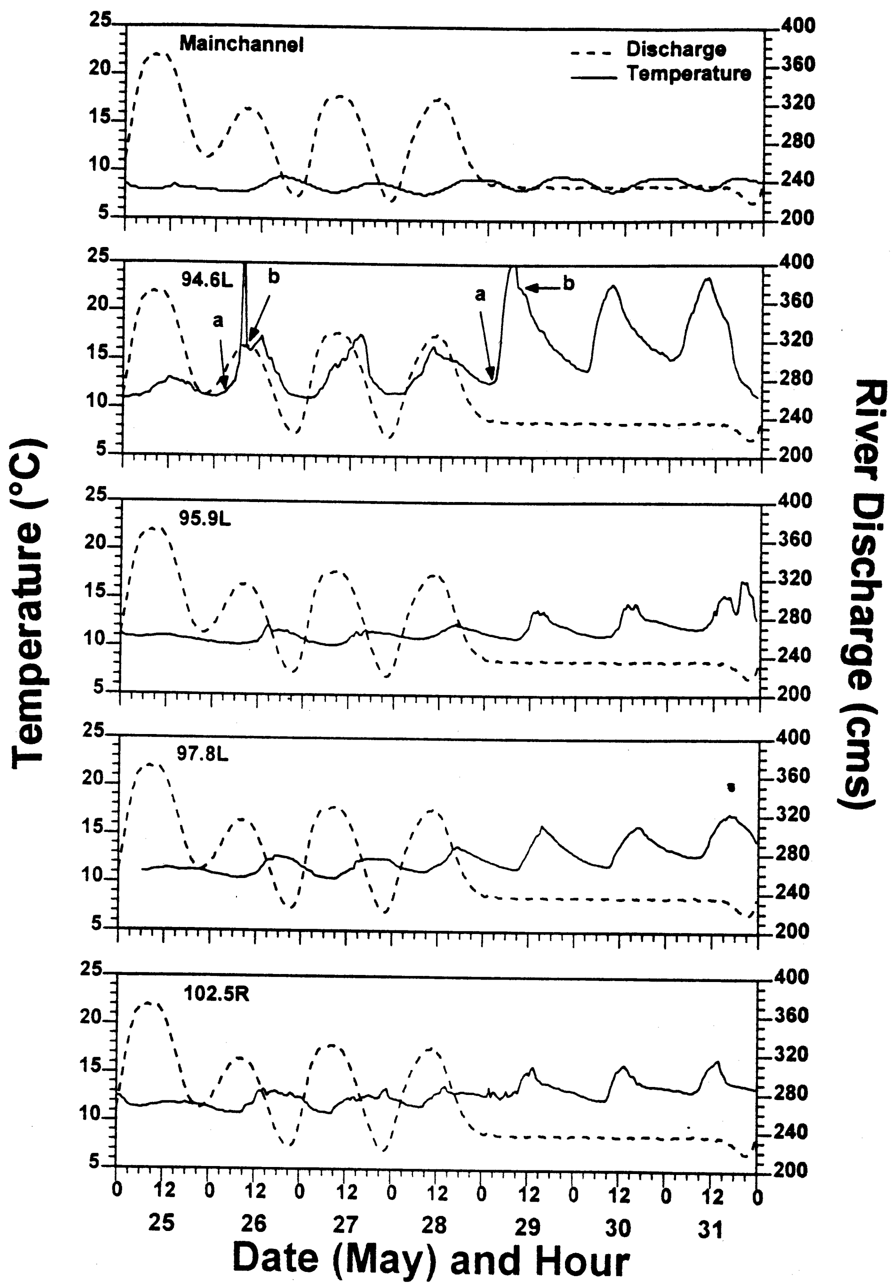

Figure A.1. Changes in temperature in mainchannel (RK 98.2) and backwaters (RK 94.6L, 95.9L, 97.8L and 102.5R), and river discharge (at RK 98.2) from 25-31 May 1994 during fluctuating and steady flows in the Colorado River, Grand Canyon. Temperature gauge in backwater at 94.6L was dewatered (a) and resubmerged (b).

Discussion

It is evident that a 64 hour (three periods of daylight) regimen of steady flows caused an increase in water temperature in both backwaters and the mainchannel Colorado River during late May 1994. Backwater temperatures are largely influenced by ambient temperature, solar radiation, and mainchannel temperature. Under fluctuating flows, backwaters may warm, but daily flushing with mainchannel river water resets the backwater temperature to approximately that of the mainchannel. Under the steady flow regime, diel fluctuations in temperature were still influenced by solar radiation and changes in ambient temperature but were less influenced by the mainchannel. With minimum ambient temperatures well above that of the mainchannel water and no surge of mainchannel water, backwaters held heat better under the steady flow regime than under fluctuating flows. Additionally, backwaters may warm further the next day, depending on ambient temperature and solar radiation. In all sites, except RK 94.6L, the highest daily mean and minimum temperatures occurred on the last day of steady flows, and at all sites the highest maximum temperature occurred on the last day, indicating an increase in temperature over time. The full potential for backwater warming was probably not reached during this short period of steady flows and these data are insufficient to estimate the limit of warming.

The diel timing of flow fluctuations near the LCR are such that temperature variation in backwaters should be maximized. During fluctuating flows, peak discharges reached the LCR gauge between 0600h and 0900h, leaving the remainder of the day under steady or decreasing discharges. This should permit backwaters in this area to warm considerably throughout the day due to little input of new, cold water from the mainchannel. In most other areas of the Colorado River, Grand Canyon, warming should occur to a lesser degree since the timing of high and low discharge occurs at different times of the day, reducing the potential for warming. If low discharge occurs in the early to mid-morning, warming of backwaters should be greatly diminished as they are filled with cold river water during daylight hours.

