

GLEN CANYON ENVIRONMENTAL STUDIES

PHASE II

1992 ANNUAL REPORT

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1. Executive Summary

The purpose of this report is to summarize progress by the Arizona Game and Fish Department (AGFD) in meeting the research objectives identified in Cooperative Agreement 9-FC-40-07940 between AGFD and Bureau of Reclamation (BR). The information contained herein has primarily been collected in 1992, however, where appropriate, information from both Phase I and from the start of Phase II research are included. In that data presented are provisional and conclusions drawn from these data may change as additional data and analysis are incorporated, the reader is cautioned to contact the author prior to citing this report.

A primary objective of this research is to identify the impacts associated with different flow conditions on the aquatic conditions of Glen and Grand canyons and select tributaries in these areas. Four specific research segments have been incorporated into the AGFD research program. Included are: ecosystem processes and lower trophic levels, native fish in the Colorado River, native fish in the Little Colorado River (LCR), and trout in the Lee's Ferry reach. Some of the key findings are identified in this Executive Summary.

Ecosystem Processes and Lower Trophic Levels

FPOM concentrations increase, but only slightly, with distance from Glen Canyon Dam. Substantial increases in flow after long periods of low flows can result in a large increase in FPOM concentrations, but this increase is both local and short-lived. Collections of *Gammarus lacustris* have occurred since May 1992 at two sites in the Lee's Ferry reach and at two flow levels. Density estimates for this organism indicate a significantly lower number at the 8,000 cfs level than at 5,000 cfs. In most months, significantly higher number of this amphipod were collected at the 3.5 mile bar than at 14.0 mile bar. Additional sampling sites have been added to investigate if this is related to sample site or actually represents a longitudinal gradient from Glen Canyon Dam. Periphyton on cobble bars above the level of permanent inundation appear to be very sensitive to flow regime. There appears to be low resistance to daytime desiccation and chronic nighttime exposure.

Native Fishes-Colorado River

From March 1991 to November 1992, 13 downriver trips took place. Data were collected for both fish and habitat parameters during these efforts. During these trips, 11,646 fish were caught (all methods combined). Speckled dace (*Rhinichthys osculus*) and fathead minnows (*Pimephales promelas*) were the most abundant species captured in most efforts. Flannelmouth sucker (*Catostomus latippinis*), bluehead sucker (*Pantosteus discobolus*), and humpback chub (*Gila cypha*) were also frequently captured on Type A trips. Type B trips used

minnow traps to identify habitat use patterns in mainchannel, tributary mouth, and backwater habitats. In mainchannel and backwater habitats 572 fish were captured in 2,887 trap sets. Based upon the distribution of habitat conditions and fish catch rates, there appears to be a selection for warmer water conditions. Opportunistic sampling was used to assess distribution of fish in mainchannel and tributary habitats. Humpback chub and flannelmouth suckers were more common in mainchannel habitats than tributaries (except LCR). Chub were relatively common in Reach 30 in fall of 1991 and 1992. Humpback chub as small as 16 mm were found in reaches 30 and 40 and likely represent fish flushed from the LCR by a high flow event. Sonde data documented warming occurred in backwater environments. In May 1991, backwater temperatures ranged from 14 C at night to 23 C the following day and returned to 14 C that night. Sonde data documented that if flows great enough to inundate the backwater occurred, the water temperature cooled to near mainchannel temperatures.

Native Fishes-Little Colorado River

Nine fish species were captured during the spring monitoring period, four of which are endemic. Of these speckled dace and humpback chub were most numerous. Using only data from AGFD marks and recaptures, the population estimate of humpback chub > 150 mm TL at the end of June 1992 was 571 (95% CI = 426-809). This value is lower than previous years. In 1992, the first larval humpback chub was found on April 30. In mid-May surveys, humpback chub larvae were found in most of the LCR. Only a single larval chub was found in June. In July and August, chub larvae were found in the lower half of the study area. Based upon these data it appears humpback spawned in late April to early May and again in July. Speckled dace mesolarvae were first encountered on May 3 and were only found in the lower reaches of the LCR until July by which time they were found throughout the river. Bluehead sucker larvae were first encountered on May 7 and were primarily observed in the lower 7 km of the LCR. It appears that bluehead spawning was synchronous with that of the first humpback spawn. Very few flannelmouth sucker larvae were encountered in the LCR in 1992. Of note is the fact that Asian tapeworm was documented from 64% of the humpback chub classified as early juvenile (50-100 mm) in 1992. This organism has been found in most chub sampled since 1990. Growth rates of humpback chub was minimal in winter. Mean size of the 1991 cohort only increased from 82 mm in November to 88 mm by May. Age-0 humpback chub up to approximately 130 mm were captured in winter months. Otoliths from select humpback chub have been analyzed to determine if daily growth rings are detectable. Counts of such increments is easily done for specimens collected from the LCR prior to the first winter of life or movement to the Colorado River. Back-calculation to hatch dates appears possible for these specimens. Daily growth rings from humpback chub collected in the mainstem are difficult to read due to narrow, poorly

defined increments. Some specimens from the mainstem show unusual patterns of very abrupt transitions in growth rates presumably due to differences in thermal regimes found between backwater and mainstem conditions.

Trout Studies

Spawning bar studies have been conducted in winter 1990, 1991, and 1992. Trout spawning (primarily rainbow trout, *Oncorhynchus mykiss*) was delayed in winter 1990 possibly due to the relatively poor condition of fish. Surveys for stranded fish have occurred in each year of the study. Under fluctuating flows, an estimated 15,000 to 20,000 adult trout were lost due to stranding between February 1990 and February 1991. An increase in the minimum flows appears to have eliminated the problem of stranding. Twenty one surveys completed since the implementation of interim flows have documented only four stranded trout. Length frequency scatterplots based upon electrofishing data have been completed. In 1989 and 1990, the distribution was unimodal, however, in subsequent years the distribution was bimodal with modes at approximately 150 and 425 mm. General growth as measured by mean total length, has declined since 1989. A one-way ANOVA comparing total lengths was significantly different between years. Relative weights were calculated for the period from 1984 to 1992. There was a significant stepwise degradation in this value between 1984 and 1991 with an increase observed in 1992. Creel data also show a decline in the quality of the fishery since 1977. Data from the creel indicated a decline in the number of fish caught per hour and harvested trout. Use of binary coded wire tags has allowed for improved assessment of natural vs. stocked trout in the Lee's Ferry reach. Based upon preliminary analysis it appears that a much larger component of the fishery is comprised of naturally reproduced trout (approximately 78% natural reproduction based upon 8/92 electrofishing data). A high percentage of trout sampled in 1990 and subsequent years were infected with a endoparasitic nematode. Although this was not a new problem, the rate of infestation in 1992 appears to be higher than in 1990. A health assessment of trout in 1992 indicated that the percent of trout with very low body fat declined since 1990. Preliminary results of a parametric approach for examining the relationships between trout relative weights and flow regimes appears to hold promise as a new analysis technique.



2. Ecosystem Processes and Lower Trophic Levels

Ted R. Angradi and Andrew D. Ayers

The purpose of this chapter is to summarize the initial findings of studies of Glen Canyon ecosystem processes and lower trophic levels conducted in 1992. In 1992, studies have focused on algal colonization and standing crop, particulate organic matter (POM) transport, and productivity of the amphipod *Gammarus lacustris*.

Previous studies of algal colonization indicated that accrual of algal biomass and chlorophyll *a* was influenced by flow fluctuations (Angradi et al. 1992). The objective of algal colonization experiments conducted in 1992 was to repeat the original field experiments under interim flows, and to expand the spatial scale of the experiments to include more of the Glen Canyon Reach. Monthly monitoring of periphyton standing crop began in August 1991 and was continued through the current period.

POM transport studies have indicated that concentration of POM exported from the Glen Canyon Reach does not greatly exceed that in water released from Lake Powell (Angradi et al. 1992, Angradi and Kubly, in press). In 1992, POM sampling was directed at exploring the longitudinal variation of FPOM concentration through Glen Canyon.

Several studies have shown that the amphipod *Gammarus lacustris* is an important component of the Glen Canyon ecosystem (reviewed by Blinn and Cole 1991). An important functional role of this organism appears to be the trophic transfer of periphyton primary production in trout biomass. Although the relative magnitude of this pathway remains to be confirmed, *G. lacustris* is an important component of trout diets in Glen Canyon (Maddux et al. 1978). A study of the productivity of *G. lacustris* was initiated in May 1992; data presented here are limited to distribution and abundance of *G. lacustris* in Glen Canyon.

Objective 1.1. Evaluate the ecosystem-level processes that determine fish production in the Lee's Ferry tailwater. The processes of concern include primary production, nutrient uptake and regeneration, and transformation of organic matter between dissolved and particulate states. These processes are affected by dam/reservoir-mediated discharge regimes, water temperature and inflow chemistry.

Methods and Progress

Water samples were collected from penstocks at the dam and 1, 2, 3, 6, 9, 12, 15, 18, 21, and 25 km downriver. FPOM was obtained as described previously (Angradi et al. 1992). All samples were collected between 1300 and 1500 h during steady diurnal flows. Samples were

collected on the first Tuesday and Wednesday of each month between February and May; samples were collected daily between May 31 and June 4, 1992. CPOM was not collected because it is time consuming to collect and it comprises <5% of the total transport of POM in Glen Canyon (Angradi and Kubly, in press; Appendix 2.1). A manuscript describing trophic linkages among aquatic biota in Glen and Grand canyons using stable isotopes is presented in Appendix 2.2.

Results and Discussion

FPOM concentration increased with increasing distance from the dam in April, May and June (Figure 2.1). The magnitude of the increase was small, as has been reported previously (Angradi et al. 1992). On June 2, a large increase (ca. twice ambient) in FPOM concentration was measured at the site 6 km below the dam. On the next two days an elevated FPOM concentration (ca. three-four times ambient) was measured at sites 15-18 km below the dam. As a result of a shift to a new release schedule at the dam, peak discharge on June 2 was higher than on any previous day since early March (Figure 2.2). These elevated peak flows partially flushed a large backwater located just upriver of the sample station (6 km). Flushed material was concentrated in large main-channel eddies further downriver (15-18 km). The effects of backwater flushing were short-lived and local; the FPOM concentration at Lee's Ferry on these dates was similar to dates when no backwater flushing occurred.

Objective 1.2. Determine the impact that Glen Canyon Dam releases have on *Gammarus lacustris* and determine how those releases affect the overall productivity of the amphipod. An effort will be made to determine the sources of organic matter required for the *Gammarus*. Both allochthonous and autochthonous organic matter inputs will be measured and evaluated as related to *Gammarus lacustris* production.

Methods and Progress

Monthly collections of *G. lacustris* were taken immediately below the 227 m³ s⁻¹ [cms](8,000 cfs) and 142 cms (5,000 cfs) river elevations with a Hess sampler (0.09 m²) fitted with a canvas cover, and preserved with 10% formalin. Eight samples were collected at each elevation and at each of two sites (14 mile bar and 3.5 mile bar) from cobble and gravel substrates and along permanent transects. *Gammarus lacustris* samples were sorted in the lab and all invertebrates were removed and counted. Future sampling will also include measurement of current velocity and sampling of benthic detritus by placing a sample tube on the substrate and vacuuming up any loose material into a carboy. The detritus will be filtered from the water using 0.45 μm glass fiber filters and an ash free dry weight will be determined. *Gammarus*

samples will be sent to the contract laboratory for length measurements, diet analysis, egg enumeration and determination of the presence of parasites. Length measurements will be used to calculate total biomass using a length-weight regression model.

The contract for length measurement, diet analysis, and egg enumeration of *G. lacustris* samples has been awarded and samples will be sent in the immediate future. Sampling is continuing with the addition of new sampling sites on the upstream side of 3.5 mile bar and the collection of additional data (i.e. flow and detritus measurements).

Results & Discussion

Figure 2.3 shows *G. lacustris* densities collected from May to November 1992. *Gammarus lacustris* density was significantly lower at the 227 cms elevations at both sampling sites ($P < 0.05$). In most months, significantly higher densities of *G. lacustris* occurred at 3.5 mile bar than 14 mile bar at the same cfs elevation ($P < 0.05$). The lack of significant *Cladophora glomerata* growth above the 142 cms elevation may explain the lower *G. lacustris* densities there. It could also be an area of desiccation and stranding.

Objective 1.3. Determine the effect of desiccation rates and time on the colonization and growth of *Cladophora glomerata* and its epiphytic diatoms. Experiments to determine the relationship of flow levels and community response are the overall objective.

Much of the work under this objective was reported by Angradi et al. (1992). A manuscript describing effects of exposure on the epilithon in Glen Canyon is presented in Appendix 2.3. Accretion of periphyton chlorophyll *a* and biomass on cobble bars was determined using artificial substrates (tiles) cut from Navajo sandstone (Angradi et al. 1992). Tiles were deployed at -14 mile bar (2 km below the dam), -3.5 mile bar (20 km below the dam), and at Cathedral Wash (30 km below the dam, 5 km below the Paria River) in late February 1992. Tiles were placed in grids of 25 tiles each at three levels: <142, 199-227 (7,000-8,000 cfs), and 425 cms (15,000 cfs); at Cathedral Wash the 425 cms level was omitted. At the sites in Glen Canyon, tiles were collected ($n=3$) at 10, 20, 30, 40, 60 and 100 days. At Cathedral Wash tiles were collected at 10, 20, 30, and 60 days.

The top and sides of each tile were scraped, and the resulting material was homogenized and subsampled twice. One subsample was ashed to determine ash-free dry mass (AFDM) of accumulated periphyton (Angradi et al. 1992); a second subsample was extracted in methanol for determination of chlorophyll *a* corrected for pheophytin (Tett et al. 1975).

Accretion of periphyton biomass and chlorophyll *a* on vertical cliff faces was determined using tiles mounted on boards bolted to the cliffs at 5-6 locations in Glen Canyon. Each vertical

substrate set of eight tiles was mounted so that some tiles were never exposed, and some were exposed at known flows. In the first trial of the experiment, substrate sets (two each) were installed at 1.5 (on river left [RL]), 6.8 (RR), 14.0 (RR), 20.5 (RL) and 23.5 (RR) km downriver from the dam on March 1, 1992. Tiles were collected at 30 and 60 days and processed as described above. In the second trial tiles were redeployed, including an additional set 15.5 km (RL) from the dam, on May 11, 1992, and collected after 30 and 60 days (only results for 30 days are reported here).

In an effort to measure species composition, and densities of benthic algae and invertebrates, two artificial substrate systems are being devised. The first will consist of small (3cm x 3cm) Navajo sandstone tiles mounted on boards and attached to the walls of the canyon at flow level elevations from 142 cms to 568 cms. The artificial substrates will be placed in triplicate at the sites just described. At predetermined times a set will be harvested and analyzed for species composition, biomass and algal density. The second artificial substrate will consist of various sizes of clay flower pots nested together to simulate the convoluted nature of the natural substrate. These also will be attached to the walls of the canyon at flow level elevations from 142 cms to 568 cms. These will be harvested in sets at predetermined times and analyzed for species composition, biomass and density of invertebrates. The contract for the identification and enumeration of the algal samples is in place and samples will be shipped as they are collected.

Results and Discussion

At -14 mile bar, accretion of periphyton chlorophyll *a* and biomass was highest on the permanently inundated tiles (< 142 cms level; Figures 2.4, 2.5), but accretion of biomass was nearly as great on tiles at the 199-227 cms level. During the experiment, the tiles at the 199-227 cms level were virtually always inundated during the day (Figure 2.2). The difference in accretion rates on tiles from the two levels can be attributed to the effects of nighttime dewatering on the 199-227 cms level tiles. Tiles at the >425 cms level were always exposed and accumulated no periphyton.

At -3.5 mile bar, much less periphyton accumulated on the tiles than at -14 mile bar (Figures 2.4, 2.5). Tiles at the 199-227 cms level actually accumulated more chlorophyll *a* and biomass than the 142 cms tiles. Wave action from boats at this site may have obscured any effect of level on periphyton accumulation because permanently inundated tiles were subject to more sediment deposition than tiles in the wave-influenced fluctuating zone.

At Cathedral Wash, more chlorophyll *a* and biomass accumulated on the tiles in the fluctuating zone initially; after 60 days, more chlorophyll *a* and biomass had accumulated on the permanently inundated tiles. At the time that tiles were installed and at 20 and 30 days, the

river was highly turbid due to sediment inputs from the Paria River. Turbidity was reduced during the second 30 days of the experiment (personal observation). Apparently, the effects of turbidity on light penetration interact with exposure effects due to the flow regime to determine periphyton colonization rates downstream of Paria River.

Accretion of periphyton chlorophyll and biomass on vertical substrates varied with exposure and distance from the dam (Figures 2.6, 2.7). The effects of exposure were most pronounced at the sites closest to the dam. In the first trial (Julian date 60-90, i.e., March-April), much more chlorophyll *a* and biomass accumulated on permanently inundated tiles than on exposed substrates. In the second trial (Julian date 132-162, i.e., mid May-mid June), accretion of chlorophyll *a* and biomass was similar for permanently inundated tiles and tiles at the 199-227 cms level. The difference in the amount of periphyton accumulated at the 199-227 cms level in the two trials is attributable to higher minimum flows in the second trial (Figure 2.2).

Much more periphyton accumulated on the vertical substrates closest to the dam in both trials. Standing biomass of periphyton on natural vertical surfaces adjacent to substrate sets showed the same trend. Differences in water velocity or orientation do not account for the longitudinal variation (Figure 2.8) in periphyton suggesting that periphyton may be nutrient limited in lower Glen Canyon.

Objective 1.4. Evaluate what effects exposure and desiccation have on the nutritional quality of *Cladophora glomerata*. The intent is to determine if exposure of the *Cladophora* to desiccation will increase the nutrient quality due to breakdown of the algal mats.

Methods and Progress

Cobbles with moderate to heavy growth of *Cladophora glomerata* will be taken from below the 142 cms river elevation and exposed to various periods of desiccation (0 to 6 hours for the first experiment then expanding to 12 or 24 hours). A subsample will be taken from each cobble at the end of the desiccation period. The cobbles will then be immersed into a tank with a constant flow of fresh water from the river. Samples will be taken from each cobble after 15 min, 30 min, 60 min, 2 hr, 4 hr, 8 hr, 16 hr, 32 hr and 64 hr. The samples will be analyzed for their chlorophyll *a*, phaeophytin, protein, lipid and carbohydrate levels in our laboratory.

Objective 1.5. Provide for comparative data collection of the water chemistry and aquatic food base elements. This work will be concentrated in the immediate area above Glen Canyon Dam and in the tailwater section from Glen Canyon Dam to Lee's Ferry. The specific techniques will follow those established under the GCES Phase II research program.

Methods and Progress

Methods used in the collection and processing of periphyton samples were identical to those described previously (Angradi et al. 1992). Samples were collected at -14 mile bar and -13.5 mile bar (3 km below the dam) from August 1991 through November 1992. No samples were collected in December 1991.

Water samples will be collected quarterly from the Lake Powell forebay at the surface and at penstock elevation, from the draft tube ports and from -14 mile bar and Lee's Ferry on the Colorado River below the dam. Samples will be filtered and preserved according to methods outlined by the contract laboratory, and sent to the contract laboratory for analysis. Zooplankton and phytoplankton will also be sampled at the same sites and preserved. The zooplankton and phytoplankton samples will be collected, identified and quantified as described in Objective 1.1. Periphyton biomass (standing crop) sampling will be continued on a monthly basis.