Backwater temperatures under fluctuating flows were not those preferred by native fish in the Grand Canyon. Humpback chub prefer water temperatures of 21 - 24.4°C (Bulkley *et al.*, 1982) and other native Colorado River fishes probably have similar preferences. These preferred temperatures are far from the 7.6 - 9.6°C temperature range recorded in the mainchannel during this study under both fluctuating and steady flows. Even in the monitored backwaters, maximum recorded temperature was 17.66°C under fluctuating flows. Mean backwater temperature under steady flows increased to 14.18°C from 11.91°C under fluctuating flows. However, under the steady flow regime diel mean temperatures in one backwater (RK 94.6L) reached 17.31 - 18.07°C, nearing the preferred temperature range for native fishes, and maximum temperatures reached 22.88 - 23.77°C, well within the preferred range for native fish. Also, temperature in most backwaters showed indications of increasing with each day of steady flows. Therefore, it appears that under a regime of steady flows, temperature in some backwaters may approach, attain, or even exceed the preferred temperature of native fishes. This is most likely to occur

during warmer months, in shallow areas of backwaters, and in warmer areas (lower reaches) of the Colorado River, Grand Canyon.

The amount of warming in the backwaters monitored in this study varied and was likely influenced by the location (accessibility to direct solar radiation), size of mouth, eddy flow patterns at the mouth, and surface area and volume of the backwater. The backwater at RK 94.6L warmed more than other backwaters under both fluctuating and steady flow regimes, probably because of its long, shallow (~20 cm) foot that is exposed to solar warming for a large part of each day. Also, the length of this backwater probably protected it from the influence of mainchannel water under steady flows. Maximum temperature at this site was 17.66°C under fluctuating flows and reached 23.77°C under steady flows on 31 May 1994. The maximum temperature recorded in any other backwater was 13.79°C under fluctuating flows and 17.27°C under steady flows, both at RK 97.8L where the shallow (~25 cm) mouth may have reduced the intrusion of mainchannel water.

The backwaters at RK 102.5R and RK 95.9L warmed the least under the steady flow regime. RK 102.5R had a wide, deep mouth that would permit a large amount of mixing with the mainchannel. The backwater at RK 95.9L was small, partially under a low undercut bank and its exposed mouth allowed intrusion of mainchannel water from regular surges in the river and waves caused by passing motorboats.

Through warming of the water, steady discharges will also affect other water quality properties of that site, such as dissolved oxygen (DO) and pH. At one site, RK 97.8L, the instrument deployed also measured dissolved oxygen and pH. In this backwater, DO and pH also varied with regular diel fluctuations under both flow regimes, as seen with temperature (Figure A.2). Daily mean, minimum and/or maximum levels of these parameters changed under the steady flow regime due to increased photosynthetic/respiratory activity by algae and macrophytes (Wetzel, 1983). Under steady flows, daily maximum DO did not significantly vary (P=0.9216) between flow regimes. Dissolved oxygen was highest during the late afternoon when O_2, produced by algal and macrophytic photosynthesis, was greatest. Daily mean and mean minimum DO significantly decreased ($P \leq 0.0015$) under steady flows as biological oxygen demand during the night used O_2 which was not replenished by the nightly influx of new water that occurs under fluctuating flows. The DO levels recorded in these backwaters were never at levels that would affect fish growth or habitat preference (Boyd, 1979; Piper *et al.*, 1982).

pH did not vary between flow regimes ($P \geq 0.0093$, α=0.0063). pH was also highest during the late afternoon due to the use of CO_2 by algal and macrophytic photosynthesis. It is unlikely that pH is limiting fish in this system, since fish generally do well in waters with a pH of 6.5 - 9.0 (Boyd, 1979; Piper *et al.*, 1982).

Therefore, it appears that fluctuations in river discharge also moderated the diel changes in DO and pH in this backwater caused by daily cycles of photosynthesis and respiration.

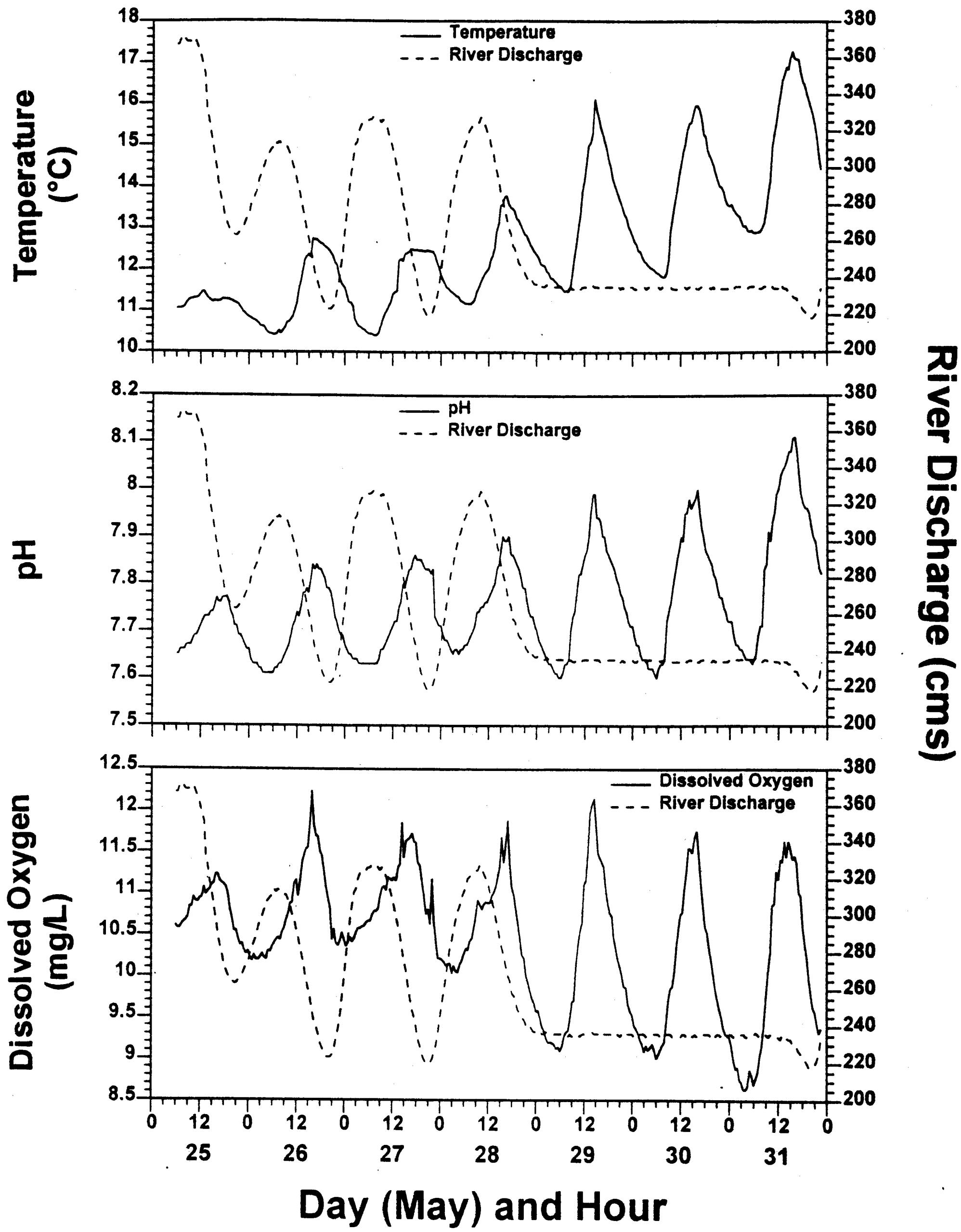

Figure A.2. Changes in temperature, pH, and dissolved oxygen in backwater at RK 97.8L and river discharge (RK 98.2) from 24-31 May 1994 during fluctuating and steady flows in the Colorado River, Grand Canyon.

However, as with the changes in temperature, the limits of these changes under an extended period of steady flow cannot be predicted from the present data.

These data show that backwaters and the mainchannel (to a lesser extent) will warm under a steady flow regime and several ecological changes may be expected to be caused by this warming. These ecological changes may be positive and/or negative for native fish populations and may include changes in: algal, invertebrate, and fish communities, and the possibility of an increase in the distribution and prevalence of diseases and parasites.

Algal and invertebrate communities in backwaters may change under steady flow conditions and these community changes may be beneficial or detrimental to native fishes. It is likely that steady flows will cause an increase in backwater invertebrate populations in response to warmer temperatures and a lack of flushing. We have already seen increases in aquatic invertebrates under the current interim flow regime as compared to a peaking power flow regime (AGFD, 1996). This would further improve backwaters as feeding areas for juvenile fishes. Although it was not examined in this study, the short duration of these flows was probably not long enough for significant changes to occur in populations of even those invertebrates with the shortest life cycles. Leibfried and Blinn (1987) reported an increase in total benthic standing crop (based on drift) in the mainchannel Colorado River under five months of steady flows as compared to fluctuating flows. It may be that use of backwaters by fish will not increase with increasing water temperature until invertebrate populations increase.

Warmer water and increased food abundance should cause an increase in fish growth and survival in all native fish. Clarkson and Lupher (1994) reared humpback chub larvae in 10°C, 14°C, and 20°C water. They found that over 30 days length increased 10%, 37%, and 83%, in the respective groups and that weight increased 28%, 195% and 951%, respectively. Similar, but less dramatic, results are expected in situ.

There are, however, potential negative aspects to long periods of steady flows for native fishes. Mainchannel temperatures will increase, particularly in lower reaches of the river, and may become hospitable to exotic predators already found in Lakes Powell and Mead, reservoirs immediately upstream and downstream from Grand Canyon, and in low numbers in the Grand Canyon (Maddux *et al.*, 1987; Valdez and Ryel, 1995; AGFD, 1996). These predators include striped bass (*Morone saxatilis*), walleye (*Stizostedion vitreum*), smallmouth bass (*Micropterus dolomieu*), and channel catfish (*Ictalurus punctatus*). Exotic competitors may also become a problem. The fathead minnow (*Pimephales promelas*) is already common, plains killifish (*Fundulus zebrinus*) is becoming increasingly common, and green sunfish (*Lepomis cyanellus*) and red shiners (*Cyprinella lutrensis*) are already found in low numbers within the system. Also, Blinn *et al.* (1989) found that epiphytic diatom communities from the Glen Canyon Dam tailwaters changed from large, upright forms to smaller, closely adnate forms with an increase in water temperature from 12°C to 18°C. Adnate forms of diatoms may be more difficult for fish to consume.

Backwater temperatures may rise too high, making these areas unsuitable for juvenile fishes, particularly in the lower reaches of the Grand Canyon and/or during the late afternoon. Maximum backwater temperatures recorded under the current discharge regime of modified fluctuations reached as high as 26.6°C in May (AGFD 1996). It is also possible that increased algae, phytoplankton, and plant growth may make backwaters anoxic during darkness, further reducing their suitability to fish.

Increased temperature may allow the invasion of new parasites and diseases. *Bothriocephalus acheilognathi*, the Asian fish tapeworm, has already invaded the lower LCR (Clarkson *et al.*, *in review*; Brouder and Hoffnagle, *in review*). Increased mainstem temperatures may allow it to expand its distribution within the Grand Canyon. This cestode is a thermophilic parasite of planktivorous cyprinid and cyprinodontid fishes. It requires copepods as an intermediate host and has been known to cause high mortality rates in fish (Hoffman and Schubert, 1984). Cold temperatures in the mainstem Colorado River presently appear to contain the reproducing population of this parasite within the Little Colorado River drainage of the Grand Canyon where it infects humpback chub, speckled dace, and fathead minnow (Clarkson *et al.*, *in review*). Granath and Esch (1983) reported that egg maturation and hatching, coracidium motility, and growth and development of *B. acheilognathi* in mosquitofish (*Gambusia affinis*) were maximized at temperatures of 25°C and 30°C, and depressed at 20°C. However, the mosquitofish is a warmwater species and *B. acheilognathi* may survive better in cold water in a host more tolerant of such conditions. Maximum mean water temperature in the LCR in 1993 was 22.4°C, with a maximum recorded temperature of 26.1°C (Gorman, 1994). The maximum temperature recorded in this study was 23.77°C and maximum daily mean temperature was 18.07°C, very close to that able to support this parasite. Brouder and Hoffnagle (*in review*) examined the distribution of *B. acheilognathi* in humpback chub, speckled dace, fathead minnow, and plains killifish throughout the Grand Canyon and found infected fish to be most common in and near the LCR. However, an infected fish was found in the mainchannel Colorado River as far as 214 km downstream and in the mouth of Kanab Creek (132 km downstream), a likely tributary for establishment of this parasite. Currently, there is no confirmation that this parasite has expanded its range in Grand Canyon and it is more likely that infected fish found outside of the LCR were infected in that tributary and dispersed elsewhere. However, increasing water temperatures to those preferred by humpback chub will likely increase the infection rate by *B. acheilognathi* in all susceptible fish. That, coupled with the continual displacement of fish downstream, will facilitate the invasion of *B. acheilognathi* into tributaries other than the LCR and possibly the mainchannel. Increased infection of humpback chub by *B. acheilognathi* could threaten this endangered fish.