Results and Discussion

During interim flows, periphyton biomass in the permanently inundated channel initially decreased to late fall-early winter minima, and then increased beginning in spring 1992 (-13.5 mile bar) or remained relatively steady (-14 mile bar; Figure 2.9). Periphyton biomass in the zone of fluctuation (227 cms) increased in winter 1992, decreased in spring, and then steadily increased to a November 1992 maximum (-14 mile bar) or remained relatively steady (-13.5 mile bar). The patterns of change in biomass of periphyton in the permanent and fluctuating zones were dissimilar because periphyton in the lower zone was undergoing seasonal variation while periphyton in the fluctuation zone was responding to flow variation. The decrease in biomass in the fluctuating zone in spring 1992 corresponded to a decrease in minimum flows (Figure 2.2). There is some evidence that the increase in minimum flow in late spring (May) was also detectable in the periphyton in the fluctuating zone, especially at -14 mile bar (Figure 2.9). There was very little colonization of periphyton on natural cobbles above 425 cms.

Conclusions

Periphyton on cobble bars above the level of the permanently inundated channel appear to be very sensitive to flow regime. During interim flows, trends in the development of

periphyton in this zone corresponded closely to changes in minimum flows. Complete recolonization of cobbles in the zone of fluctuation may be possible under interim flows, but this is doubtful since complete recolonization of permanently inundated substrates to natural ambient levels may require 100-300 days (e.g., compare Figures 2.5, 2.9). Periphyton in Glen Canyon appears to lack resistance to daytime desiccation and is also sensitive to chronic nighttime exposure. Seasonal changes in minimum flows, especially on Sundays when low flows are minimal and most protracted, will determine the development rate of periphyton on cobble bars in Glen Canyon.

Evidence for nutrient limitation in Glen Canyon is still preliminary. It seems likely, however, that water quality and flow regime interact to determine periphyton development in Glen Canyon. In lower Glen Canyon, nutrient limitation may modify the magnitude of the exposure/desiccation effect on periphyton standing biomass.

POM in water released from Lake Powell appears to constitute the bulk of the POM exported from the Glen Canyon reach. This is additional evidence for the importance of Lake Powell forebay limnology on downstream ecosystem processes. For example, lake level determines the level at which water is withdrawn which may influence the particulate and dissolved nutrient content of released water.

Gammarus lacustris density varies among sites and degree of exposure. The higher density of *G. lacustris* at the -3.5 mile site suggests that periphyton biomass, which is low at that site, is not the only determinant of *G. lacustris* density. More likely, velocity and its effect on the availability of fine detritus exert a strong effect on *G. lacustris* distribution and abundance in Glen Canyon.

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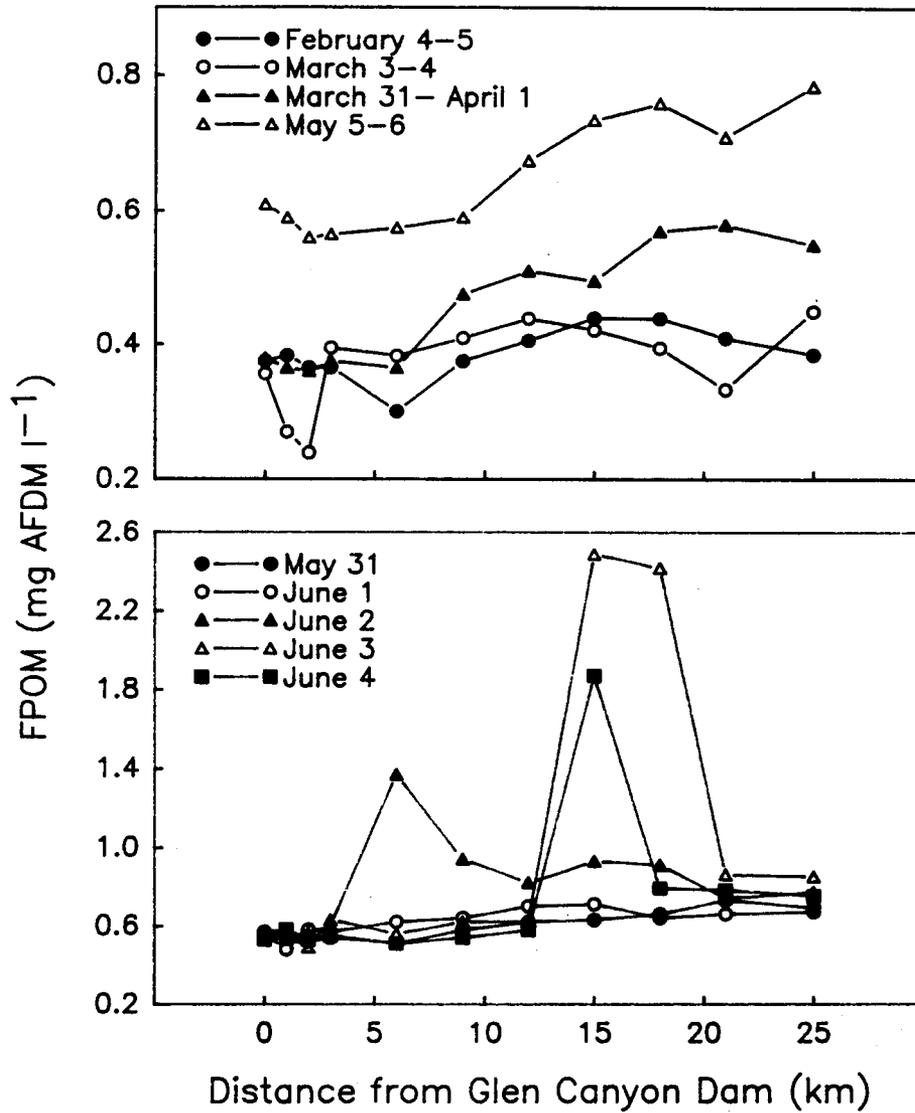


FIGURE 2.1. Longitudinal variation in mean FPOM concentration in Glen Canyon (n=10 except in June, n=5). Samples for 0 km were collected from Glen Canyon Dam penstocks. Error bars were omitted for clarity.

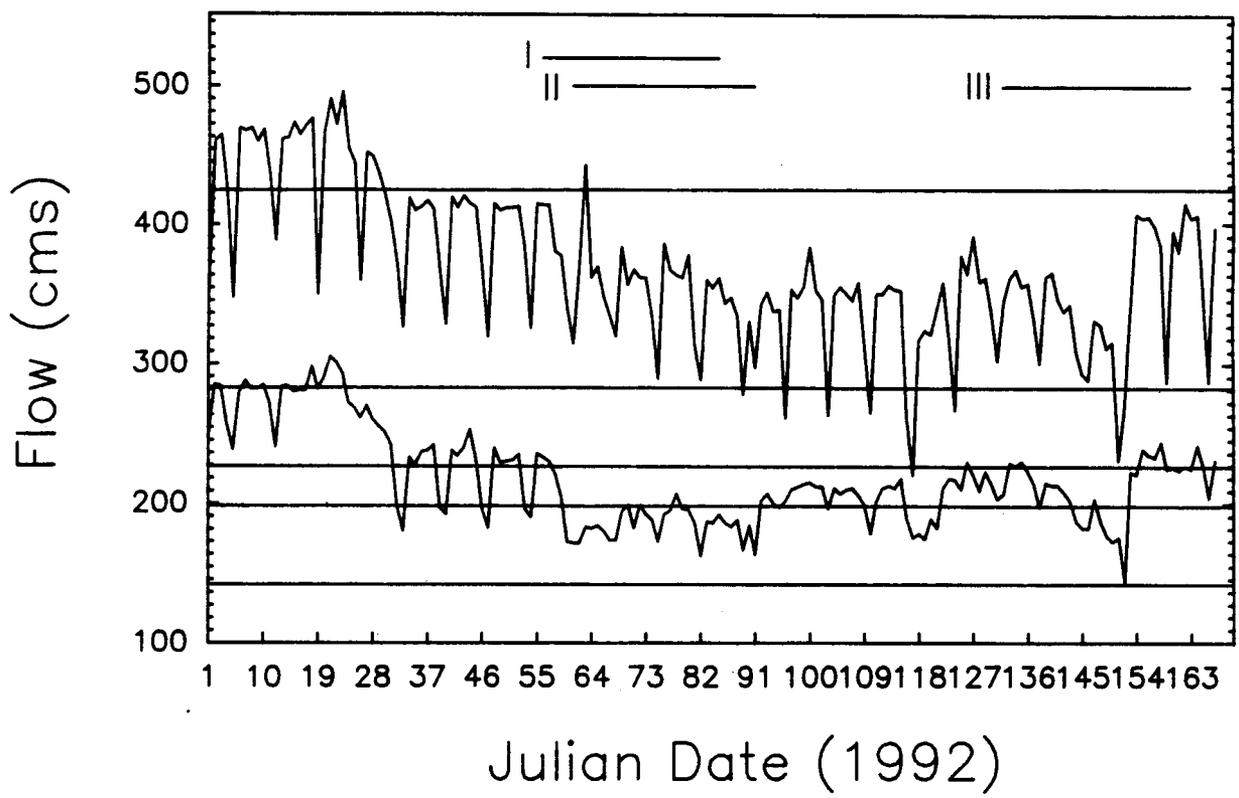


FIGURE 2.2. Minimum and maximum flows (cubic meters per second [cms]) during 1992 through June 15, 1992. Horizontal lines indicate significant levels (142, 199, 227, 285, 425 cms). Lines at the top of the figure indicate the time period of the cobble bar colonization experiment (I), and the two vertical substrate trials (II, III). Evenly spaced minima in maximum daily flow are Sundays. Data are from Glen Canyon Dam water release records.

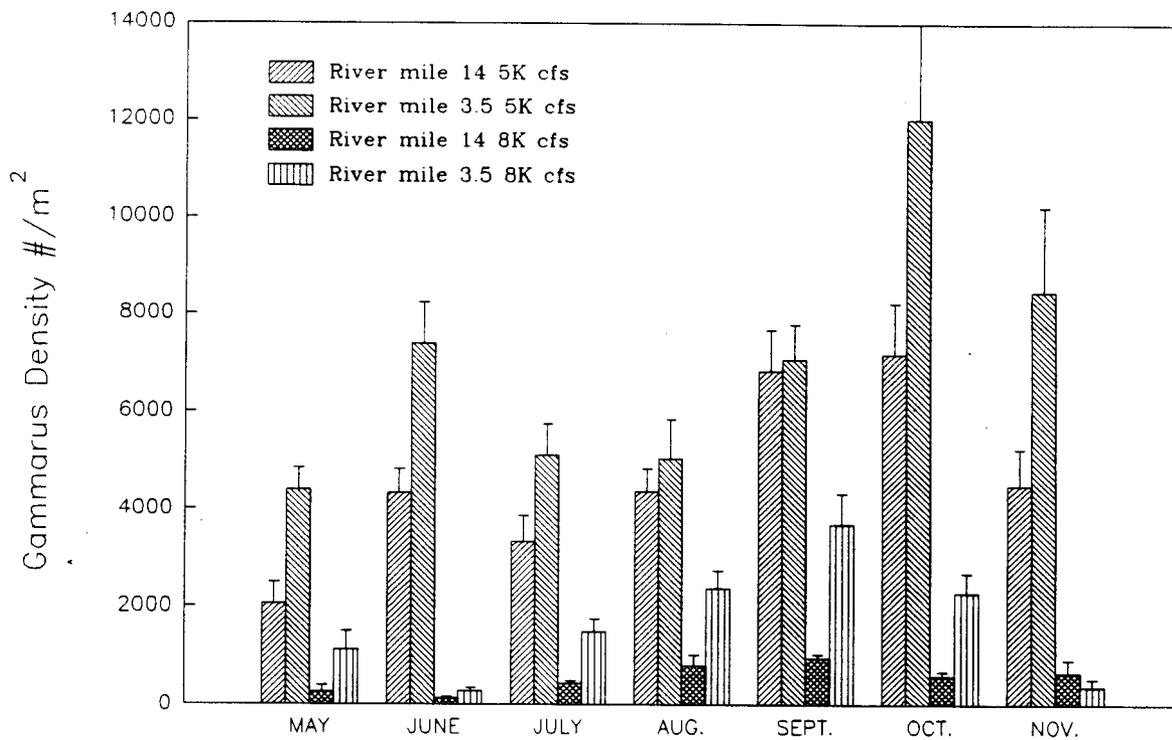


FIGURE 2.3. Mean (± 1 SE) *Gammarus lacustris* density (number/m²) at 14 and 13.5 mile bar in Glen Canyon from May through November 1992.

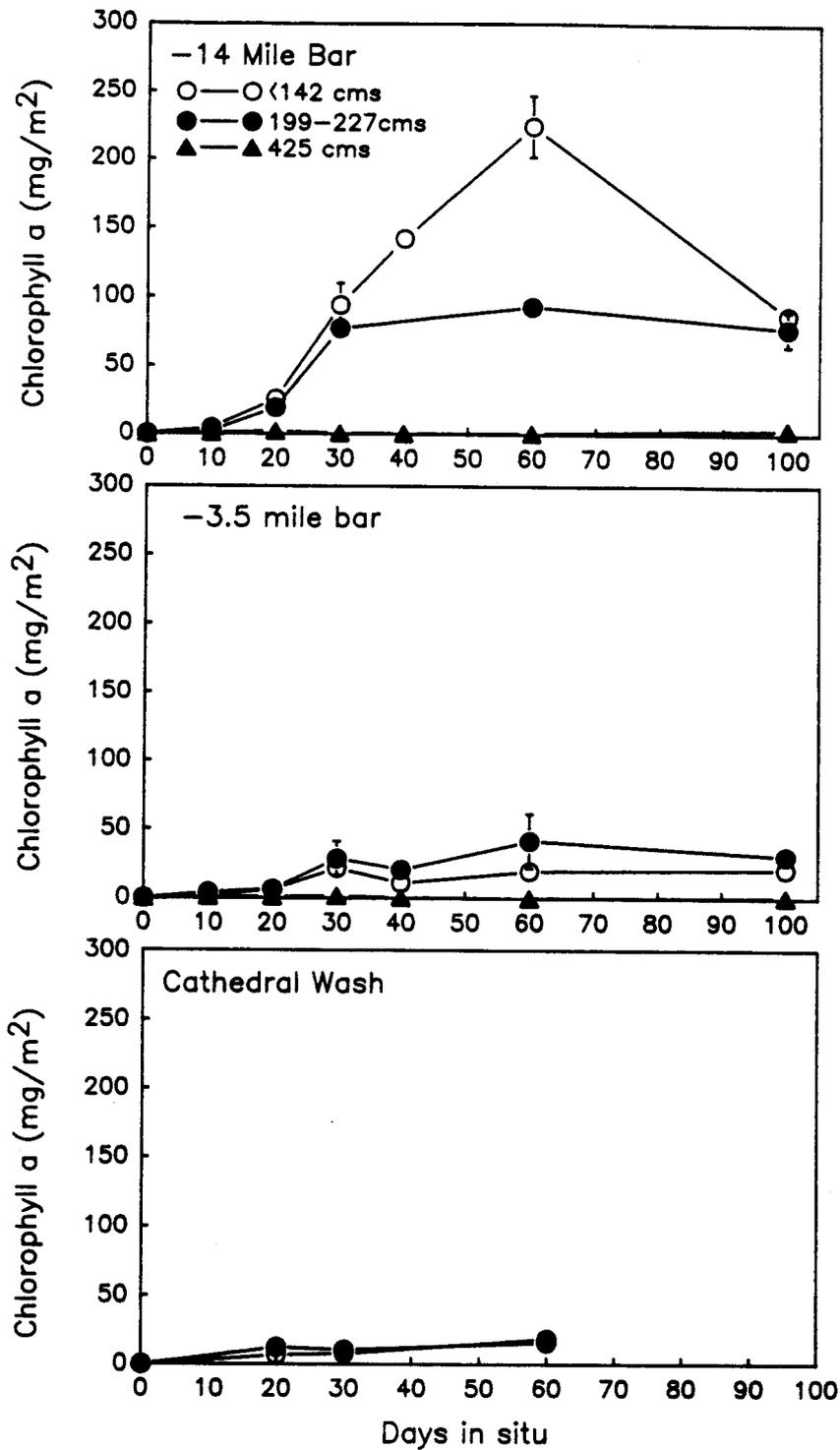


FIGURE 2.4. Accretion of chlorophyll a on sandstone tiles at three Glen Canyon sites in spring 1991 at three levels (cubic meters per second[cms]). Error bars are ±1 SE of the mean.

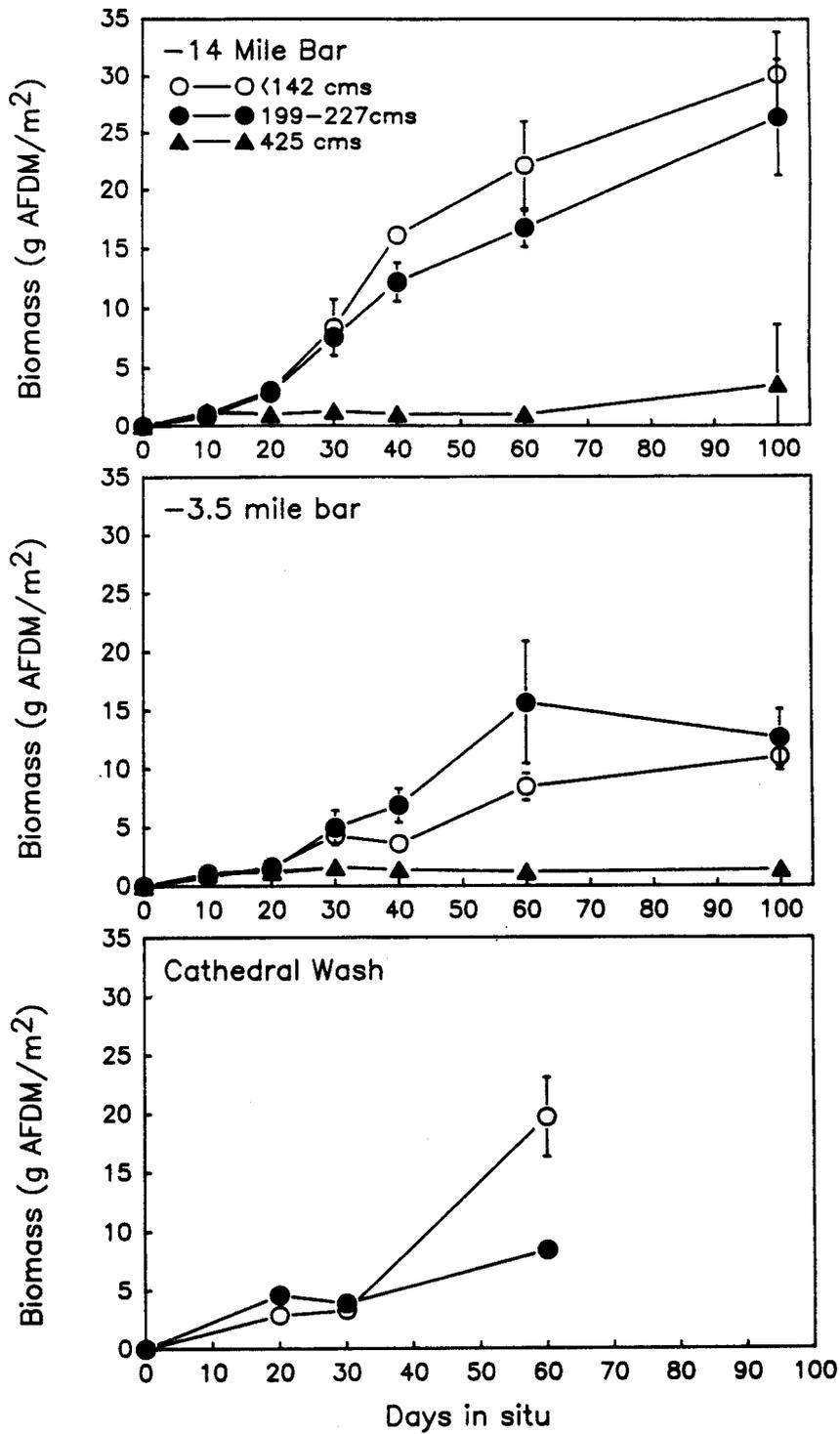


FIGURE 2.5. Accretion of biomass on sandstone tiles at three Glen Canyon sites in spring 1991 (cubic meters per second [cms]). Error bars are ± 1 SE of the mean.

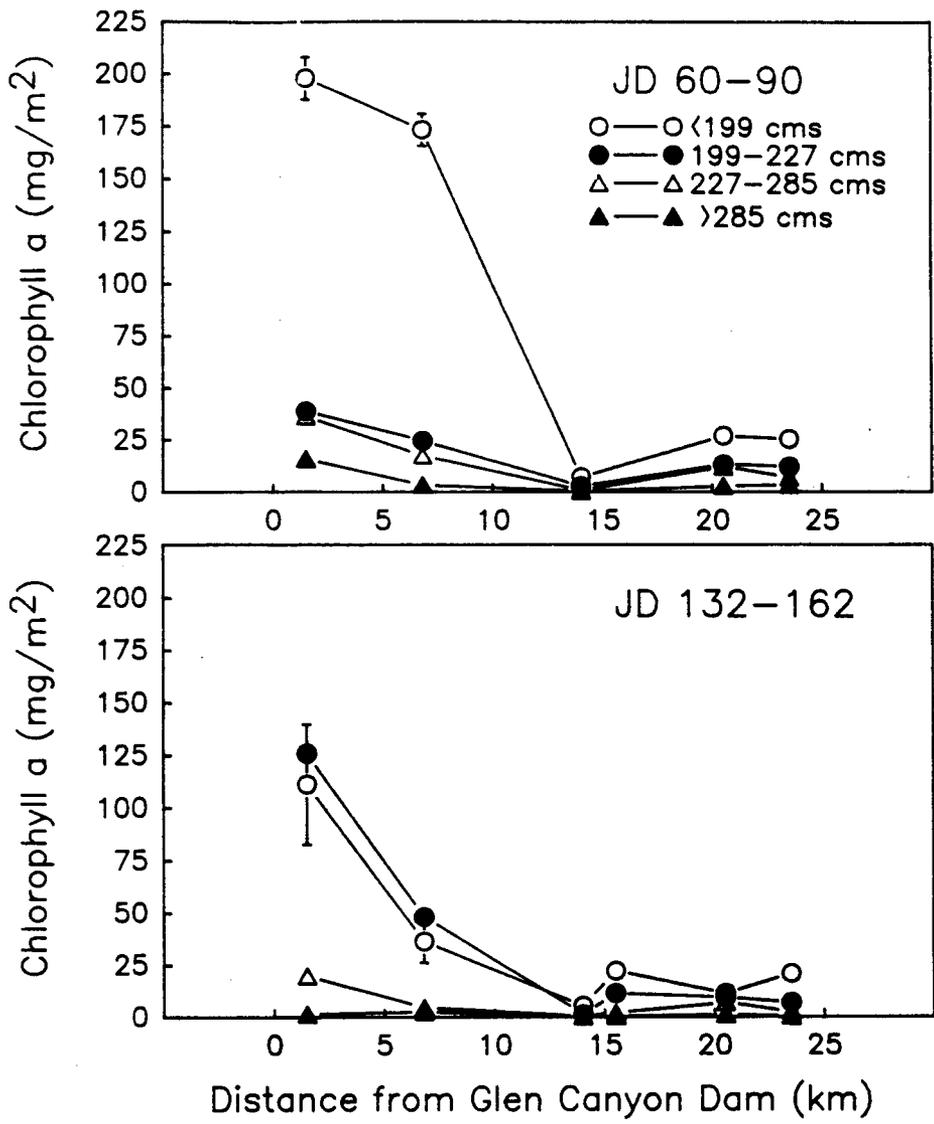


FIGURE 2.6. Accretion of chlorophyll *a* on vertical substrate sets in two experimental trials conducted from Julian date (JD) 60-90 and from JD 132-162 at four levels (cubic meters per second [cms])

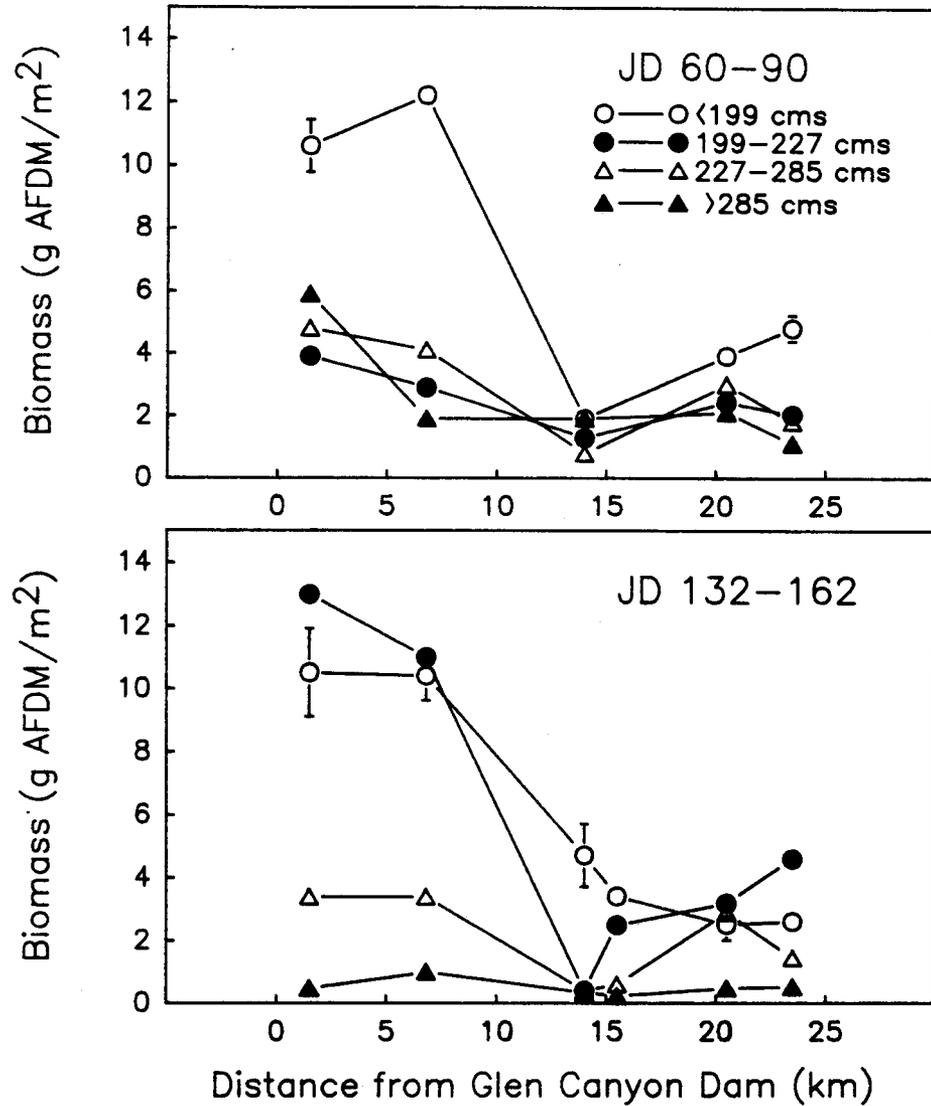


FIGURE 2.7. Accretion of biomass on vertical substrate sets in two experimental trials conducted from Julian date (JD) 60-90 and from JD 132-162 at four levels (cubic meters per second [cms]).

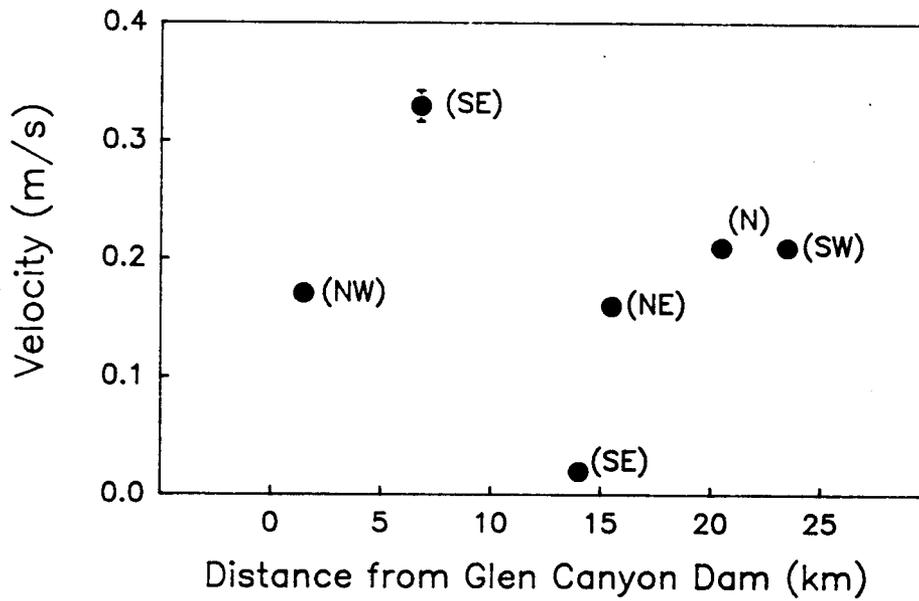


FIGURE 2.8. Water velocity (± 1 SE) and (orientation) of vertical substrate sets in Glen Canyon. Velocity data were collected on June 10, 1992 from 1300-1500 h.

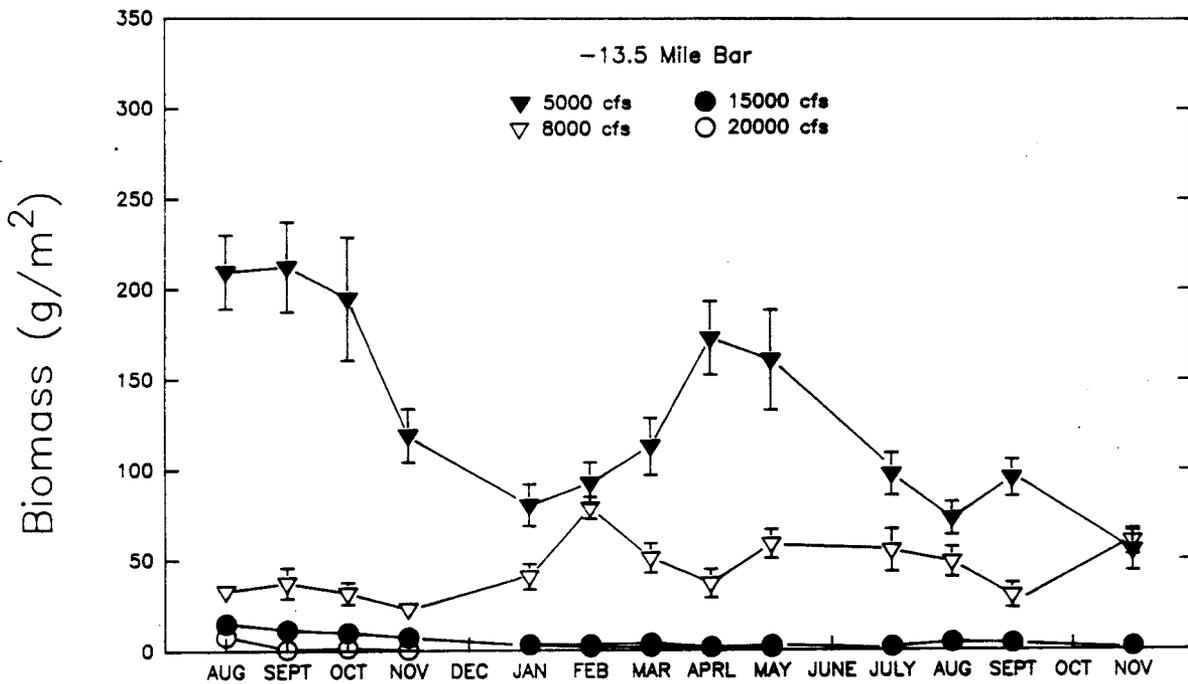
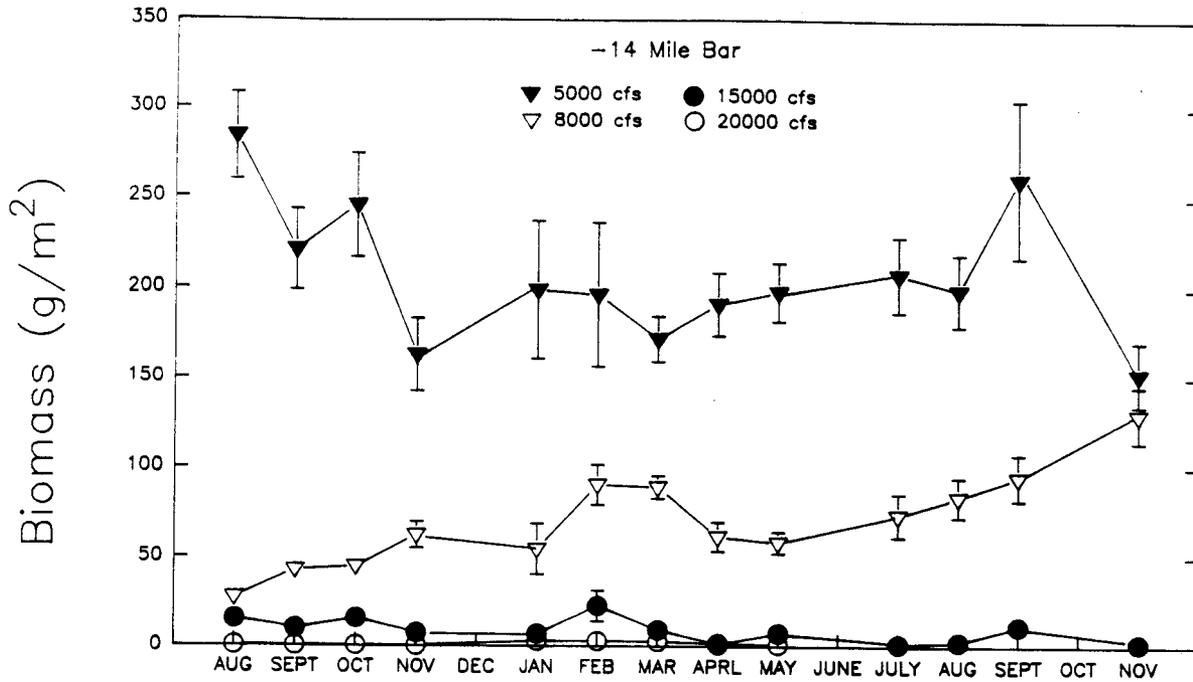


FIGURE 2.9. Accretion of biomass on natural cobbles at four levels (cubic meters per second [cms]) at -14 mile bar and -13.5 mile bar in 1991-1992. Error bars are ± 1 SE of the mean ($n > 10$).

APPENDIX 2.1

CONCENTRATION AND TRANSPORT OF PARTICULATE ORGANIC MATTER
BELOW GLEN CANYON DAM ON THE COLORADO RIVER, ARIZONA

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ABSTRACT

Particulate organic matter (POM) concentration and transport were investigated in a 25 km tailwater reach below Glen Canyon Dam on the Colorado River, Arizona. The concentration of coarse particulate organic matter (CPOM, $> 750 \mu\text{m}$) was positively related to flow during periods of daily fluctuating flows (for hydropower); there was no diel variation in CPOM concentration during constant flows. Fine particulate organic matter concentration (FPOM, $0.7\text{-}750 \mu\text{m}$) was only weakly related to flow; FPOM exported from the reservoir (Lake Powell) dampened diel and seasonal variation in tailwater FPOM concentrations. FPOM concentration in released water (sampled directly from dam penstocks) was not related to discharge. Export of total POM from the reach substantially exceeded imports only in spring. Otherwise, temporal variation in FPOM concentration 25 km downriver from the dam closely tracked variation in the FPOM concentration of water released from the dam. Overall, mean FPOM concentration ($> 96\%$ of the total POM) 25 km from the dam (0.58 mg l^{-1}) was only slightly higher than penstock concentrations (0.55 mg l^{-1}). A series of FPOM collections in the tailwater indicated that downriver increases in POM concentration were gradual and continuous, suggesting that localized POM sources or sinks had little effect of POM concentration except when elevated peak flows flushed a large backwater. Our results indicate that some lotic algal debris was exported as CPOM ($< 4\%$ of POM), but that lotic autochthonous contributions did not elevate tailwater POM concentrations much above reservoir inputs.

INTRODUCTION

Fluctuations in flow below hydroelectric dams can influence the concentration and transport of particulate organic matter (POM) imported into and exported from the tailwater reach (reviewed by Petts 1984). POM dynamics are an important component of river ecosystem function (Vannote *et al.* 1980); changes in the spatial and temporal distribution of organic particles caused by flow regulation may precipitate effects at several trophic levels (Cushman 1985).

Flow fluctuations may influence the concentration of POM in at least four ways: (1) daily stage changes may entrain or strand particles originating on the previously dewatered or inundated substrate (e.g., desiccated algal filaments, Leibfried and Blinn 1987); (2) changes in flow may alter stream competence causing POM to become entrained or deposited (Webster *et al.* 1979); (3) an increase in peak discharge may flush side channels and backwaters (Lieberman and Burke 1991); (4) the POM concentration in water released from the dam may depend in part on the volume of water withdrawn from the reservoir.

Glen Canyon Dam on the Colorado River regulates flows for 400 km between Lake Powell and Lake Mead. This reach includes Glen Canyon, which extends for 25 km below the dam, and Grand Canyon which extends thence to Lake Mead. The influence of the existence (since 1963) and operation of Glen Canyon Dam on downriver ecosystems in Glen and Grand Canyons has come under scrutiny in recent years (National Research Council [NRC] 1987, 1991; United States Department of the Interior 1987). Two potential effects of dam operations on downriver resources which involve POM dynamics have been identified: (1) the flow regime may affect the availability of suspended particles eaten by introduced trout and native fishes (Leibfried and Blinn 1986, NRC 1987, Minckley 1991); (2) water releases may influence the export of organic matter from the Glen Canyon reach to Grand Canyon where it may be processed and assimilated by primary and secondary producers (NRC 1987).

Objectives of this study were to determine how water releases from Glen Canyon Dam affect the concentration of particulate organic matter, and to examine seasonal and longitudinal variation in POM inputs and outputs in Glen Canyon.

SITE DESCRIPTION AND METHODS

POM samples were collected from penstocks within Glen Canyon Dam on the Colorado River, and from the 25 km tailwater reach between the dam and Lee's Ferry, Arizona. Glen Canyon Dam forms Lake Powell, a long (300 km), deep (average depth = 51 m), warm

monomictic reservoir that retains virtually all of the 44-154 million Mg annual suspended sediment input (Evans and Paulson 1983). Water releases from the reservoir are hypolimnial (from a depth of ca. 48-52 m during this study). As a result, released water is perennially cold (7-11 C), chemically stable, and transparent (Stanford and Ward 1991).

Glen Canyon tailwater hydrodynamics are determined by dam releases. During this study the river received water in a variety of daily flow regimes ranging from peaking flows with a daily range of from < 100 to $> 700 \text{ m}^3 \text{ s}^{-1}$ to steady flows of ca. 225 and $420 \text{ m}^3 \text{ s}^{-1}$ (United State Geological Survey [USGS], unpublished data). The river in the tailwater reach flows through deeply incised (> 300 m) Glen Canyon. It ranges in width from 50-220 m, and in depth from < 1 m to > 15 m. Substrate is mostly cobble and sand; surficial substrate size on cobble bars decreases with increasing distance from the dam due to armoring (Pemberton 1976, Angradi *et al.* 1992).