Mainchannel turbidity and backwater dissolved oxygen levels will likely decrease under steady flows. Sabo *et al.* (1991) found that high quality nursery ponds along the Mississippi River contained higher turbidity, dissolved oxygen, and conductivity than low quality nursery areas. Decreased turbidity may result in increased predation on larval and juvenile fish.

Mainchannel turbidities are probably already sufficiently low to affect the behavior of fish. Valdez and Ryel (1995) reported increased catches of sub-adult and adult humpback chubs in trammel nets at night and during periods of high turbidity in the Colorado River. AGFD (1996) also reported increased catches of humpback chub, flannelmouth sucker, speckled dace, and fathead minnow under turbid conditions.

The time required to observe a response by fish to steady flows is expected to be longer than the three days monitored in this study. This response will be measured by changes in growth, survival, recruitment, and reproduction in each species. Extended periods of steady flow will be required for fish populations and growth rates to be altered. At a minimum, backwater usage under steady flows by larval and juvenile fish probably will not increase until food (zooplankton and benthic invertebrates) availability increases. Increases in numbers of these organisms will probably take at least a couple of weeks, depending on the amount of the increase in backwater temperature and the life cycle of the invertebrate species of concern.

These results clearly show that water temperature will increase under a regime of steady flows during periods of warm weather, but the duration of these steady flows was insufficient to determine the ultimate temperature of these backwaters. Additionally, evidence is provided that dissolved oxygen was affected by this flow regime and that pH changes may also be expected under longer-term steady flows. The effects of steady flows and changing river and backwater conditions on plankton, aquatic invertebrates, and fishes were not tested but could be considerable. Therefore, it is apparent that further study is needed to assess the potential changes of long-term steady flows on larval and juvenile native fishes, their food sources, parasites, and habitat before such changes are made. These studies, both laboratory and in situ, should provide significant information on the utility of steady releases for management of native fish populations in the Colorado River, Grand Canyon.

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Appendix 14. Distribution and Prevalence of the Asian Fish Tapeworm, *Bothriocephalus acheilognathi*, in the Colorado River and Tributaries, Grand Canyon, Arizona, Including Two New Host Records

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Abstract

The Asian fish tapeworm, *Bothriocephalus acheilognathi*, has invaded the lower Little Colorado River (LCR), a tributary of the Colorado River, where it infects humpback chub (*Gila cypha*), speckled dace (*Rhinichthys osculus*), and fathead minnow (*Pimephales promelas*). This study examined the distribution of *B. acheilognathi* in the Colorado River and tributaries in Grand Canyon. In 1994, 22.5% of humpback chub, 10.3% of plains killifish (*Fundulus zebrinus*), 3.8% of speckled dace, and 2.2% of fathead minnow were infected. In 1995, 2.4% of fathead minnow and 1.4% of speckled dace were infected. Humpback chub, an endangered species, and plains killifish are new host records for this parasite. Nearly all (66.7 - 100%) infected fish were captured in areas near the LCR and were probably the result of infected fish emigrating from that tributary. However, four infected fish (one plains killifish, one speckled dace, and two fathead minnows) were caught 92.8 - 202.1 km downstream from the LCR. Another speckled dace was caught in the lower section of Kanab Creek, a warm tributary, indicating a potential expansion of the parasite's range. Infection of humpback chub by *B. acheilognathi* is of concern due to the endangered status of this fish. Because *B. acheilognathi* requires high water temperature for completion of its life cycle, this species is largely confined to the LCR by the cold water of the mainstem Colorado River. The potential effects of plans to seasonally warm the Colorado River on *B. acheilognathi* are discussed.

The closure of Glen Canyon Dam in 1963 turned the Colorado River in Grand Canyon from a seasonally warm and muddy river into a typically clear and constantly cold one due to hypolimnetic discharge from Lake Powell. The drastic changes in the riverine environment, particularly water temperature and turbidity, caused by the closure of Glen Canyon Dam, have had a severe negative impact on the native fishes in Grand Canyon (Minckley 1991). Of the original eight endemic fishes in Grand Canyon, reproducing populations of only four remain, one of which is endangered. Lost to this reach of the Colorado River are the Colorado squawfish (*Ptychocheilus lucius*), bonytail chub (*Gila elegans*), and roundtail chub (*G. robusta*), and the razorback sucker (*Xyrauchen texanus*) is extremely rare and probably not reproducing. Remaining are humpback chub (*G. cypha*; federally endangered), flannelmouth sucker (*Catostomus latipinnis*; category II), bluehead sucker (*Catostomus discobolus*), and speckled dace (*Rhinichthys osculus*). Reproduction of these fishes is now largely restricted to a few perennial tributaries (AGFD 1996), however, backwaters of the mainstem Colorado River are important rearing areas for larval and juvenile native and exotic fishes (Holden 1978; Valdez and Clemmer 1982; Carter et al. 1985; AGFD 1996).

Recently, a management proposal (Bureau of Reclamation 1995) suggested the installation of a multi-level intake structure (MLIS) in Glen Canyon Dam to increase downstream water temperatures seasonally and improve conditions for native fish. Changing from hypolimnetic releases to epilimnetic releases in the spring may provide sufficient temperature elevation for increased mainstem reproduction and survival and growth of native young-of-the-year (YOY) fishes. However, an important consideration of warming the river is the potential for an increase in the incidence of fish parasites and diseases.