The epilithic filamentous green algae Cladophora glomerata (L.) Kütz. and its diatom epiphytes dominate the aquatic flora of the tailwater (Blinn and Cole 1991). The epilithon attained a high biomass during this study, especially in the upper half of the tailwater reach ($> 500 \text{ mg chlorophyll } a \text{ m}^{-2}$; $> 250 \text{ g ash-free dry mass [AFDM] m}^{-2}$, Angradi *et al.*, 1992). A densely vegetated 1-30 m wide riparian zone exists along much of the shoreline in Glen Canyon. Woody riparian vegetation in the post-dam high water zone is dominated by Tamarix ramosissima and Salix spp. (Johnson 1991).

POM collection

POM was collected in two phases. In the first sampling phase (September 1990 - December 1991), POM was collected simultaneously from penstocks within the dam and at Lee's Ferry, 25 km downriver. At Lee's Ferry, a sample was collected at ca. 1000, 1600, 2200 h, and at 0400 and 1000 h of the following day in an attempt to sample ascending, maximum, descending, and minimum flows. In actuality, the 2200 h sample was typically just prior to the daily reduction to nighttime flow levels (Figure 1). At the dam, the second 1000 h sample was not collected. Mean POM concentrations at 1000 h on the first day did not differ from the concentration at 1000 h on the second day. Flow data were obtained from USGS gauging stations located at Lee's Ferry and 1.5 km below the dam. Samples were collected on 15 dates (roughly monthly) between September 1990 and December 1991; POM was collected only four times in the September 1990 sample. On three sample dates, water releases from the dam were constant or nearly so (Table 1); releases otherwise varied according to variation in hydropower demands.

In the first sampling phase (1990-1991), water samples for fine particulate organic matter (FPOM; 0.7-750 μm) were collected at Lee's Ferry using a diaphragm pump. A depth-integrated water sample was obtained by raising and lowering the inlet hose as the boat was maneuvered back and forth normal to flow. At the dam, a water sample was withdrawn directly from the penstocks. Coarse particulate organic matter (CPOM; $>750 \mu\text{m}$) was collected at Lee's Ferry by deploying a metered high-speed Miller tube (10-cm diameter mouth, 750 μm -mesh) behind a boat maneuvered across a transect as was done for FPOM. CPOM was not collected at the dam but was negligible in penstock samples.

FPOM was obtained by filtering prefiltered (750- μm) samples (1-3 l) of river water through tared, pre-ashed glass fiber-filters (Whatman GF/F; 0.7 μm pore size). Samples were dried for 24 h at 105 C, desiccated, weighed, ashed for 2 h at 550 C, desiccated and reweighed. All POM concentrations are expressed as mg AFDM l^{-1} .

In the second sampling phase (1992), water samples for FPOM were collected from penstocks at the dam and 1, 2, 3, 6, 9, 12, 15, 18, 21, and 25 km downriver and processed as described above. All samples were collected between 1300 and 1500 h during steady flows at the peak of the daily hydrograph (Figure 2). Samples were collected on the first Tuesday and Wednesday of each month between February and May; samples were collected daily from May 31 to June 4, 1992.

Analysis of variance (ANOVA) was used to examine the effect of sample station (Lee's Ferry versus dam penstocks) on POM concentration. Two techniques were used to examine the effects of flow on POM concentration: ANOVA, in which a grouping variable and surrogate of flow, time of day, was the factor of main effect, and log-log rating plots of flow versus concentration (Ferguson, 1987). Least-squares linear regression was used to examine the relation between distance downriver from the dam and FPOM concentration.

RESULTS

Flow effects

CPOM concentration varied with time of day during fluctuating flows (Figure 3; $F_{3,44} = 2.37$, $p = 0.08$) but not during steady flows ($F_{3,8} = 0.82$, $p = 0.52$). During fluctuating flows, mean (\pm SE) CPOM concentration at 1600 h ($0.03 \pm 0.009 \text{ mg l}^{-1}$) was three times higher than at 0400 h ($0.01 \pm 0.003 \text{ mg l}^{-1}$; t-test, $p < 0.05$). Qualitative examination of CPOM indicated that it was predominately Cladophora glomerata debris. Macrophyte and terrestrial debris and macroinvertebrates were present in far lesser amounts.

At Lee's Ferry, FPOM concentration varied with time of day during fluctuating flows (Figure 3), although the effect was not significant ($F_{3,44} = 1.92$, $p = 0.14$). However, maximum mean concentration at 1600 (0.70 ± 0.07 mg l⁻¹) exceeded the minimum mean concentration at 0400 (0.50 ± 0.05 mg l⁻¹; t-test, $p < 0.05$). During steady flows there was no effect of time of day ($F_{3,8} = 0.79$, $p = 0.54$) on FPOM concentration. At Glen Canyon Dam penstocks, there was no effect of time of day during fluctuating ($F_{3,43} = 0.39$, $p = 0.76$) or steady flows ($F_{3,8} = 0.01$, $p = 0.99$).

A weak but statistically significant relationship existed between flow and CPOM concentration at Lee's Ferry ($r^2 = 0.21$, $n = 72$; Figure 4). Hysteresis (different discharge-concentration relationships for ascending and descending portions of the daily hydrograph) could partially account for the scatter about the trend, because equal flows at different times of day would not correspond to equal seston concentrations. Our data are not replicated within sample dates, so we were unable to test for this effect. There was no relationship between flow and FPOM at either Lee's Ferry ($r^2 = 0.01$, $n = 72$) or the dam ($r^2 = 0.004$, $n = 58$).

Seasonal variation

CPOM concentration varied significantly among sample dates ($F_{14,45} = 2.88$, $p < 0.01$). Concentration was higher in spring and fall and lowest in winter (Figure 5). FPOM concentration varied significantly among dates at Lee's Ferry ($F_{14,45} = 5.51$, $p < 0.01$) and Glen Canyon Dam penstocks ($F_{14,44} = 4.72$, $p < 0.01$).

Concentration of FPOM at Lee's Ferry was higher than FPOM concentration in the penstocks only in spring. At other times, FPOM concentration at Lee's Ferry closely tracked FPOM concentration in dam releases (Figure 5). For all dates combined (September 1990 - December 1991), the FPOM concentration at Lee's Ferry (0.58 ± 0.03 mg l⁻¹) was not significantly higher than the concentration at the dam (0.55 ± 0.02 mg l⁻¹; $F_{1,89} = 1.49$, $p = 0.23$); however, the interaction of site and date was significant ($F_{14,89} = 3.18$, $p < 0.01$).

As for concentration, total export of POM (g AFDM s⁻¹) from the tailwater reach was highest in spring (Table 1). For several samples, inputs to the reach substantially (>50%) exceeded outputs. When the effects of the spring 1991 data are excluded, there is little net export from the reach (Table 1). Of the three sample dates in which flow did not vary much (October 23-24, 1990; December 17-18, 1990; May 28, 1991), there was net export from the reach only in the May sample. There is little evidence that during fluctuating flows, flow

regime influenced POM concentration. For example, total POM concentration at Lee's Ferry was not correlated with discharge range ($r^2 = 0.11$, $n = 15$).

Longitudinal variation

FPOM concentration increased with increasing distance from the dam in April ($r^2 = 0.41$, $n = 110$) and May ($r^2 = 0.25$, $n = 110$), and on May 31 ($r^2 = 0.54$, $n = 53$), June 1 ($r^2 = 0.37$, $n = 55$), June 3 ($r^2 = 0.23$, $n = 55$), and June 4 ($r^2 = 0.16$, $n = 54$) (Figure 6). In all cases, downstream increases were moderate (<25%). In some months (e.g., February, March) there was a decrease in FPOM concentration for 2-6 km below the dam followed by a gradual increase, suggesting that a partial shift from reservoir-derived to river-derived particles occurred in the upper third of the reach.

On June 2, a large increase (ca. twice ambient) in FPOM concentration was measured at the site 6 km downriver from the dam. On the next two days an elevated FPOM concentration (ca. three-four times ambient) was measured at sites 15-18 km below the dam (Figure 6). In each case the increase diminished downriver. As a result of a shift to a new release schedule at the dam, peak discharge on June 2, the first day of elevated FPOM concentration, was higher ($> 400 \text{ m}^3 \text{ s}^{-1}$) than on any previous day since early March 1992 (Figure 2). Our observations indicate that these elevated peak flows partially flushed a large (ca. 1.5 ha) backwater located just upriver of the sample station. Flushed material was concentrated in large main-channel eddies further downriver (15-18 km below the dam). The effects were short-lived and local; the FPOM concentration at Lee's Ferry on these dates was similar to dates when no backwater flushing occurred.

DISCUSSION

CPOM concentration varied as a function of flow. Of two possible major sources of CPOM, Cladophora sloughed from the bed of the permanently inundated channel or Cladophora sloughed from the zone of daily fluctuation, the former is the more likely since several protracted dewatering episodes before and during this study eliminated nearly all of the Cladophora in the zone of fluctuation (Angradi *et al.* 1992). Furthermore, exposed Cladophora filaments are rapidly bleached (in $< 24 \text{ h}$; Usher and Blinn 1990, Angradi *et al.* 1992). Cladophora filaments collected as CPOM were bright green.

The effects of diel flow variation on FPOM concentration were less than for CPOM. FPOM concentration in penstocks at the dam did not vary with flow, and was largely independent of the volume of water withdrawn from Lake Powell. FPOM concentration at

Lee's Ferry was only weakly related to flow, suggesting that FPOM exported from Lake Powell dampens diel (i.e., flow-related) variation in FPOM concentration. Seasonal variation in the POM concentration in the dam forebay at penstock intake depth is probably low (Angradi *et al.* 1992) suggesting that limnologic processes in Lake Powell, which is intensely stratified most of the year (Stanford and Ward 1991), may dampen seasonal variation in downriver POM concentration.

POM concentration often increases with distance downriver from dams as a result of tributary inputs and enhanced autochthonous production (e.g., Ward 1976, Webster *et al.* 1979, Gilvear 1987, cf. Kondratieff and Simmons 1984). In some impounded rivers, considerable lentic plankton remains entrained for many kilometers (Petts 1984). Under such conditions, and where tributary and allochthonous inputs are negligible, as they are in Glen Canyon, downriver increases in POM concentration represent lotic autochthonous contributions in excess of losses of lentic inputs.

FPOM sampling at intermediate sites between the dam and Lee's Ferry indicated a moderate (ca. 25 %) downriver increase in FPOM concentration within the reach in spring. An initial decline in FPOM concentration in the first few km below the dam on some dates suggests that a part of the FPOM from the reservoir was deposited in the relatively slack water in the large (0.25 km²) pool just below the dam. Net export of POM in late winter and spring resulted from processes in the tailwater rather than from depressed FPOM concentration in water releases (Figure 5).

In Glen Canyon, where epilithon biomass on cobble substrates is high, a positive relationship between cumulative upriver area of cobble substrate and epilithon-derived POM would be predicted (Swanson and Bachmann 1976). However, cobble substrates in Glen Canyon are largely restricted to the upstream half of the tailwater (about 85% are in the first 12 km), and the bottom area colonized by algae decreases substantially between the dam and Lee's Ferry (T. R. Angradi, personal observation). Whereas cumulative upstream algal production increases in the downriver direction, it is at a decreasing rate, and high concentrations--compared to dam penstocks--of river-derived POM do not develop. The strong temporal concordance between Lee's Ferry and dam penstock FPOM concentrations, and lack of concordance with CPOM concentration (Figure 5) indicate that the measure FPOM concentration at Lee's Ferry resulted from lotic organic matter inputs in excess of the lentic inputs which remain entrained through the reach.

The effects of benthic POM storage on POM dynamics in the reach are poorly understood. Longitudinal sampling (Figure 6) revealed no consistent interruption--POM

source or sink--in the progressive, albeit slight, downriver increase in FPOM concentration except in June when side channels were flushed by elevated peak flows. Our observation that the importance of backwaters as contributors of POM to the river is contingent on antecedent flow conditions agrees with the findings of Lieberman and Burke (1991). They reported that the abundant backwaters of the lower Colorado River appeared to have little effect on thalweg POM concentration except during storm events. The effects of backwater flushing appear to be short-lived; sustained high flows flush out stored POM in a day or two.

Although the reach was always a net exporter of CPOM, this conspicuous size fraction accounted for only 3 or 4 percent of the total POM at Lee's Ferry. The ecological significance of CPOM exports from the tailwater to downriver communities is uncertain. There are no large-particle detritivores (shredders) present in the mainstem Colorado River in Grand Canyon (W.C. Leibfried and D. W. Blinn, in litt.) to consume reliable and highly nutritious CPOM (C:N \leq 12, Angradi *et al.* 1992). Exported CPOM is probably assimilated into downriver food webs only after it is processed to finer fractions.

We consider it unlikely that vigorous processing of retained POM obscured POM export from the tailwater reach: mean concentration of dissolved organic carbon in spring of 1991 (2.9 mg l⁻¹) did not differ between Lee's Ferry and the penstocks (Angradi *et al.* 1992). More likely, infrequent events such as floods (including planned increases in peak dam releases), dewaterings, and seasonal pulses in algal sloughing account for the majority of the export of autochthonous POM that is in excess of reservoir inputs.

Mean total POM concentration at Lee's Ferry during this study (0.6 ± 0.04 mg l⁻¹) was lower than the tailwater POM concentrations reported by Lieberman and Burke (1991) for the lower Colorado river below Lake Mojave (0.80 mg l⁻¹) and Lake Havasu (0.89 mg l⁻¹). Reasons for the difference are unknown, but are probably related to increased nutrient levels in these downriver reservoirs (Paulson and Baker 1984). Nonetheless, our findings support their conclusion that in lower Colorado River tailwaters, downstream increases in total POM concentrations due to lotic autochthonous sources are generally small.

ACKNOWLEDGMENTS

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FIGURE CAPTIONS

Figure 1. Mean (\pm SE) percent change in flow between diel POM samples at Lee's Ferry and Glen Canyon Dam (GCD) for September 1990 - December 1991 excluding dates on which flow did not vary. At Lee's Ferry, 1000 h and 1600 h samples were during ascending flow; flows during the 2200 h sample were 100 percent of flows at 1600 h; 0400 h sample was during minimum diel flows.

Figure 2. Daily hydrographs at Lee's Ferry and 1.5 km below Glen Canyon Dam (GCD) for 1992 dates when longitudinal FPOM samples were collected (for February - May, the hydrographs for the first sample day are shown). Missing are data from the upper gauge on May 31, and data from both gauges for several hours on June 2. Apparent higher peak flows at the upper gauge in June are due to malfunctioning of the upper gauge (as verified by comparison to actual dam releases). Reduced flows on May 31 are the normal case for a Sunday.

Figure 3. Diel variation in POM concentration in Glen Canyon. Values are means (\pm SE) pooled across sample dates (September 1990 - December 1991). Dates of constant flows are given in Table 1. CPOM was not collected from penstocks.

Figure 4. Plots of POM concentration versus flow for all dates combined (September 1990 - December 1991). Regression was significant for CPOM only; $\text{Log}_{10} \text{CPOM} = -4.33 + 0.98 \text{Log}_{10} \text{Flow}$, $r^2 = 0.21$.

Figure 5. Among-sample date variation in CPOM and FPOM concentration in Glen Canyon (September 1990 - December 1991). Values are means (\pm SE) pooled across time of day, excluding the second 1000 h sample at Lee's Ferry.

Figure 6. Longitudinal variation in mean FPOM concentration ($n = 10$ except in June, $n = 5$) in Glen Canyon, February - June 1992. Error bars were omitted for clarity. Samples for 0 km were collected from Glen Canyon Dam penstocks.

Table 1. Daily mean flow-weighted POM transport (g AFDM $s^{-1} \pm SE$) in Glen Canyon. Discharge range is as recorded at the Lee's Ferry USGS gauging station.

Sampling date	Discharge range ($m^3 s^{-1}$)	Lee's Ferry		Dam Penstocks
		CPOM	FPOM	FPOM
09-27-90	81-735	10.0 ± 3.5	254.3 ± 87.6	306.0 ± 73.5
10-04-90	96-362	4.3 ± 1.0	121.6 ± 24.0	159.5 ± 35.6
10-23-90	229-231	2.7 ± 0.3	103.8 ± 14.0	110.8 ± 6.6
12-17-90	229-288	2.5 ± 0.4	141.2 ± 6.5	140.9 ± 1.3
01-07-91	241-558	3.2 ± 0.9	291.7 ± 42.7	265.2 ± 27.4
01-22-91	205-472	2.6 ± 0.5	193.2 ± 21.6	211.3 ± 20.3
02-04-91	150-414	2.5 ± 0.5	182.9 ± 19.2	137.6 ± 14.5
03-11-91	106-495	16.2 ± 5.9	272.5 ± 45.6	161.9 ± 23.8
04-23-91	142-480	24.4 ± 4.7	304.2 ± 47.5	196.4 ± 29.8
05-28-91	424-426	8.9 ± 1.5	207.4 ± 16.5	161.1 ± 11.4
06-24-91	181-664	10.8 ± 2.8	338.6 ± 60.0	352.6 ± 48.2
08-16-91	311-517	7.3 ± 0.9	122.2 ± 6.5	225.0 ± 32.3
09-24-91	323-539	11.1 ± 2.4	171.0 ± 17.5	176.1 ± 18.2
10-30-91	201-377	8.1 ± 0.5	165.1 ± 8.1	152.7 ± 19.3
12-17-91	249-390	7.9 ± 0.7	201.6 ± 13.6	153.8 ± 5.1

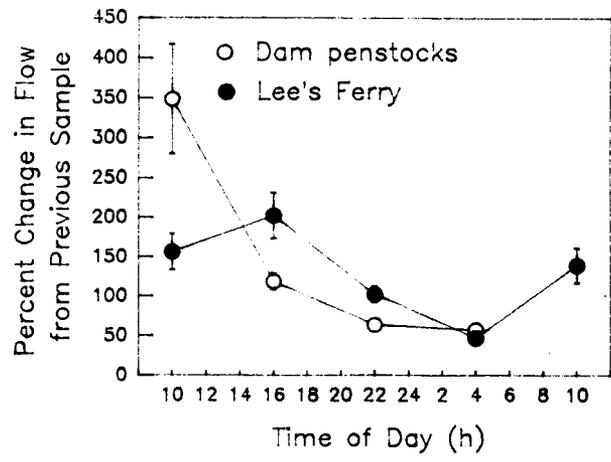


FIGURE 1.

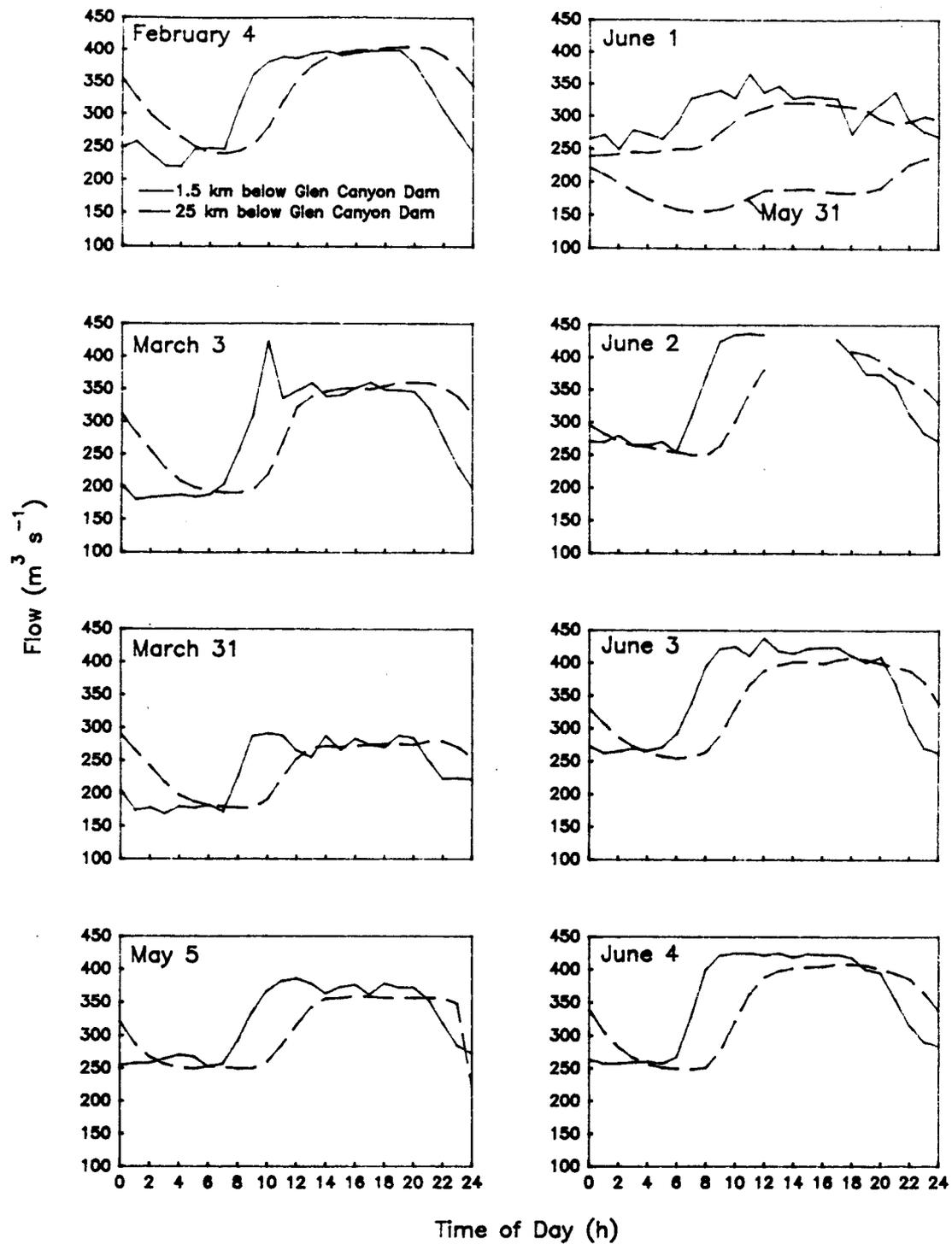


FIGURE 2.

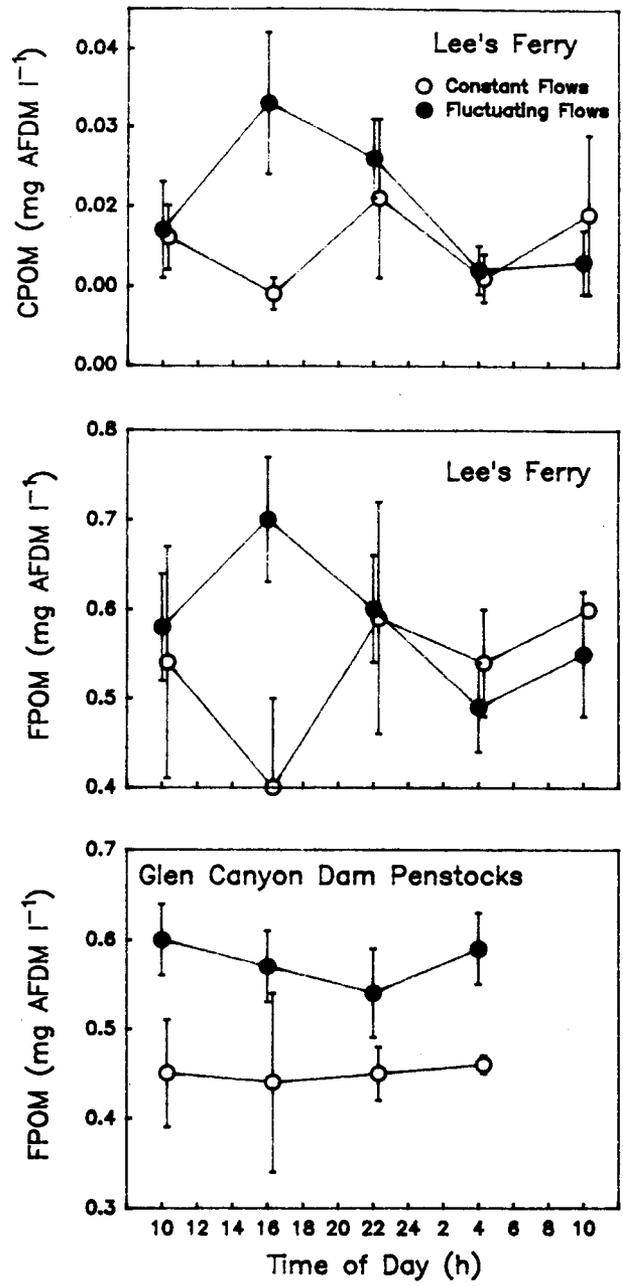


FIGURE 3.

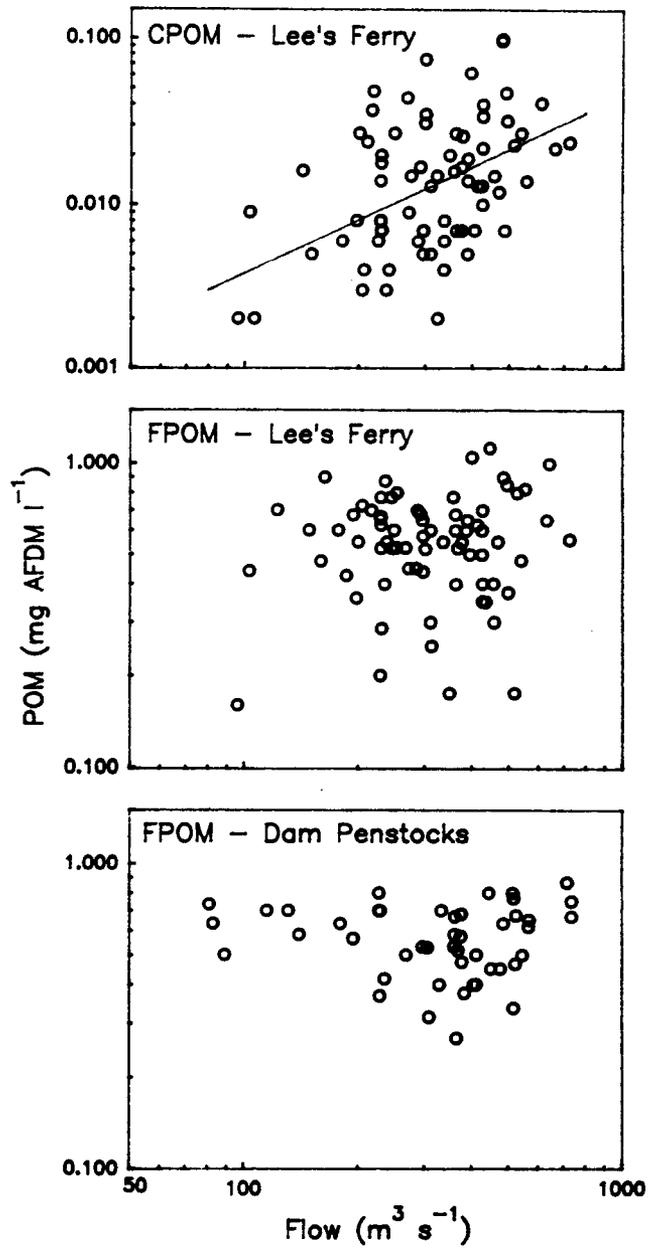


FIGURE 4.

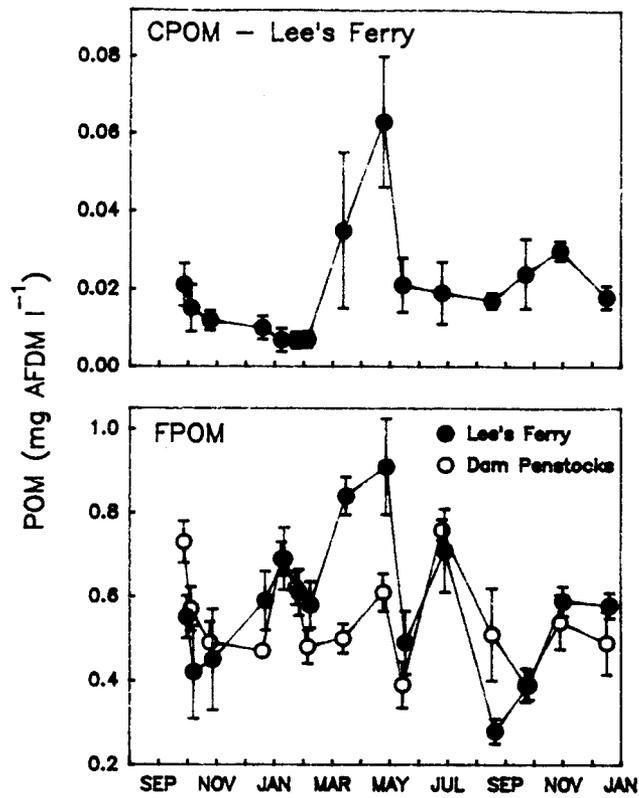


FIGURE 5.

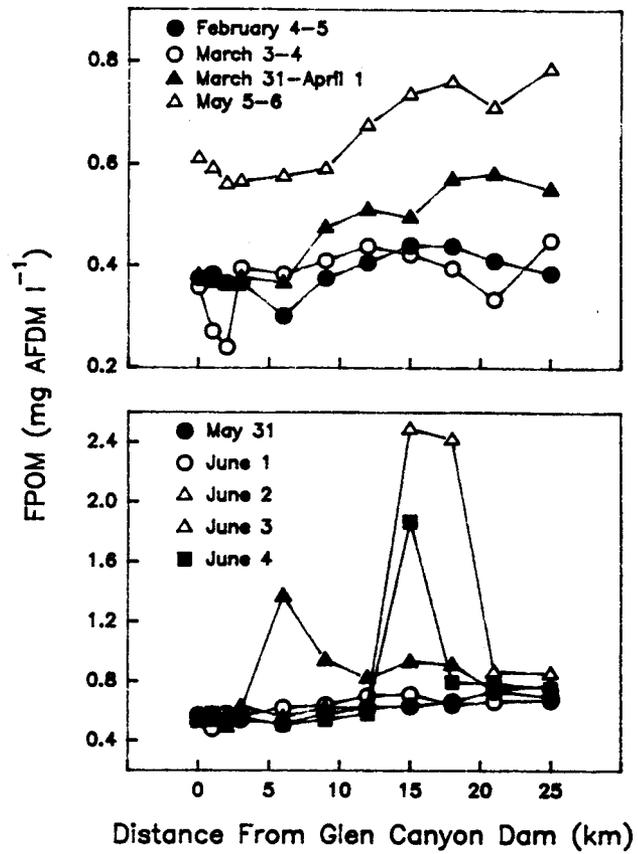


FIGURE 6.

APPENDIX 2.2

TROPHIC LINKAGES IN THE LOWER COLORADO RIVER
BELOW GLEN CANYON DAM: STABLE ISOTOPE EVIDENCE

T. R. ANGRADI

ABSTRACT

Stable isotope analysis was used to examine trophic linkages in Glen and Grand canyons of the lower Colorado River downstream from Glen Canyon Dam. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of seston, plant, animal, and dissolved inorganic carbon were determined. The $\delta^{13}\text{C}$ value of DIC varied among sites. DIC from the epilimnion of the reservoir above the dam was more $\delta^{13}\text{C}$ enriched than DIC in the river; DIC from a tributary was more enriched than Colorado River sites. Upland vegetation, riparian vegetation, and algae were isotopically distinct from each other. Seston from the Colorado River was derived from algae and zooplankton, except for the ultrafine fraction (< 0.053 mm) which was mostly phytoplankton from the reservoir. Seston from a tributary (the Paria River) was derived from a mixture of upland and riparian vegetation and was isotopically distinct from Colorado River seston. Isotope analysis revealed three trophic levels in Glen Canyon: algae (*Cladophora glomerata* and diatoms), macroinvertebrates (e.g., *Gammarus lacustris* and chironomids), and fish (primarily rainbow trout, *Oncorhynchus mykiss*). Direct assimilation of algal N by trout was not indicated despite the high incidence of algae in trout stomachs. Isotope values of fishes (trout and speckled dace, *Rhinichthys osculus*) from Grand Canyon tributaries indicated a food web depending in part on the Colorado River in some streams. In other streams, a food web based on riparian or upland vegetation was indicated. The potential usefulness of stable isotopes in examining trophic linkages in a large regulated river was demonstrated; suggestions for future research are given.

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INTRODUCTION

Stable isotopes of carbon and nitrogen (^{13}C , ^{15}N) can be used to establish a chemical outline of the trophic structure of aquatic communities (Fry 1991). These isotopes undergo fractionation, a change in the ratio of heavy to light isotopes, in biochemical reactions. As a result, biogenic materials often have unique isotope ratios ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$) which can be used to trace carbon and nitrogen through ecosystems (Fry and Sherr, 1984; Rounick and Winterbourn, 1986; Peterson and Fry, 1987; Fry, 1991; Gearing 1991). Stable isotopes are used in trophic studies because they move with little or predictable alteration through food chains (Rounick and Winterbourn, 1986). For ^{13}C , the isotope value of animals reflects that of the assimilated part of the diet averaged over weeks or months, but with about a 1 part per thousand (‰) enrichment per trophic level (Fry and Sherr, 1984). For ^{15}N , the isotope values of animals are usually 3-5 ‰ to their diet (Minagawa and Wada, 1984; Peterson and Fry, 1987).

Stable isotopes have been used to examine trophic linkages in a variety of lotic ecosystems including high-latitude rivers and streams (Bunn et al. 1989, Angradi 1989; Kline et al., 1989; Rosenfeld and Roff, 1992), New Zealand rivers and streams (Rounick et al., 1982; Rounick and Hicks, 1985; Collier and Lyon, 1991), a British river system (Winterbourn et al., 1986), and a regulated Rocky Mountain River (Angradi, in press).

The work described here was part of a larger study of how the operation of Glen Canyon Dam influences the structure and function of ecosystems in Glen and Grand canyons of the Colorado River, USA. Research findings on dam effects, and on mechanisms by which the timing, rate, and volume of water released from the dam influence the downstream aquatic biota are impossible to interpret fully without an understanding of the trophic structure of Colorado River aquatic communities, including tributary streams, and of the linkages among communities (e.g., reservoir-tailwater, upstream-downstream, riparian-lotic, upland-lotic, and tributary-mainstem linkages).

The objective of this study was to use stable isotopes of carbon and nitrogen to examine the trophic structure of the dam tailwater (Glen Canyon) and to survey trophic linkages in the downstream Colorado River and its tributaries, with emphasis on fishes. Several questions were considered amenable to stable isotope analysis: (1) What is the trophic basis of production for

important Glen Canyon macrofauna? (2) How many trophic levels are there in Glen Canyon? (3) Is there spatial variation in the origin of seston (suspended particulate organic matter) within Glen Canyon? (4) How much trophic interaction is there between tributaries and the Colorado River in Grand Canyon? and; (5) Is the trophic basis of production different in Glen Canyon, Grand Canyon, and tributaries?

MATERIALS AND METHODS

Study Site

Glen Canyon Dam, located on the Utah-Arizona (USA) border, forms Lake Powell, a 653 km² warm-monomictic reservoir (Stanford and Ward, 1991). Glen Canyon extends 26 km downstream from the dam to the confluence of the first tributary, the Paria River; Grand Canyon extends another 375 km to Lake Mead. The physical environment of the Colorado River was greatly altered by the construction and operation of Glen Canyon Dam. Flows from hypolimnetic releases are perennially cold and are more transparent than were pre-dam flows (Stanford and Ward 1991). The existing flora and fauna of the river below the dam are depauperate (Blinn and Cole, 1991). The filamentous green algae *Cladophora glomerata* (L.) Kutz. is the dominant attached algae and is an important substrate for diatoms (Blinn et al., 1992). Epilithic *Cladophora* thrives in Glen Canyon, often attaining biomasses in excess of 500 mg chlorophyll/m² (Angradi et al., 1992). High turbidity caused by suspended sediment exported from tributaries greatly limits the growth of *Cladophora* in Grand Canyon (Usher and Blinn, 1990). The crustose blue-green algae *Oscillatoria* is abundant in some reaches of the Grand Canyon (Blinn et al., 1992)

Chironomids, oligochaetes, and the amphipod *Gammarus lacustris* predominate the depauperate Glen Canyon macroinvertebrate fauna (Blinn and Cole, 1991). The invertebrate faunas of most tributary streams within the Grand Canyon are typical of southwestern streams (Hofknect, 1981).

The fish fauna consists of five native species, two of which are threatened or endangered, and 15-20 introduced species (Minckley, 1991). The speckled dace (*Rhinichthys osculus* Girard) is the most widespread and abundant native species in Grand Canyon and its tributary streams. The fish fauna of Glen Canyon is dominated by an introduced salmonid, the rainbow trout

(*Oncorhynchus mykiss* Walbaum). The native flannelmouth sucker (*Catostomus latipinnis* Baird and Girard) and the nonnative carp (*Cyprinus carpio* Linn.) and are common; other species are rare.

Woody vegetation of the Glen Canyon riparian zone is dominated by tamarisk (*Tamarix ramosissima*), willow (*Salix* spp.), and seepwillow (*Baccharis* spp.) (Johnson, 1991). Upland vegetation of the inner gorge of the Grand Canyon is Great Basin desertscrub and Mojave desertscrub; larger tributaries drain juniper-pinyon woodlands (Brown and Lowe, 1980).

Sample Collection and Analysis

Samples for stable isotope analysis were collected in March, April, and May of 1992. Water samples for dissolved inorganic carbon were collected from the epilimnion (6 m), and hypolimnion (46 m) of Lake Powell at a site 100 m in front of the dam. Water samples were also collected from dam penstocks, from sites 2, 11, and 25 km downriver from the dam (all Colorado River distances given here are relative to the dam), and from the Paria River 0.7 km upstream from its confluence with the Colorado River. DIC samples were filtered (millipore, 0.47- μ m pore size) and preserved with HgCl. Seston was collected at the same sites using the following methods: in Lake Powell, seston < 0.08 mm was collected by pumping lake water through a plankton net (0.08 mm mesh). Water samples were then filtered with glass-fiber filters (0.7- μ m pore size). seston > 0.08 mm was collected by pumping 1500 l of lake water through a 0.08-mm mesh plankton net. Insufficient material > 0.08 mm was collected in the hypolimnetic sample for analysis. Samples from dam penstocks were filtered (glass-fiber) without prefiltering. Seston > 0.053 mm was collected at river sites by towing a pair of plankton nets (1.5 m long, 0.25 m diameter, 0.053-mm mesh) behind a boat maneuvered back and forth across the channel. At the Paria River site, a net was fixed to a bridge support in midchannel. Collected material was acidified (1 N HCl) to prevent carbonate contamination (Boutton 1991), washed, and wet sieved into three size fractions: coarse particulate organic matter (CPOM, > 1 mm); fine particulate organic matter (FPOM, < 1 mm and > 0.25 mm); and very fine particulate organic matter (VFPOM, < 0.25 mm and > 0.053 mm). Ultrafine particulate organic matter (UFPOM, < 0.053 mm and > 0.7 μ m) was collected by filtering (glass-fiber) samples of prefiltered (0.053 mm) river water. On both collecting trips to the Paria River, discharge was above baseflow, and no UFPOM sample could be collected due to the high

silt load. On one occasion a sample of Paria River CPOM was collected using a fish seine with a mesh size of about 3 mm.