The Asian fish tapeworm, *Bothriocephalus acheilognathi*, a pseudophyllidean cestode, was originally described from *Acheilognathus rhombea* in Japan (Yamaguti 1934). It has spread to Europe, Russia, and North America with introductions of grass carp (*Ctenopharyngodon idella*) in the early 1970's (Hoffman and Shubert 1984). *Bothriocephalus acheilognathi* is now well established in golden shiner (*Notemigonus crysoleucas*), red shiner (*Cyprinella lutrensis*), fathead minnow (*Pimephales promelas*), grass carp, and mosquitofish (*Gambusia affinis*) in the mid-south and southeastern United States (Hoffman and Schubert 1984; Riggs and Esch 1987). More recently, Heckmann et al. (1987) found *B. acheilognathi* in speckled dace (*Rhinichthys osculus*), red shiner, and the endangered woundfin (*Plagopterus argentissimus*), Virgin River chub (*G. robusta seminuda*), and Virgin spinedace (*Lepidomeda mollispinis*) from the Virgin River, Utah, Nevada, and Arizona. Heckmann et al. (1993) found *B. acheilognathi* elsewhere in Nevada: in red shiner in the Muddy River, roundtail chub from the Moapa Power Plant cooling pond, and golden shiner from bait shops around Las Vegas. Font and Tate (1994) have also reported *B. acheilognathi* from native Hawaiian freshwater fishes.

Cyclopoid copepods are the intermediate hosts of *B. acheilognathi* (Marcogliese and Esch 1989a) and the definitive hosts are a broad range of fishes, particularly cyprinids (Hoffman and Schubert 1984). Temperatures in excess of 20°C are required for maturation of this cestode (Granath and Esch 1983a). Currently, *B. acheilognathi* appears to be confined to the LCR, probably by cold mainstem water temperatures which do not reach 20°C (Stanford and Ward 1991). Temperatures in many of the other tributaries throughout Grand Canyon are to be similar to those in the LCR (AGFD 1996) and thus should be capable of colonization by *B. acheilognathi*. This study examined the present distribution and prevalence of *B. acheilognathi* in native and exotic fishes of the Colorado River, Grand Canyon, and its tributaries.

Methods

Native and exotic fishes were collected in 1994 and 1995. In 1994, as part of a diet study of small (<150 mm) fish, we attempted to collect five fish from each of two size classes, ≤30 mm and >30 mm total length, from each of the eight mainstem Colorado River reaches (Figure A.3.)

during each of three river trips. These species included: humpback chub, speckled dace, flannelmouth sucker, bluehead sucker, rainbow trout (*Oncorhynchus mykiss*), fathead minnow, and plains killifish (*Fundulus zebrinus*). In 1995, we further examined the distribution of this parasite by attempting to collect five speckled dace and five fathead minnows from each of the eight reaches and seven tributaries on each of three river trips. We were not permitted to collect humpback chub in 1995 due to its endangered status. Fishes were collected using seines, hoop nets, dip nets, minnow traps, and electrofishing. Total length (TL; mm) and weight (g) of fish and date and location of capture (tributary or river kilometer (RK) downstream from Lee's Ferry) were recorded. Fish were then preserved in either 70% ethanol or 10% formalin, as field examination was not practical. In the laboratory, fish were examined to determine the presence or absence of Asian fish tapeworms in each fish. A representative specimen of *B. acheilognathi* has been deposited in the U. S. National Parasite Collection, Beltsville, MD (USPNC Coll. No. 86818).

Results

A total of 1,902 fish representing seven species in four families were examined for *Bothriocephalus acheilognathi* in this study. These fish included all four remaining native species and three common exotic species. Species sampled included: humpback chub, speckled dace, and fathead minnow (Cyprinidae); plains killifish (Cyprinodontidae); bluehead and flannelmouth suckers (Catostomidae); and rainbow trout (Salmonidae).

In 1994, 1,669 fish were sampled from the mainstem Colorado River. Twenty-seven of 120 (22.5%) humpback chub (12-110 mm TL; $\bar{x}$=36.2 mm), seven of 185 (3.8%) speckled dace (12-132 mm TL; $\bar{x}$=35.7 mm), five of 234 (2.2%) fathead minnows (12-78 mm TL; $\bar{x}$=35.1 mm), and three of 29 (10.3%) plains killifish (21-57 mm TL; $\bar{x}$=35.1 mm) were infected with *B. acheilognathi* (Tables A.1, A.2, and A.3). None of 329 flannelmouth suckers (15-98 mm TL; $\bar{x}$=34.2 mm), 562 bluehead suckers (12-106 mm TL; $\bar{x}$=29.0), or 210 rainbow trout (22-416 mm TL; $\bar{x}$=267.4 mm) were infected.

In 1995, 148 speckled dace and 85 fathead minnows were examined from the Colorado River and seven tributaries in Grand Canyon. Two of 85 (2.4%) fathead minnows and 2 of 148 (1.4%) speckled dace were infected with *B. acheilognathi*.

In both 1994 and 1995, the majority of the fish infected with *B. acheilognathi* were captured in the reach directly above (Reach 2) and two reaches directly below (Reaches 3 and 4) the confluence of the Little Colorado and Colorado Rivers. Of the infected fish, all of the 27 humpback chub, seven of nine (77.8%) speckled dace, five of seven (71.4%) fathead minnow, and two of three (66.7%) plains killifish were captured in this area. Of greater interest are the fish captured outside of this area. One infected fathead minnow was captured at RK 265.2 and another at RK 301.1. One infected plains killifish was captured at RK 191.8. An infected speckled dace was captured in Kanab Creek (RK 230.9) and another in a backwater at RK 266.6. No infected fish were captured in Nankoweap, Shinumo, Royal Arch, Stone, or Havasu Creeks.

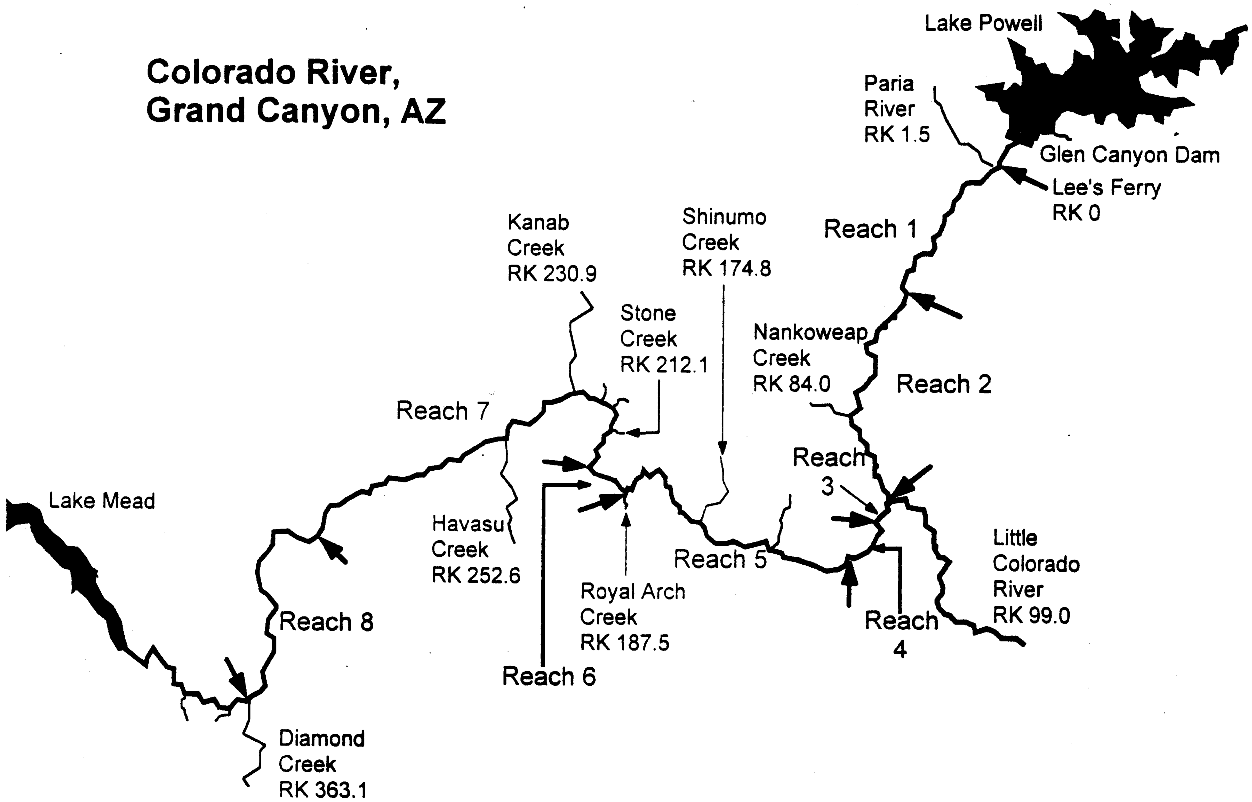

Figure A.3. Boundaries (arrows) of eight designated fish sampling reaches and location of sampled tributaries of the Colorado River, Grand Canyon, Arizona. River Kilometer (RK) is distance downstream from Lee's Ferry. Colorado River reach boundaries are as follows: Reach 1 - Lee's Ferry (RK 0) to Shinumo Wash (RK 47.17); Reach 2 - Shinumo Wash to Little Colorado River (RK 99.0); Reach 3 - LCR to Lava Chuar Rapid (RK 105.44); Reach 4 - Lava Chuar Rapid to Hance Rapid (RK 123.47); Reach 5 - Hance Rapid to Elve's Chasm (Royal Arch Creek, RK 187.54); Reach 6 - Elve's Chasm to Forster Rapid (RK 197.68); Reach 7 - Forster Rapid to Hell's Hollow (RK 293.78); Reach 8 - Hell's Hollow to Diamond Creek (RK 363.16).

Table A.1. Prevalence of *Bothriocephalus acheilognathi* in humpback chub and plains killifish collected from the Colorado River and tributaries, Grand Canyon, Arizona, 1994. Dashes indicate that no collections were attempted at that location.

	Humpback Chub			Plains Killifish		
Reach/Tributary	N	Number Infected	Percent Infected	N	Number Infected	Percent Infected
1	0	0	0.0	0	0	0.0
2	4	1	25.0	1	0	0.0
Nankoweap Creek	-	-	-	-	-	-
Little Colorado River	-	-	-	-	-	-
3	39	16	41.0	9	1	11.1
4	58	10	17.2	12	1	8.3
5	0	0	0.0	1	0	0.0
Shinumo Creek	-	-	-	-	-	-
Royal Arch Creek	-	-	-	-	-	-
6	9	0	0.0	5	1	20.0
7	7	0	0.0	1	0	0.0
Stone Creek	-	-	-	-	-	-
Kanab Creek	-	-	-	-	-	-
Havasu Creek	-	-	-	-	-	-
8	3	0	0.0	0	0	0.0
Total	120	27	22.5	29	3	10.3

Table A.2. Prevalence of *Bothriocephalus acheilognathi* in speckled dace collected from the Colorado River and tributaries, Grand Canyon, Arizona, 1994 and 1995. Dashes indicate that no collections were attempted at that location.

	1994			1995		
Reach/Tributary	N	Number Infected	Percent Infected	N	Number Infected	Percent Infected
1	7	0	0.0	0	0	0.0
2	18	0	0.0	3	0	0.0
Nankoweap Creek	-	-	-	6	0	0.0
Little Colorado River	-	-	-	11	1	9.1
3	16	2	12.5	13	0	0.0
4	17	4	23.5	15	0	0.0
5	0	0	0.0	1	0	0.0
Shinumo Creek	-	-	-	25	0	0.0
Royal Arch Creek	-	-	-	7	0	0.0
6	17	0	0.0	5	0	0.0
7	32	1	3.1	14	0	0.0
Stone Creek	-	-	-	3	0	0.0
Kanab Creek	-	-	-	4	1	25.0
Havasu Creek	-	-	-	24	0	0.0
8	78	0	0.0	17	0	0.0
Total	185	7	3.8	148	2	1.4

Table A.3. Prevalence of *Bothriocephalus acheilognathi* in fathead minnow collected from the Colorado River and tributaries, Grand Canyon, Arizona, 1994 and 1995. Dashes indicate that no collections were attempted at that location.