Riparian vegetation and litter grab samples were collected at various sites. At the Paria River, two flood-deposited litter accumulations were sampled. These deposits consisted of an admixture of conifer needles, cones, berries, nuts, bark, and small pieces of wood, as well as much unidentifiable material. A cottonwood (*Populus fremonti*) leafpack was also collected. Seston, plant and litter samples were dried (60 °C) and ground in a mill prior to analysis.

Cladophora glomerata was collected at sites 2 and 22 km below the dam. At each site samples of bright green as well as dark brownish-green filaments were collected. Other work (Angradi et al., 1992) has shown that the bright green filaments support very few diatom epiphytes compared to the heavily colonized brownish-green filaments. A subsample of the brownish-green *Cladophora* from the 2 km site was partially stripped of epiphytes by placing the filaments in a plastic bag with distilled water and shaking vigorously. Detached material was collected on pre-ashed glass fiber filters, from which *Cladophora* fragments were removed with forceps. To examine the effects of *in situ* processing on the stable isotope ratios of *Cladophora* filaments, fresh samples of each type of *Cladophora* from the 2 km site were placed in litter bags (2-mm mesh), four each, and fastened to a heavy block in the permanently inundated channel. Samples were collected at 25 and 52 days.

A sample of the green algae *Ulothrix tenuissima* Kutz. was collected from the dam spillway. An algal crust presumed to contain the blue-green algae *Oscillatoria* was collected from a cobble bar on the Colorado River 330 km below the dam. Algal samples were acidified, rinsed, dried, and ground in a mill prior to analysis.

Gammarus lacustris was collected by a diver with a small dipnet at sites 2, 11 and 22 km below the dam. The animals were held live in mesh bottom cages for 48 h to clear their guts, dried, ground with a mortar and pestle, acidified, rinsed, and redried. Oligochaetes were collected at the 11 km site and processed similarly.

Adult rainbow trout (> 350 mm) were collected in Glen Canyon at sites <1.0 and 19 km below the dam by angling (upper site) or trammel net. At the 19 km site, trout were collected from a

connected backwater used for spawning by trout and suckers. Four fish were collected at each site. Rainbow trout fry (<50 mm) were collected with a seine at sites 2 and 25 km below the dam. Two flannelmouth suckers (>400 mm) were collected at the 19 km site. Two adult rainbow trout (>200 mm) were collected in Nankoweap Creek 10 m above the confluence with the Colorado River (109 km below the dam). Rainbow trout fry (< 35 mm) were collected 1370 m above the confluence of Bright Angel Creek and the Colorado River (166 km), and 75 m above the confluence of Deer Creek and the Colorado River (244 km). Speckled dace (40-100 mm) were collected at six sites: > 2 km up the Paria River; 45 and 1500 m up Nankoweap Creek, 500 m up Crystal Creek (183 km); and 10 and 700 m up Shinumo Creek (200 km).

Boneless, skinless filets were removed from the dorsal musculature of adult trout and suckers. Trout fry and speckled dace were eviscerated, skinned, and the head and fins were removed. The vertebrae of small fish were assumed to produce no bias in isotope ratios relative to a pure muscle sample (Gearing, 1991). Fish tissue was dried and ground with a mortar and pestle. Selected gut contents of adult trout were dried and ground for analyses [these data not yet available].

Isotope ratios were determined by mass spectrometry at the Stable Isotope Laboratory at Boston University. Isotope ratios are reported in delta (δ) as parts per thousand (‰) deviation from isotope standards, atmospheric nitrogen for ^{15}N and PeeDee belemnite carbonate for ^{13}C :

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} \text{ ‰} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where R denotes $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ (Peterson and Fry, 1987). Well homogenized replicates are usually within a 0.2 ‰ range (Bob Michener, personal communication).

RESULTS AND DISCUSSION

Dissolved Inorganic Carbon--Dissolved inorganic carbon (DIC) was more $\delta^{13}\text{C}$ -depleted in the river and the hypolimnion of Lake Powell than in the epilimnion or the Paria River (Figure 1). The $\delta^{13}\text{C}$ value of DIC in freshwater depends on the extent to which it is in equilibrium with air (atmospheric $\text{CO}_2 = -7$ to -8 ‰, DIC of water in equilibrium with air = ca. 0‰), the rates

of photosynthesis and respiration, and the contribution from dissolution of $\delta^{13}\text{C}$ -enriched carbonate rock (Oana and Deevey, 1960; Quay et al., 1986; Boutton, 1991). Lake Powell is generally stratified by April when samples were taken, and the productivity of the epilimnion (as indicated by particulate chlorophyll *a* concentration) is more than twice that of the hypolimnion at penstock depth (Angradi et al., 1992).

Photosynthesis increases the $\delta^{13}\text{C}$ of DIC as isotopically light (i.e., $\delta^{12}\text{C}$ -enriched) dissolved CO_2 of atmospheric origin is incorporated into plankton (Quay et al., 1986). Hypolimnetic and river DIC are probably more depleted as a result of contributions of dissolved CO_2 from respiration of plankton (Oana and Deevey, 1960). Variation in $\delta^{13}\text{C}$ of DIC among Colorado River sites is very small (Figure 1). Therefore, any variation in the $\delta^{13}\text{C}$ of river-collected phytoplankton (UFPOM) must result from factors other than a longitudinal gradient in $\delta^{13}\text{C}$ values of DIC in Glen Canyon.

The $\delta^{13}\text{C}$ -enriched condition of Paria River DIC probably results from dissolution of carbonate rock ($\delta^{13}\text{C}$ ca. 0 ‰, Deevey and Stuiver, 1964). The concentration of bicarbonate ions in the Paria River (3.5 meq/l) exceeds that of the Colorado River (2.8 meq/l; Kubly and Cole, 1979). Variation in the $\delta^{13}\text{C}$ of phytoplankton exported from tributaries or backwaters with different DIC $\delta^{13}\text{C}$ values could be used to study trophic relations of planktivorous organisms.

Trophic Basis of Production

The $\delta^{13}\text{C}$ range of terrestrial and aquatic plant material was from -33.5 to -24 ‰ (Figure 2a). Aquatic material was all < -31 ‰ except *Oscillatoria* (-21 ‰); terrestrial plants and plant litter were all > -29 ‰. *Cladophora* with and without epiphytes, and an extract of epiphytes (diatoms), all had similar $\delta^{13}\text{C}$ values (ca. -33 ‰). *Cladophora* from 22 km below the dam, and *Ulothrix* from the dam spillway were slightly enriched (2 ‰) compared to other algal samples.

Litter from the Paria River was isotopically similar to published ^{13}C values for leaves and twigs of one-seed juniper (*Juniperus monosperma*), Utah juniper (*Juniperus osteosperma*), and pinyon (*Pinus edulis*) collected in Arizona (-20 to -23 ‰; Leavitt and Long, 1982, 1986). Riparian litter (tamarisk and cottonwood) was more $\delta^{13}\text{C}$ -depleted (< 27 ‰).

The $\delta^{15}\text{N}$ range of plant material was from ca. -1 to 9 ‰, but most values were from 5 to 9 ‰ (Figure 2b). Isotopically distinct were Paria litter and, to a lesser extent, cottonwood and tamarisk litter. The relatively enriched value for *Oscillatoria* (8.8 ‰) was unexpected since nitrogen-fixing algae usually have a $\delta^{15}\text{N}$ near 0 ‰ (Estep and Macko, 1985) or are at least $\delta^{15}\text{N}$ depleted (e.g., Estep and Vigg, 1985; Angradi, in press). Possible explanations are that the non-heterocystous *Oscillatoria* does not fix nitrogen on Grand Canyon substrates, although it has been reported to do so in unialgal cultures (Stewart, 1973), or, that the high $\delta^{15}\text{N}$ value is an artefact. *Oscillatoria* is found in a matrix of sediment and $\delta^{15}\text{N}$ detritus of unknown composition; the isotope value of the bulk sample may represent a mixture of N-containing materials. Blinn et al. (1992) reported that the biomass of *Oscillatoria* increases downriver in Grand Canyon in inverse proportion to the standing biomass of *Cladophora*, but they found no *Oscillatoria* filaments in the stomachs of Grand Canyon chironomids. The sample we analyzed was isotopically unique among lower trophic level components since it had enriched $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values; additional dual isotope analysis would clarify the role of *Oscillatoria* in the Grand Canyon food web.

There was little effect of *in situ* incubation of *Cladophora* samples on $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values. $\delta^{13}\text{C}$ values for high-epiphyte-load samples after 0, 25, and 52 days (-33.4, -33.8, -33.0 ‰, respectively) and for low-epiphyte-load samples (-33.2, -33.8, -32.6 ‰) were within a 1 ‰ range. $\delta^{15}\text{N}$ values for high-epiphyte-load samples after 0, 25, 52 days (7.0, 6.7, 6.6 ‰) and for low-epiphyte-load samples (5.2, 4.6, 5.7 ‰) were both within a 1.1 ‰ range. Angradi (in press) also reported little alteration of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of whole and finely ground allochthonous and autochthonous organic matter after up to three months of incubation in an Idaho river. These findings have implications for the use of isotope tracers in rivers, since particles resulting from the comminution of algal filaments will be isotopically similar to the intact filaments.

Seston

The $\delta^{13}\text{C}$ range of seston was from ca. -35 to -23 ‰ (Figure 3a). Values were in three groups: > -25 ‰ for Paria River seston; -27 to -30 ‰ for all seston in the ultrafine range including Lake Powell plankton < 0.08 mm; and < -32 ‰ for CPOM, FPOM, and VFPO from all Colorado River sites and plankton > 0.08 mm from the epilimnion of Lake Powell. There did

not appear to be a relationship between $\delta^{13}\text{C}$ and either particle size or collection site or seston > 0.053 mm. The $\delta^{15}\text{N}$ range of seston was from ca. 0 to 13 ‰ (Figure 3b). Only epilimnetic zooplankton (> 0.08 mm, 13 ‰) and Paria River seston (< 2 ‰) were distinct from the majority of values (6.5 to 11 ‰). Most $\delta^{15}\text{N}$ values for Glen Canyon seston were very similar (9.5 to 11 ‰).

The co-plotted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges of seston > 0.053 mm from Glen Canyon indicate that this size fraction, which includes CPOM, FPOM, and VFPOM, was mostly derived from benthic algae (Figure 4). No distinction could be made among the two forms of *Cladophora* and diatoms. Many seston samples were $\delta^{15}\text{N}$ -enriched by 2-3 ‰ relative to algae, indicating the presence of zooplankton. An alternative explanation for the enrichment of seston over algae is that the particles were colonized by microbes which substantially enriched the net $\delta^{15}\text{N}$ value (Macko and Estep, 1984). This interpretation would contradict the results of the litter-bag assay. Furthermore, CPOM, FPOM, and VFPOM samples from the site nearest the dam (2 km) were the most $\delta^{15}\text{N}$ -enriched (Figure 3b). Autochthonous material from this site would be the least processed, however, since it was collected closer to its point of origin than seston from any other site (none is produced above the dam). Finally, seston from the most upstream site would be expected to include the most zooplankton, since the amount of entrained zooplankton usually decreases rapidly below dams (Ward, 1975).

The dual-isotope range of Glen Canyon UFPOM is contained within the dual isotope range for reservoir plankton < 0.08 mm. Clearly, comminution of particles derived from lotic algae does not contribute much seston to the UFPOM fraction in Glen Canyon. The uniqueness of the $\delta^{13}\text{C}$ compared to larger fractions, and its dual-isotope similarity to phytoplankton indicates that this fraction is dominated by material exported from the reservoir. This finding corroborates that of Angradi and Kubly (in press) who showed that the seston in Glen Canyon was dominated by particles < 0.75 mm, and that the concentration of seston in water released through the dam was maintained, with little alteration, through Glen Canyon. Collection of seston down a transect in Grand Canyon might reveal the distance at which the ultrafine fraction loses its isotopic distinctiveness. Such a study would reveal the direction of isotopic shift with distance downstream and answer the question: do isotope values of Grand Canyon seston continue to resemble that of Glen Canyon as local inputs of autochthonous organic matter replace

reservoir-derived seston exported from Glen Canyon, or does the seston increasingly reflect allochthonous tributary and riparian inputs?

The dual-isotope range of Paria River seston indicates that it is a mixture of particles derived from riparian and upland vegetation (Figure 4). Large CPOM (> 3 mm) collected during a runoff event was most similar, isotopically, to upland vegetation. Flows during and prior to sampling, especially in Grand Canyon tributaries subject to flash floods, probably exert a large influence on the origin of seston in a given sample. The dual isotope range of riparian vegetation was large (Figure 4); Paria River seston was isotopically more similar to litter (tamarisk, cottonwood) than to live vegetation (tamarisk, willow, *Equisetum*).

Glen Canyon Food Web

With the exception of plankton < 0.08 mm from the hypolimnion of Lake Powell, primary producers and primary consumers had $\delta^{13}\text{C}$ values between -31 and -34 ‰ (Figure 5a). There was no consistent pattern of $\delta^{13}\text{C}$ -enrichment of primary consumers over primary producers; secondary consumers, fish, were more enriched ($\delta^{13}\text{C}$ > -30 ‰). Enrichment in $\delta^{15}\text{N}$ with trophic level was 2 - 4 ‰ for invertebrates versus algae, and ca. 5 ‰ for fish versus macroinvertebrates (Figure 5b).

A dual-isotope plot (Figure 6a) indicates three trophic levels in Glen Canyon: algae, benthic macroinvertebrates, and fish. Plankton (see Figure 4) and terrestrial organic matter were not important in the diet of *Gammarus* in Glen Canyon.

The relative importance of diatoms versus *Cladophora* in the food web could not be determined using stable isotopes (e.g., Figure 2). However, Pinney (1991) showed that > 90% of the diet of *Gammarus* in Glen Canyon was comprised of diatoms. There appears to be a tight linkage between diatoms and secondary production in Glen Canyon--a relationship that depends on the physical substrate for diatoms provided by *Cladophora* (Usher and Blinn, 1990).

Fish had enriched $\delta^{13}\text{C}$ values (+6 ‰ for adult trout) relative to the benthos. Two explanations for this are (1) that there was an unmeasured, $\delta^{13}\text{C}$ -enriched food source, or (2) that the enriched $\delta^{13}\text{C}$ for fish reflect slower turnover of fish tissue carbon relative to lower trophic levels. I

consider the first explanation less likely, because although feeding intensively on terrestrial insects with $\delta^{13}\text{C}$ values similar to riparian vegetation could account for the unexpectedly high $\delta^{13}\text{C}$ values, no study of Glen and Grand Canyon trout diet has reported terrestrial animals to be more than a minor component of the diet in most months (Angradi et al., 1992; Maddux et al., 1987; Carothers and Minckley, 1981). Furthermore, the isotopic signature of the flannelmouth sucker was similar to adult trout (Figure 6); the sucker is a benthic forager whose reported food habits do not include terrestrial animals (Minckley 1991).

Angradi (in press) reported that summer-collected periphyton samples were 3 - 4 ‰ more $\delta^{13}\text{C}$ -enriched than winter or spring samples in a regulated Idaho river. He also found a large difference in the $\delta^{13}\text{C}$ values for *Cladophora* collected at sites 9 km apart on the same river (-36.9 versus -12.1 ‰). He attributed these differences to seasonal and downstream shifts in the $\delta^{13}\text{C}$ of the dissolved inorganic carbon utilized by algae resulting from processes in an upstream reservoir. In Lake Powell, DIC varied 2 ‰ between the epilimnion and hypolimnion. Deep penetration of the epilimnion in the drawn-down reservoir in late summer and fall could result in a supply of $\delta^{13}\text{C}$ -enriched DIC to algae in the river.

The turnover rate of carbon in animal tissue is fastest in growing animals. (Fry and Arnold, 1982). Fish, which grow slower than invertebrates, would have slower carbon turnover rates, and would respond slower, isotopically, to a seasonal change in the $\delta^{13}\text{C}$ of the diet (macroinvertebrates that feed on diatoms) caused by an altered $\delta^{13}\text{C}$ value of the DIC supply and its effect on the $\delta^{13}\text{C}$ of algae. Trout fry, which grow faster than adults, had $\delta^{13}\text{C}$ values closer the expected range (+ 1 ‰ enriched relative to food). Thus, the measured $\delta^{13}\text{C}$ of adult trout in Glen Canyon may reflect the isotopic structure of the food webs of past seasons, including summer when terrestrial insects are likely to be most important in the diet. This complicated explanation illustrates a potential limitation of using only isotopes of carbon and nitrogen.

A third isotope, of sulfur, $\delta^{34}\text{S}$, has used to overcome problems of unaccounted shifts in $\delta^{13}\text{C}$ of fish predators and their prey in a river (Hesslein 1991). Inclusion of $\delta^{34}\text{S}$ measurements in future Colorado River food web studies is recommended.

Studies of trout diet in Glen and Grand Canyon have found that *Cladophora* filaments are generally the predominant food item by weight and volume (Carothers and Minckley 1981;

Maddux et al., 1987; Leibfried, 1988; Angradi et al. 1992). Leibfried (1988) felt that trout consume *Cladophora* intentionally for the nutritional value of its epiphytes. I offer no new explanation for the presence of so much algae in the stomachs of trout. However, the stable isotope data show that not much algal nitrogen is assimilated directly into trout tissue, because the 7-9 ‰ enrichment in $\delta^{15}\text{N}$ of trout over algae indicates an intermediate trophic level: aquatic macroinvertebrates. This finding corroborates that of Leibfried (1988) who showed that very little protein (the source of tissue nitrogen) derived from *Cladophora* or diatoms was assimilated by trout. Algae may provide some energy for maintenance, but it seems unlikely that trout are able to grow very well on a diet so dominated by this food source.

Fish

Isotopic separation among sample sites was greater for $\delta^{15}\text{N}$ than for $\delta^{13}\text{C}$, and was independent of species (Figure 7). Fish from Glen Canyon and Nankoweap Creek were more $\delta^{13}\text{C}$ depleted and $\delta^{15}\text{N}$ enriched than fish collected elsewhere. Rainbow trout and speckled dace from the Paria River, Deer Creek, Bright Angel Creek, and Crystal Creek were isotopically similar (Figure 7, 6b). Adult trout from Nankoweap Creek were isotopically indistinguishable from Glen Canyon trout. Glen Canyon trout fry and Nankoweap Creek speckled dace also had very similar isotope values. Speckled dace from Shinumo Creek were isotopically distinct from dace collected elsewhere.

The similarity in the stable isotope values of Colorado River and Nankoweap fish suggest that the fish from Nankoweap had assimilated C and N from the Colorado River, because *Gammarus* are not found in tributary streams (Carothers and Minckley, 1981; Hofknecht, 1981), and *Cladophora* is scarce or absent in the tributaries from which fish were collected (Carothers and Minckley, 1981). Rainbow trout, at least, are known to ascend Nankoweap Creek from the Colorado River in winter to spawn (B. Brown and W. Leibfried, in litt).

The dual-isotope range of speckled dace from Shinumo Creek (Figure 6b) indicates that the food web there was more strongly based on organic matter derived from upland vegetation than were other sampled tributaries. Hofknecht (1981) found that the macroinvertebrate biomass, abundance, and family diversity in Shinumo Creek was less than in Bright Angel, Crystal, or Deer Creek. Lower Shinumo Creek is in a deep canyon and lacks a riparian zone. Hofknecht

(1981) felt that the reduced allochthonous and autochthonous inputs partially accounted for the relatively depauperate invertebrate fauna. The same explanation may apply to the food web: local algal and riparian inputs are lacking, so the isotope values of the speckled dace reflect a macroinvertebrate fauna dependent largely on detritus exported from upland catchments. The isotopic similarity of speckled dace from the mouth of Shinumo Creek (10 m upstream of the confluence) and from above a barrier falls (700 m upstream of the confluence) suggests the lack of mainstem foraging.