	1994			1995		
Reach/Tributary	N	Number Infected	Percent Infected	N	Number Infected	Percent Infected
1	0	0	0.0	0	0	0.0
2	17	0	0.0	3	1	33.3
Nankoweap Creek	-	-	-	0	0	0.0
Little Colorado River	-	-	-	8	0	0.0
3	78	0	0.0	16	0	0.0
4	36	3	8.3	18	1	6.3
5	0	0	0.0	0	0	0.0
Shinumo Creek	-	-	-	0	0	0.0
Royal Arch Creek	-	-	-	0	0	0.0
6	29	0	0.0	13	0	0.0
7	42	1	2.4	15	0	0.0
Stone Creek	-	-	-	0	0	0.0
Kanab Creek	-	-	-	7	0	0.0
Havasu Creek	-	-	-	0	0	0.0
8	32	1	3.1	5	0	0.0
Total	234	5	2.2	85	2	2.4

Discussion

Bothriocephalus acheilognathi was found in four of seven species of fish examined from the Colorado River, Grand Canyon: three cyprinids (humpback chub, speckled dace, and fathead minnow) and one cyprinodontid (plains killifish). The Colorado and lower Little Colorado Rivers are new localities for this parasite, which likely invaded via infected nonnative fish species or copepods from the upper LCR. Although *B. acheilognathi* has not been documented in the upper LCR, common carp, fathead minnow, and plains killifish are all potential hosts of this parasite and are common upstream, in the perennial headwaters of the LCR in the White Mountains area of eastern Arizona. Although the middle portion of the LCR is ephemeral (from Lyman Lake to 21 km above the confluence with the Colorado River) infected fish or copepods may easily have been flushed downstream into the lower LCR during floods. Although Heckmann et al. (1987) found *B. acheilognathi* in speckled dace at Beaver Dam Wash, Virgin River, AZ, it is highly unlikely that any of these fish moved down to Lake Mead, then upstream over 400 km and through many large rapids to the LCR. The paucity of infected fish in the lower part of the canyon and the absence of infected fish from the upper canyon, above the LCR, casts doubt on invasion of this area via migration up or down the Colorado River.

This is the first report in the refereed literature of *B. acheilognathi* in the endangered humpback chub. *Bothriocephalus acheilognathi* has been reported in humpback chub and speckled dace in the LCR in 1990 in an Arizona Game and Fish Department agency report (Clarkson and Robinson 1993). This cestode was first discovered in the Grand Canyon in May 1990 in humpback chub from the LCR (C.O. Minckley, U.S. Fish and Wildlife Service, personal communication). Kaeding and Zimmermann (1983) examined 26 humpback chub for pathogens from the LCR and Colorado River from 1979-1981. They reported 13 bacteria, 6 protozoans, one fungus, and the parasitic copepod *Lernaea cyprinacea*, but not *B. acheilognathi*. Heckmann et al. (1987) and Heckmann et al. (1993) reported *B. acheilognathi* in the closely related roundtail chub. Infection of humpback chub by *B. acheilognathi* is expected since copepods were found in 7.2% of the humpback chub stomachs collected in 1994 (AGFD 1996).

The occurrence of *B. acheilognathi* in 10.3% of the plains killifish examined is also the first report of this species as a host for this parasite. However, mosquitofish, another cyprinodontid, is also susceptible to this parasite (Granath and Esch 1983b; Riggs and Esch 1987; Marcogliese and Esch 1989). None of the 29 plains killifish examined from 1994 contained copepods in their stomachs (AGFD 1996). Plains killifish is a surface feeder and is omnivorous with insects and aquatic invertebrates being dominant food items (Shute and Allen 1980), but they may also consume benthic material (Simon 1946). Although copepods do not appear to be a dominant food item for plains killifish, infection with *B. acheilognathi* indicates that copepods are occasionally ingested.

Neither flannelmouth sucker, bluehead sucker, nor rainbow trout contained *B. acheilognathi*. Copepods were ingested by both species of suckers, more so by flannelmouth suckers (AGFD 1996). Presumably, all species that ingested copepods were exposed to this parasite since they were collected from the same sites as infected species. Therefore, since both sucker species contained copepods in their stomachs, it appears that they are not susceptible to infection by the Asian fish tapeworm. This result supports Heckmann et al. (1987) who found no *B. acheilognathi* in the three flannelmouth suckers they examined. No copepods were found in rainbow trout stomachs. Although most of the trout were caught upstream from the LCR, to our knowledge, *B. acheilognathi* has never been reported in salmonids.

Bothriocephalus acheilognathi was found in fishes collected throughout the entire mainstem Colorado River and two tributaries from RK 97.9 to RK 301.1. However, the majority of the fish that were infected by *B. acheilognathi* were captured in reaches directly above and below the confluence of the Little Colorado and Colorado Rivers (Reaches 2, 3, and 4) and were probably the result of fish emigrating from the LCR. The fish caught upstream from the LCR were captured in a backwater only 1.1 km from the mouth of the LCR and did not need to negotiate any rapids to get there. Therefore, it appears that *B. acheilognathi* is currently only able to complete its life cycle within the LCR.

Five infected fish were captured outside of the LCR and nearby reaches, at least 92.8 km and as far as 202.1 km downstream from the LCR. Of particular concern is the speckled dace captured in Kanab Creek. Water temperatures of Kanab Creek are warm enough to allow for reproduction by *B. acheilognathi*, with mean temperatures exceeding 20°C from May through August and reaching as high as 34°C (Otis 1994; AGFD 1996). Whether this occurrence of an infected speckled dace is indicative of a separate, reproducing population of *B. acheilognathi* or simply an infected fish that had emigrated downstream from the LCR is not clear. This fish was caught in the lower section (<500 m from the mouth) of Kanab Creek, so either alternative is possible. In any event, since speckled dace and fathead minnow are resident and humpback chub are occasionally found in Kanab Creek (AGFD 1996), the potential certainly exists for this parasite to become established in this tributary. Therefore, although the cold water temperature of the mainstem Colorado River seems to be limiting the distribution of this parasite, there is an indication that it may have colonized Kanab Creek. Further examination of the potential colonization of Kanab Creek by *B. acheilognathi* is warranted and planned.

Three of the four components for successful invasion by *B. acheilognathi* are present in the mainstem of the Colorado River, Grand Canyon. First, definitive hosts (native and exotic cyprinid fishes) are present throughout the river. Secondly, the intermediate host, cyclopoid copepods, are abundant in the mainstem of the Colorado River (AGFD 1996) and are ingested by native and exotic fishes. Thirdly, *B. acheilognathi* is present in the lower reaches of the LCR (Clarkson and Robinson 1993). The fourth and apparently limiting factor is water temperature. Although the temperature in the mainstem of the Colorado River is currently too cold for the parasite to disperse throughout the entire Grand Canyon, the proposed MLIS could increase the water temperature in the mainstem by 3 - 10°C (Bureau of Reclamation 1995). This could cause water in the mainstem to reach the minimum temperature required for *B. acheilognathi* to complete its life cycle. Even if mainchannel temperatures do not reach 20°C, backwater temperatures will certainly exceed 20°C and may permit *B. acheilognathi* to complete its life cycle in these habitats or improve the chances of its colonizing other tributaries.

The major factor affecting egg maturation, coracidium motility, growth, development of adult worms, and ultimately the size and composition of *B. acheilognathi* populations is water temperature. Granath and Esch (1983a) found that growth and development of this parasite was stimulated by temperatures above 25°C and that temperatures of 25 - 30°C maximized egg maturation, hatching, and coracidium motility. At temperatures outside that range these activities were depressed. Temperatures exceeding 35°C caused a decrease in recruitment of this parasite in mosquitofish (Granath and Esch 1983b). Water temperature in the LCR is suitable for *B. acheilognathi*, exceeding 20°C from May through September in 1993 and reaching as high as 26.1°C (Gorman 1994). Conversely, temperatures in the mainchannel Colorado River are unsuitable for this parasite, reaching only 18.4°C from 1991-1994 (AGFD 1996). Maximum backwater temperatures reached 28.0°C in shallow areas, suitable for *B. acheilognathi* to complete its life cycle. However, the water level in the Colorado River, Grand Canyon, fluctuates daily with the demand for electric power. This dynamic nature causes inundation and desiccation of backwaters, prevents these temperatures from being stable, and flushes zooplankton from the backwaters. Mean backwater temperatures never exceeded 20°C during four years of study (AGFD 1996). However, construction of an MLIS or implementation of steady flows, another suggested mitigation measure (U.S. Fish and Wildlife Service 1994), will likely cause mean backwater temperatures to increase above 20°C and may regularly approach 25°C, aiding the completion of the life cycle of *B. acheilognathi*. Copepods inhabit backwaters which are important rearing areas for larval and juvenile native and exotic fishes (AGFD 1996). These fish are planktivorous and regularly ingest copepods (AGFD 1996). Therefore, warming of the river may permit *B. acheilognathi* to expand its range beyond the LCR.

The infection rates for speckled dace (1.4 - 3.8%) and fathead minnow (2.2 - 2.4%) in this study were relatively low. Only 1.4% of the speckled dace and none of the fathead minnows sampled from 1994 contained copepods in their stomachs (AGFD 1996). The fact that fathead minnows were infected with *B. acheilognathi* indicates that copepods are ingested. Clarkson and Robinson (1993) also found low prevalence (0.4%) in speckled dace from the LCR captured in 1991 but higher prevalence (17.0%) in 1992. Heckmann et al. (1987) found 17% of 107 speckled dace were infected from Beaver Dam Wash, Virgin River, AZ. Riggs and Esch (1987) found prevalence of *B. acheilognathi* in fathead minnows in Belews Lake, NC, to range from approximately 15 - 95%, depending on season and site. The low prevalence of *B. acheilognathi* in speckled dace and fathead minnow in our study may be due to the dynamic nature of the LCR. The base discharge of the LCR, approximately 5.6 m^3/s, comes from a series of springs approximately 21 km from the mouth (Minckley 1991). However, flooding is common in spring (rain and snow melt) and in late summer (monsoonal rains) and can exceed 850 m^3/s. Differences in the frequency and severity of these floods may have dramatic effects on copepod populations, which would then affect *B. acheilognathi* populations, as noted by Marcogliese and Esch (1989b). These low prevalences of *B. acheilognathi* in speckled dace and fathead minnow also reflect our inclusion of samples from areas where the parasite was not found.

The infection of humpback chub by *B. acheilognathi* (rates as high as 41% in Reach 3 and an overall infection rate of 22.5% in 1994) is of concern, considering the endangered status of this fish. Clarkson and Robinson (1993) reported infection rates in juvenile humpback chub in the LCR as high as 78.9% in 1990 and 77.8% in 1992 and as low as 12.4% in 1991 and 0% in 1989 (1989 may have bee pre-invasion). Valdez and Ryel (1995) reported finding *B. acheilognathi* in 3.6% of 168 adult (≥250 mm) humpback chub. However, the prevalence of *B. acheilognathi* in these fish may have actually been higher since their data were from stomach contents obtained by flushing the gastrointestinal (GI) tract and may not have dislodged parasites from all infected fish. High intensity infections can lead to mortality by blockage of the GI tract, intestinal perforation and/or destruction of the intestinal mucosa, killing the fish (Hoffman 1980; Schäperclaus 1986). The humpback chub in and around the Little Colorado River comprise the largest remaining population of this species (Maddux et al. 1993). Douglas and Marsh (1996) used various models to estimate population size of humpback chub (≥150 mm TL) in Grand Canyon which ranged from 4,508 to 10,444 fish. This small population size, high infection rates, and potential for mortality do not bode well for this endangered fish.

The proposed MLIS may increase water temperatures of the mainstem Colorado River 3-10 °C (Bureau of Reclamation 1995). This increase in mainstem water temperature may be high enough to allow *B. acheilognathi* to become established in other tributaries and possibly the mainstem of the Colorado River in Grand Canyon. This is a more likely scenario in streams further downstream from Glen Canyon Dam where the water is warmer. Increasing mainstem water temperature may initially increase growth and survival of YOY native fishes. However, it may also prove to be detrimental to these fish in the long run due to an increase in the prevalence of *B. acheilognathi* and/or other parasites and diseases.

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