The invertebrate fauna of the Paria River is even more depauperate than that of Shinumo Creek (Hofknecht, 1981) yet isotope values of speckled dace suggest riparian influence. Algal and invertebrate production in the Paria River is limited by high turbidity, unstable substrate, and frequent spates (Hofknecht, 1981). The aquatic food web that exists there appears to be linked to the well-developed riparian corridor. Confirmation of this hypothesis will require examination of lower trophic levels, but these preliminary findings suggest that multiple stable isotopes provide sufficient resolution to identify spatial variation in the trophic basis of production among Grand Canyon tributaries.

Applications

Distinct isotope ratios for the trophic basis of production in the Colorado River versus its tributaries in Grand Canyon (e.g., Figure 6a) might be exploited for examining trophic linkages between tributaries and the mainstream. Analysis of isotopic gradients in fish, invertebrates, algae, and seston from the confluence zone of tributaries upstream to and beyond barrier falls might reveal the degree of trophic interaction among these habitats. Such an approach might also be applied to tributary-using endangered fishes, such as the humpback chub (*Gila cypha* Miller), which may not be destructively sampled. Since only a few mg of dried material is needed for $\delta^{13}\text{C}$ analysis of animal tissue, chub scales might substitute for muscle tissue. Estep and Vigg (1985) found a consistent relationship between the $\delta^{13}\text{C}$ and muscle tissue for trout and suckers in a Nevada lake.

Stable isotopes can also be used to examine aquatic-terrestrial linkages for semiaquatic or terrestrial organisms in the canyon. For example, Mizutani et al. (1992) reported that the $\delta^{13}\text{C}$ of 7600 year old bat guano from a cave in Grand Canyon was $\delta^{13}\text{C}$ enriched (-21.5 ‰)

compared to modern guano (-24.4 ‰). They reasoned that increased development of $\delta^{13}\text{C}$ -depleted woody riparian vegetation following construction of Glen Canyon Dam could partially account for the $\delta^{13}\text{C}$ shift in bat guano as a result of a shift in the trophic basis of bat diets from upland to riparian plant species (e.g., see Figure 2a).

This study has demonstrated the usefulness of stable isotopes in tracing organic matter and identifying trophic linkages in Glen and Grand Canyons: all of the questions posed at the beginning of this paper have been answered at least partially. Future studies should consider seasonal variation in the isotope values of food web components, including dissolved inorganic carbon, and should examine macrosatial variation in the importance of upland and riparian vegetation versus autotrophic production. Water releases from Glen Canyon dam probably influence the Colorado River ecosystem in multiple ways at every trophic level. Studies of trophic linkages in the Colorado and other regulated rivers will provide insight into how dam operations influence aquatic communities and processes.

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FIGURE CAPTIONS

- Figure 1. Mean stable carbon isotope ratios of dissolved inorganic carbon from Lake Powell, Glen Canyon Dam, the Colorado River (CR) in Glen Canyon, and the Paria River. Error bars represent the range of measure values, $n = 2$. Distances downstream from Glen Canyon Dam are given for Colorado River values.
- Figure 2. Mean stable carbon (a) and nitrogen (b) isotope ratios for the trophic basis of production in Glen and Grand Canyons. *Cladophora* samples were with (w) or without (wo) diatom epiphytes. $\delta^{13}\text{C}$ values for juniper and pinyon are from Leavitt and Long (1982, 1986). Sample size = 2, except for cottonwood leaves, *Ulothrix*, *Equisetum*, and tamarisk: $n = 1$. Labels are otherwise as in Figure 1.
- Figure 3. Mean stable carbon (a) and nitrogen (b) isotope ratios for seston in Glen Canyon. Error bars represent the range of measure values. Sample size = 2, except for plankton < 0.08 mm, GCDP plankton, UFPOM, and Paria CPOM: $n = 1$. Symbol types identify sample site: LPEP, Lake Powell epilimnion; LPHY, Lake Powell hypolimnion; GCDP, Glen Canyon Dam penstocks; CR, Colorado River. Labels are otherwise as in Figure 1.
- Figure 4. Dual isotope plot for seston, plankton, and organic matter sources in Glen Canyon and the Paria River. Box dimensions are the range of measured values for each isotope. Upland vegetation includes Paria River litter deposits and published values for juniper and pinyon (approximate $\delta^{15}\text{N}$ values are from Angradi, in press). Labels are otherwise as in Figures 2 and 3.
- Figure 5. Mean stable carbon (a) and nitrogen (b) isotope ratios for components of the Glen Canyon food web. Error bars represent the range of measured values. Sample size is as in Figures 2 and 3; otherwise, $n = 2$ except for oligochaetes, chironomids, sucker, and trout fry: $n = 1$, and adult trout: $n = 4$. Symbol types indicate predicted trophic status. Labels are otherwise as in Figures 2 and 3.

Figure 6. Dual isotope plots for the Glen Canyon food web (a), and for all fish collected in the study (b). Box dimensions are the range of measured values for each isotope. Hatched boxes indicate organic matter sources not generally observed in Glen Canyon. Labels are otherwise as in Figures 2 and 3.

Figure 7. Mean stable carbon (a) and nitrogen (b) isotope ratios for fish collected in Glen Canyon, and in Grand Canyon tributaries. Error bars represent the range of measured values. Sample size is as in Figure 5; otherwise, $n = 2$ except trout fry at Deer Creek and Bright Angel Creek: $n = 1$, and Paria River dace: $n = 3$. Labels are otherwise as in Figures 2 and 3.

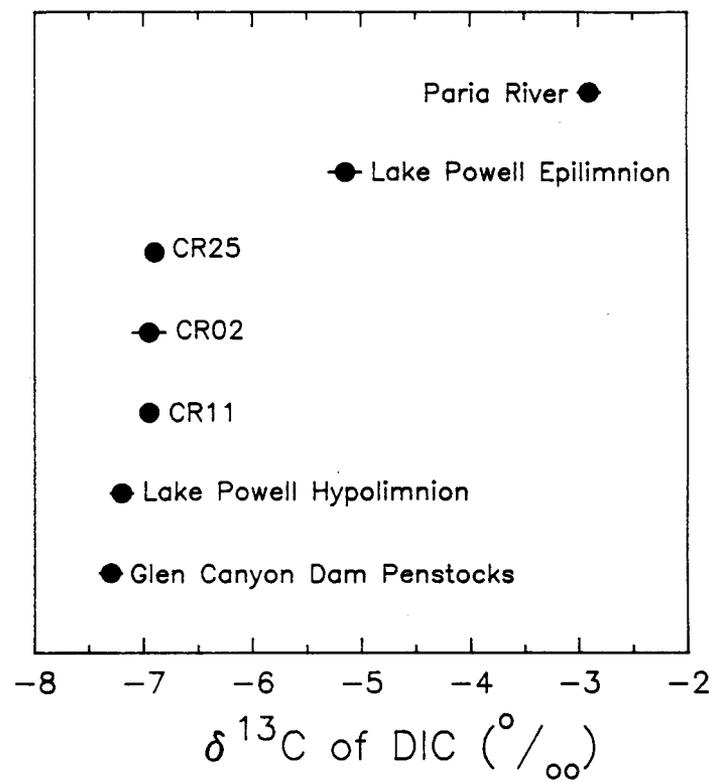


FIGURE 1.

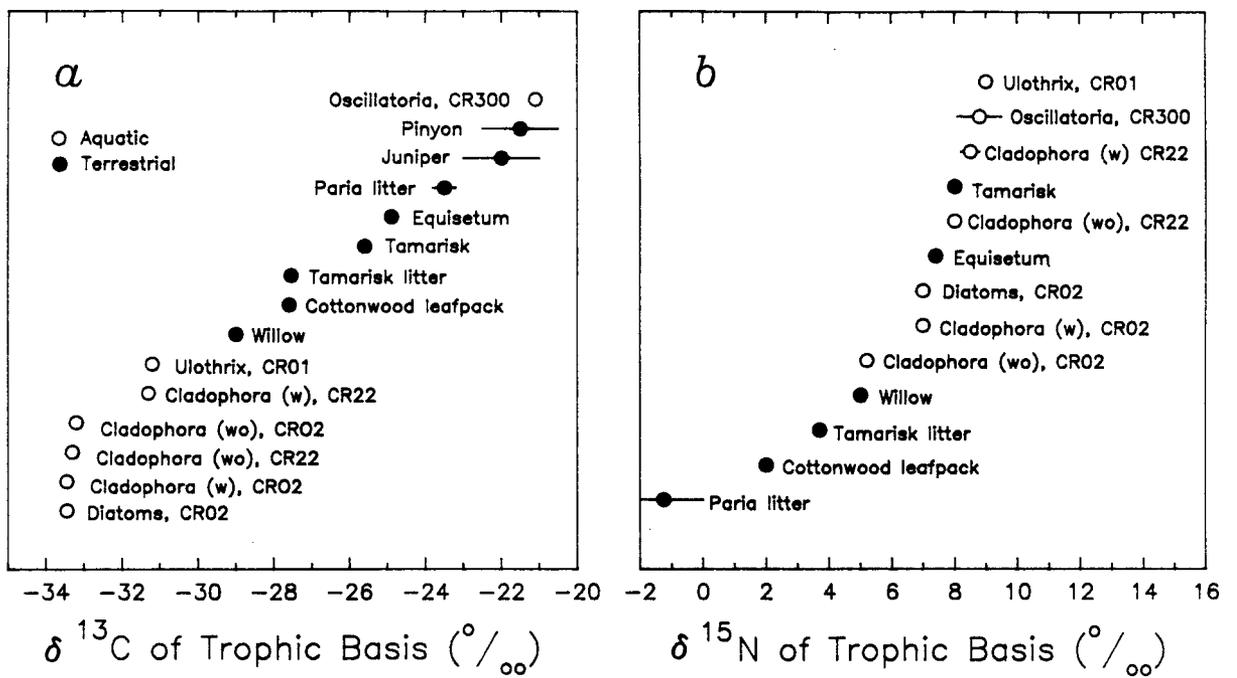


FIGURE 2.

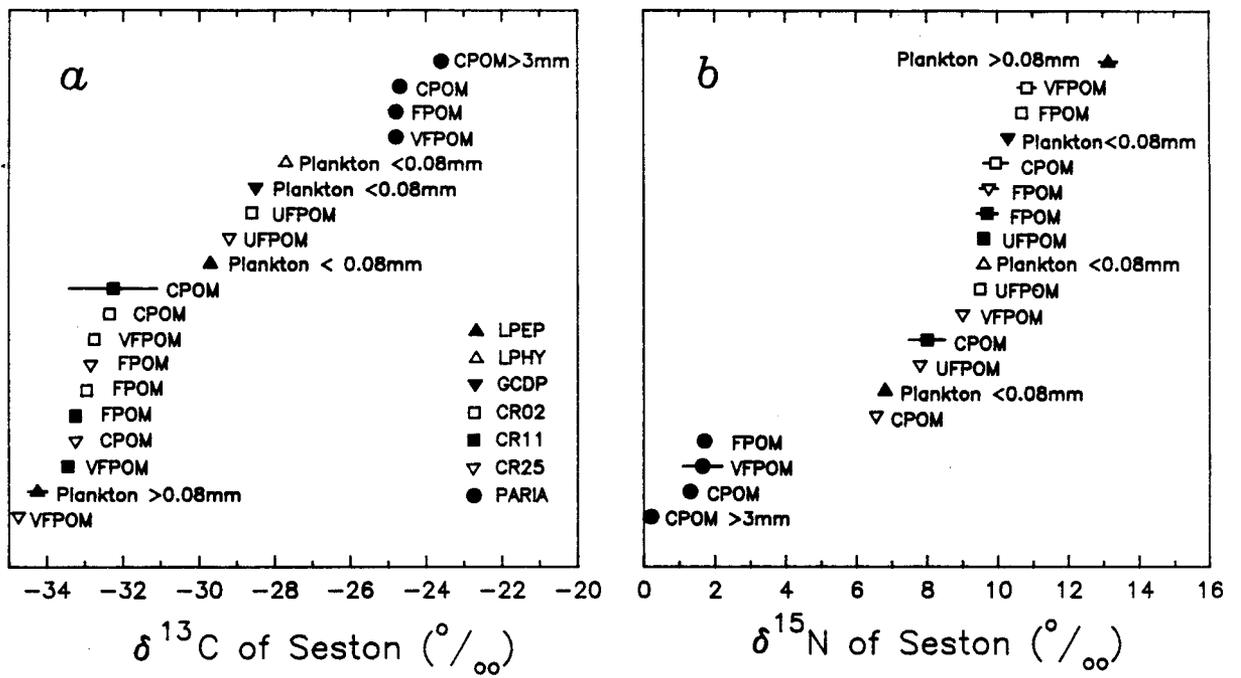


FIGURE 3.

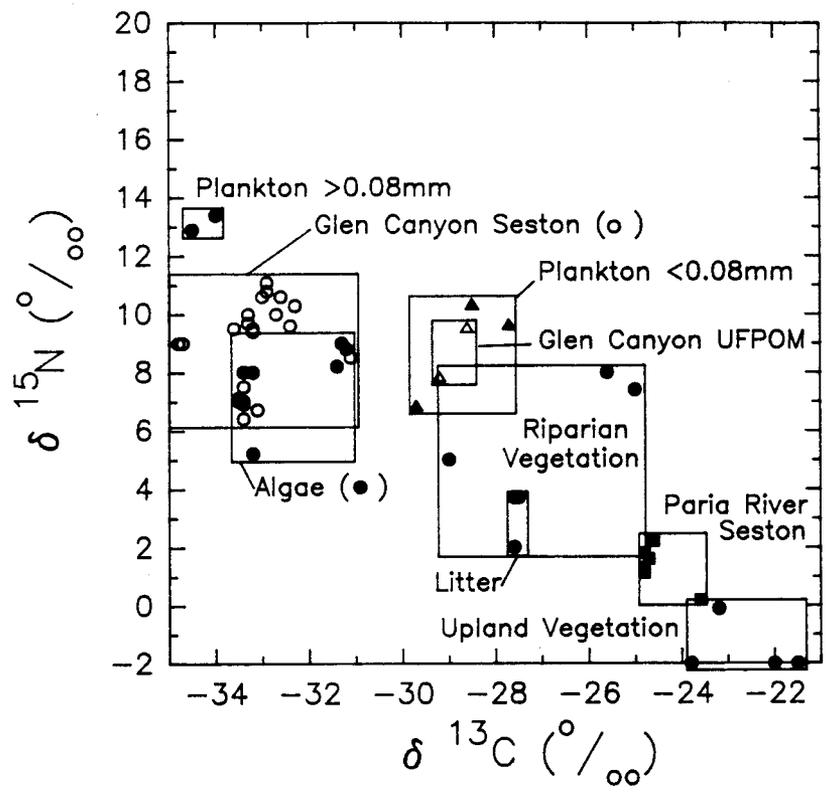


FIGURE 4.

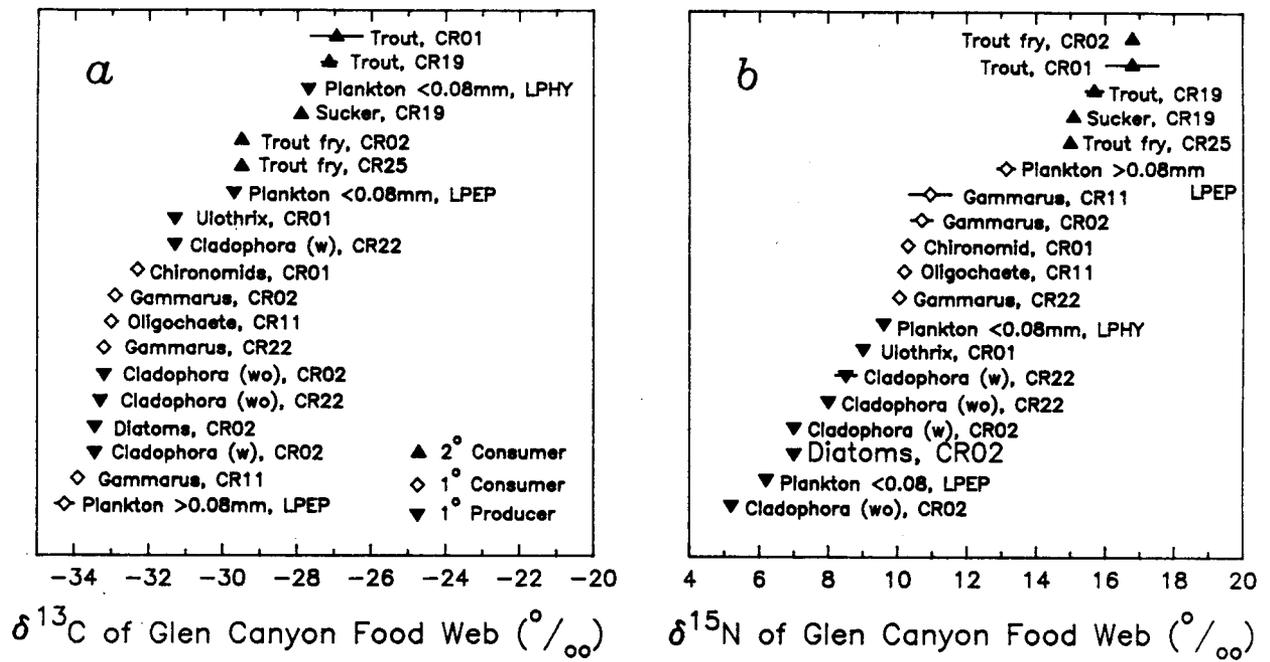


FIGURE 5.

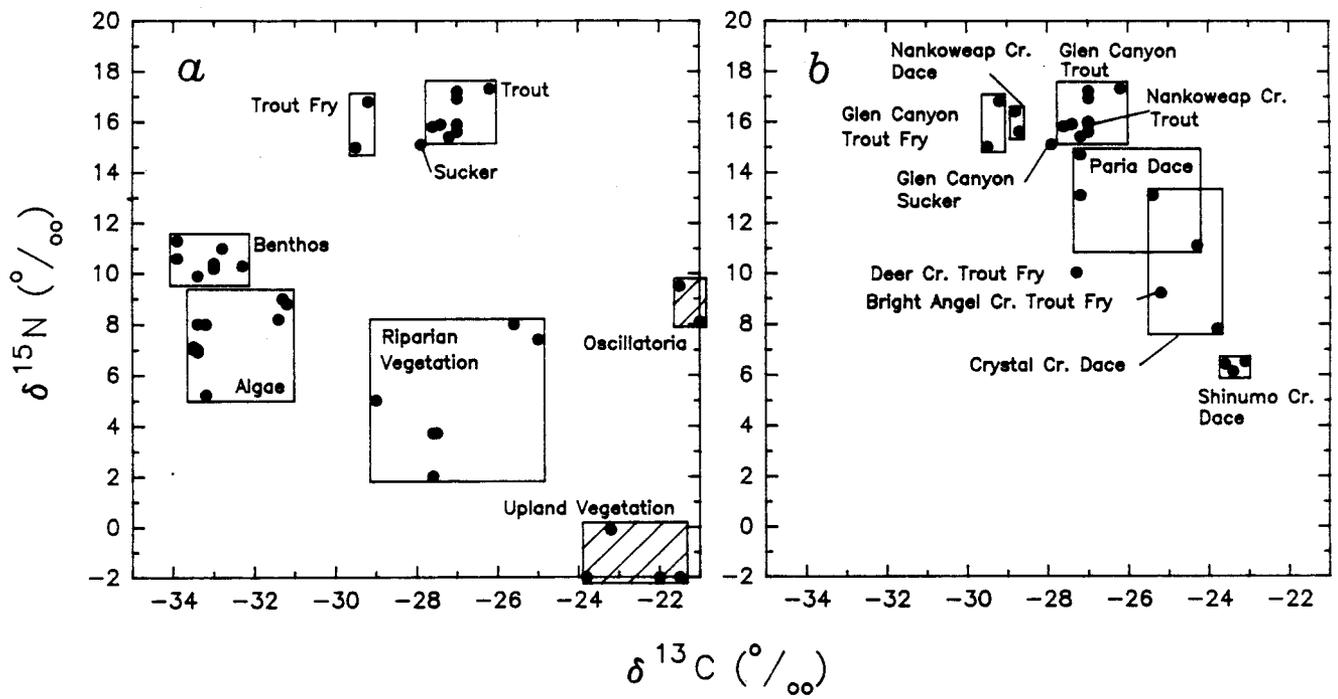


FIGURE 6.

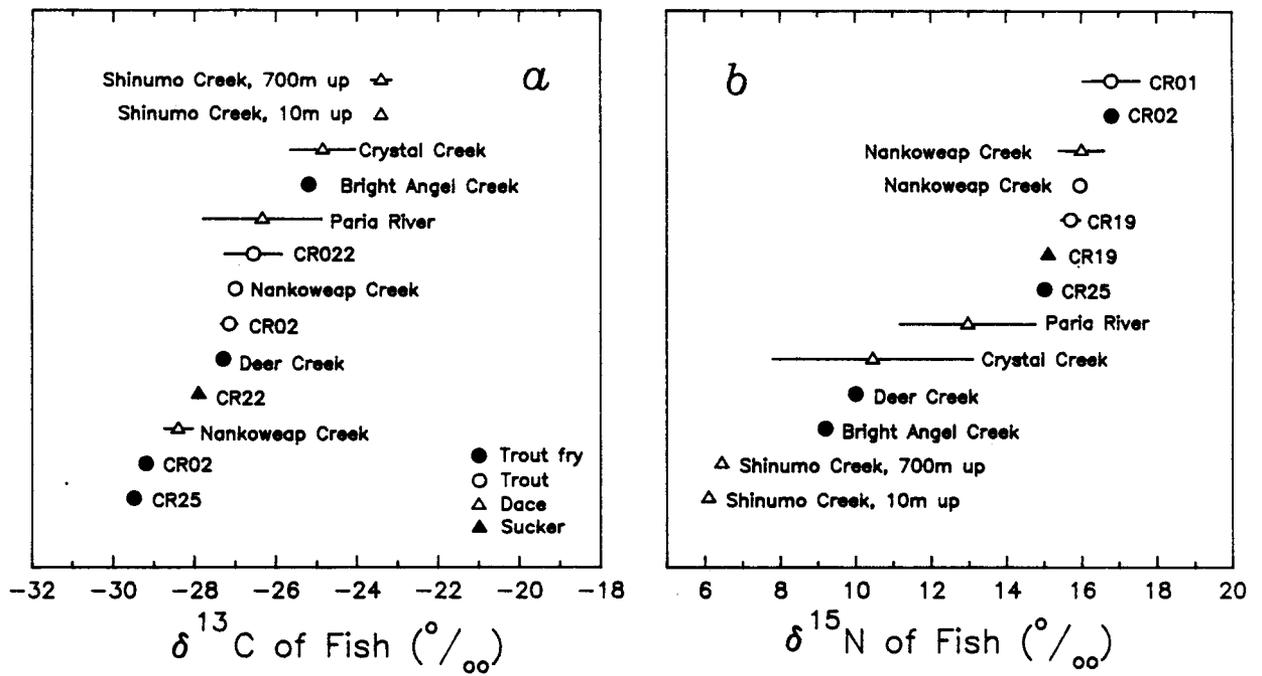


FIGURE 7.

APPENDIX 2.3

EFFECTS OF EXPOSURE ON THE CHLOROPHYLL *a* CONTENT, BIOMASS, AND
PRODUCTIVITY OF THE EPILITHON OF A TAILWATER RIVER

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ABSTRACT

A series of field experiments was conducted to determine the effect of exposure on the chlorophyll *a* content, biomass and gross primary productivity (GPP) of littoral epilithon in the Colorado River below Glen Canyon Dam, Arizona. Chlorophyll *a* content was much more sensitive to exposure than was biomass. The epilithon was rapidly bleached during summer daytime exposures. The percent of initial chlorophyll *a* remaining following one day of exposure was not different from the percent remaining following two days of exposure. Significant reductions in chlorophyll *a* content were detected for exposures as short as six hours. There were close inverse relationships ($r^2 = 0.7 - 0.8$) between time exposed or cumulative solar radiation (400-700 nm) and the percent of initial chlorophyll *a* remaining after reinundation. GPP of *Cladophora glomerata*-dominated epilithon from the permanently inundated channel was ten times higher than the GPP of epilithon from the zone of daily water level fluctuation. Experimental exposure reduced the GPP of epilithon, but not the assimilation ratio (GPP per unit of chlorophyll *a*). The Glen Canyon epilithon has low resistance to exposure disturbances, and recolonization is slow under hydropower peaking flow regimes. Disruption of the epilithon is likely to precipitate effects at higher trophic levels.

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KEY WORDS: Epilithon, Periphyton, *Cladophora glomerata*, Stranding, Chlorophyll *a*, Biomass, Disturbance, Primary Production, Colorado River, Flow, Dam

INTRODUCTION

Most studies of the effects of flow-related disturbance on periphyton have examined changes resulting from floods in unregulated streams (e.g., Fisher et al., 1982; Biggs and Close, 1989; Grimm and Fisher, 1989). Stranding and desiccation of periphyton resulting from a decrease in flow is a more likely cause of disturbance in regulated streams, particularly those used for irrigation storage and hydroelectric power generation (Petts, 1984). Although flow regulation may produce physical and chemical conditions which enhance periphyton growth (reviewed by Lowe, 1979), periphyton generally is not well adapted to conditions of stranding caused by large unnatural fluctuations in stage (Neel, 1963; Kroger, 1973; Steinman and McIntire, 1990).

This paper describes a study of the effects of stranding on the epilithon (periphyton growing on cobbles) of the Colorado River downstream from Glen Canyon Dam, Arizona, USA. Epilithon in the Glen Canyon tailwater is dominated by the filamentous chlorophyte, *Cladophora glomerata* (L.) Kutz. (Blinn and Cole, 1991), which often attains a high biomass (>200 g ash-free biomass m⁻²). The significance of the epilithon to other trophic levels in Glen and Grand Canyon has been recognized (National Research Council, 1991), but the effects of dam operations on the ecological role of the epilithon are not well understood (Blinn and Cole, 1991).

In Glen Canyon, *Cladophora* provides habitat for trout and macroinvertebrates. The tailwater macroinvertebrate community relies on epiphytic diatoms and detritus associated with *Cladophora* filaments for food (Pinney, 1991; Blinn et al., 1992). Effects of dam operations on Glen Canyon epilithon may also have consequences for downstream ecosystems. For example, *Cladophora* sloughed from the substrate in Glen Canyon is exported downriver to the seasonally turbid and light-limited Grand Canyon (Kubly and Cole, 1979; M. D. Yard, in litt.) where it enters detrital pathways (Angradi and Kubly, in press).

Controlled studies of the effects of stranding on lotic epilithon are few. Usher and Blinn (1990) examined the effects of laboratory-simulated stranding on Colorado River *Cladophora* from a site 25 km below Glen Canyon Dam. Peterson (1987) examined the effects of short-term desiccation on diatom communities below Hoover Dam on the same river. No data exist describing the effects of stranding on lotic *Cladophora*-dominated epilithon *in situ*, nor for the relationship between stranding and primary productivity.

Our study consisted of six field experiments conducted in the summers of 1991 and 1992. Specific objectives were: 1) to quantify the effects of exposure duration on the chlorophyll *a* content and biomass of epilithon (experiments I-V); 2) to compare the effects of exposure on these variables among epilithon communities with different previous exposure histories (experiments IV-V), and; 3) to examine the effect of exposure on epilithon primary productivity (experiment VI).

STUDY AREA

Glen Canyon Dam (36° 56' N, 111° 29' W), is a large peaking power hydroelectric facility operated by the Bureau of Reclamation. The dam forms Lake Powell, a long (300 km), deep (average depth = 51 m), warm monomictic reservoir. Water releases from the reservoir are hypolimnial, perennially cold (7-10° C), chemically stable, and transparent (Stanford and Ward, 1991). Total oxidized nitrogen averaged ca. 0.3 mg l⁻¹; orthophosphate concentrations were very low, rarely exceeding 0.01 mg l⁻¹; N:P is typically > 30 (Angradi et al., 1992).

The algal material used in this study was collected at 14 Mile Bar, a 300 m long cobble bar located 2 km downriver from the dam. This site is representative of the upper half of the 25 km Glen Canyon reach. Eighty-five percent of the littoral cobble habitat in Glen Canyon is in the upper 12 km; sand and sandstone headwall dominate in the lower half of the reach.

Cobbles were collected from two littoral zones at 14 Mile Bar: the permanently inundated zone and the fluctuating flow zone. For purposes of this study, the littoral zone was defined as the zone that could be sampled without SCUBA at flows of > 142 cubic meters per second (cms). The permanently inundated zone was defined as the littoral habitat inundated at flows of 142 cms. This zone only could be sampled during early morning flows. Flows < 142 cms did not occur during the study. The fluctuating flow zone was defined as the littoral habitat inundated at flows > 142 cms and ≤ 226 cms. Flows > 226 cms occurred throughout the study, but epilithon development above the 226 cms level was almost nonexistent (Angradi et al., 1992).

Algae in the fluctuating flow zone had, in the year previous to the beginning of this study, been subjected to daily exposure, mostly at night, and to more protracted exposure (2-3 days) on some weekends and during controlled special releases. During this study, cobbles in the permanently

inundated zone supported 2-3 times more epilithic chlorophyll *a* than did cobbles in the fluctuating flow zone. *Cladophora* filaments in the permanently inundated zone were dark-green and had high epiphyte loads (Angradi et al., 1992). Epilithon on cobbles in the fluctuating flow zone was dominated by diatoms and the crustose blue-green algae *Oscillatoria* spp. (T. Angradi, personal observation). Colonization by *Cladophora* of cobbles in this zone was slow and appeared to be frequently reset by repeated exposure (T. Angradi, personal observation).

METHODS

General

Six field experiments were conducted. A single method for collecting epilithon samples was used throughout. Cobbles were removed from the river, and a randomly located 4.15 cm² circular area was isolated on the upper surface of each cobble with a template. Algal filaments, including those attached outside the sample area, and other material within the template were sheared off, scraped loose with a chisel-shaped knife (#17 X-acto) and placed in a vial. Our method probably results in biased estimates of epilithon biomass and chlorophyll content m⁻², because we only sampled colonized cobbles, whereas occasional gaps in the epilithon occur naturally on cobble bars. Also, we made an effort to collect cobbles of a similar size to reduce variability within and among replicates. Substrate size has been shown to affect the biomass of attached *Cladophora* (Dodds, 1991).

Two methods were used for the determination of chlorophyll *a*. In experiments I-III (1991), samples were ground with a teflon pestle and chlorophyll *a* was extracted for 24 h in 90% acetone. In experiments IV-VI (1992), chlorophyll *a* was extracted from unground samples by boiling in methanol. The pheophytin-corrected chlorophyll *a* concentration of extracts was determined by spectrophotometry (Spectronics 21) using the method of APHA (1990) for acetone, and of Tett et al. (1977) for methanol. More chlorophyll *a* could be extracted in methanol, so comparisons of absolute chlorophyll *a* content among experiments using different methods were not made. The ash-free dry mass (AFDM) of samples was determined from loss on ignition (550 C, 2h).

In experiments I-V, treatment manipulations were performed on replicate experimental units which consisted of open-sided plastic boxes (modified utility crates, 40 x 40 x 10 cm) each containing four cobbles. In experiment VI, individual cobbles were tested.

Ambient photosynthetically available radiation (PAR, $\mu\text{moles s}^{-1} \text{m}^{-2}$, 400-700 nm) was measured with quantum sensors (Li-Cor). Cumulative PAR (moles m^{-2}) was used as an index of the total amount of solar radiation to which exposed cobbles were subjected. Atmospheric data (air temperature and relative humidity) for periods of exposure were obtained from sensors located at the dam (Table 1). Water quality data (temperature, specific conductance, dissolved oxygen, pH) for periods of inundation were obtained from unpublished United States Geological Survey records from a gaging station located just upstream from 14-Mile Bar (Table 2).

Experiment I

In experiment I, we evaluated the rate of chlorophyll *a* decomposition on cobbles subjected to prolonged exposure to the atmosphere. Twenty cobbles were collected from the permanently inundated zone at 14 Mile Bar, placed in five boxes--four cobbles in each box--and exposed to the atmosphere. The geometric mean diameters ($[(l \times w)^{0.5}]$) of cobbles used in experiments I, II, and III was 161, 147, and 152 mm; all cobbles were collected in the same vicinity, and mean diameter did not differ among treatments or experiments. A single sample was collected from each cobble in each replicate at 0, 10, 24, 58, 130, and 336 h (two weeks).

The chlorophyll *a* content and AFDM of all samples were determined, and the individual values for the four cobbles in each replicate unit (plastic box) were averaged. Cumulative PAR (moles m^{-2}) received by the exposed cobbles was calculated from 15 minute averages.

Experiment II

In experiment II, we examined epilithon chlorophyll *a* and AFDM as a function of exposure duration and time since reinundation of cobbles following exposure. The experiment was conducted in a 30 m section of a concrete sluiceway channel at the base of Glen Canyon dam. The channel conveys seepage from within the dam to the river. It has a trapezoid profile, is 0.5 m deep, 0.6 m wide at the bottom, and 0.9 m wide at the top. Discharge in the sluiceway is

regulated by a sump, and was ca. 0.03 cms. A 0.2 m high weir was installed at the halfway point and at the downstream end of the 30 m section to create two sections (blocks) of nearly equal depth and velocity. Prior to the experiment, flow was diverted from the sluiceway and attached algae were removed.

For the experiment, 48 cobbles were collected at 14 Mile Bar, transported to the dam in river water, randomly placed in 12 boxes, and the boxes were placed, six each, into two 15-m sluiceway sections. After four days, cobbles were exposed for 0, 24 (one day and night), or 48 h (two days and two nights; $n = 4$ for each treatment), reinundated in the sluiceway, and resampled after one day, one week, and two weeks. Chlorophyll *a* content and AFDM were determined as in experiment I.

To quantify the rate of algal colonization in the sluiceway during the experiment, 25 sandstone tiles (approximately 15 x 15 x 2 cm) were placed in each sluiceway section. Five tiles were collected from each section after 5, 10, 15, 20, and 25 days. Accrued material was removed from each tile with a stiff brush, homogenized, subsampled, and analyzed for chlorophyll *a* and AFDM as in experiment I.

A continuous record of water quality was not available for the sluiceway. Concurrent grab samples from the sluiceway and river indicated that water in the sluiceway was slightly warmer (1-3 °C) and had a slightly higher specific conductance (ca. 100 $\mu\text{S cm}^{-1}$ higher) than river water as a result of seeping through the dam; sluiceway water had a higher dissolved oxygen content than the river (ca. 2 mg l^{-1} higher) as a result of high turbulence upon exiting the base of the dam.

Experiment III

In experiment III, we attempted to verify the findings of experiment II under more natural conditions. Thirty-six cobbles from 14 Mile Bar were placed in 9 boxes and exposed for 0, 24, or 48 h ($n = 3$ for each treatment), reinundated in the permanently inundated zone at 14 Mile Bar, and resampled after one day, one week, and two weeks.

Experiments IV and V

In experiments IV and V we examined the effects of short duration daytime exposure (≤ 8 h) on epilithon from the permanently inundated (experiment IV) and fluctuating flow zones (experiment V). For each experiment, 96 cobbles were collected at 14 Mile Bar, placed in 24 boxes, exposed for 0, 1, 2, 4, 6, or 8 h ($n = 4$ for each treatment), reinundated in the permanently inundated zone, and resampled after one, two, and four weeks. The four samples from each replicate were combined, homogenized and subsampled. One subsample was extracted in methanol for chlorophyll *a* determination, and a second subsample was ashed for AFDM. PAR data were collected at 15 minute intervals while cobbles were exposed.

Experiment VI

In experiment VI we examined the effect of exposure on the primary productivity of epilithon from the permanently inundated and fluctuating flow zones. Primary productivity was measured in a plexiglass photosynthesis-respiration chamber (37 x 23 x 12 cm; after Bott et al., 1978). An electric pump circulated water in the chamber at 10-15 l s⁻¹. Chamber water was circulated past a probe (Hydrolab Datasonde III) that measured dissolved oxygen and temperature. The chamber, pump, and probe were submerged in a 150 l bath at the river's edge. Fresh river water was continuously circulated through the bath with a pair of diaphragm pumps. This allowed water temperature within the chamber to be held within 2 C of the river during incubations.

Incubations were made using cobbles in four treatment groups: unexposed and exposed cobbles from the permanently inundated and fluctuating flow zones. Cobbles were exposed for one or two days depending on ambient conditions. Exposed cobbles were tested after 6-10 days of reinundation. Prior to incubation, a circular template (35 cm²) was used to isolate one or two patches of epilithon on the upper surface of the cobble; epilithon outside the template was removed with a wire brush. Mean geometric diameter of cobbles was 170 mm, and did not differ among treatments.

Net primary productivity (NPP, gO₂ m⁻² h⁻¹) measurements were made between 1000-1400 h. Light intensity during incubations was varied using greenhouse shading. Incubations at each light intensity lasted 20-60 min depending on the rate of dissolved oxygen change; chamber water

never became supersaturated with O₂. PAR at the water surface was recorded at five minute intervals. Community respiration (R_C, gO₂ m⁻² h⁻¹) was measured at night. Gross primary productivity (GPP, gO₂ m⁻² h⁻¹) was calculated as NPP + R_C (Bott et al., 1985). The chlorophyll assimilation ratio (AR, mgO₂ mg chlorophyll *a*⁻¹ h⁻¹) provided an estimate of photosynthetic activity per unit of plant pigment.

Following incubations, cobbles were scraped, and the material was analyzed as in experiment IV. For exposed cobbles, before-and- after exposure samples were collected to allow determination of the reduction in chlorophyll *a* content.

Statistical Analysis

In experiment I, the rate of chlorophyll *a* decomposition and rate of biomass loss were calculated as the slope of a linear regression of the log₁₀ of the percent of the initial chlorophyll *a* or biomass remaining as a function of time and cumulative PAR. For all experiments, residual plots indicated heteroscedasticity; thus, appropriate logarithmic transformations were performed (Zar, 1984). In experiments II - V, one way ANOVA was used to examine the effect of treatment (duration of exposure) on the log₁₀-transformed percent of initial chlorophyll *a* and biomass remaining on each sample date following reinundation; Tukey comparisons ($\alpha = 0.05$ experimentwise error rate) revealed treatments that were significantly different. A preliminary analysis indicated no block (sluiceway section) effect for any dependent variable in experiment II, so data for blocks were combined. In experiment VI, analysis of covariance was used to examine the effects of treatment on GPP and AR; PAR was the covariate. Photosynthesis-irradiance relationships were examined with linear regression of log₁₀-transformed variables.

RESULTS

Experiment I

Epilithon was rapidly bleached from dark green to tan-brown during exposure. After 10 h of exposure, 57% of the initial chlorophyll *a* remained; after two weeks, 16% remained (Figure 1). Linear regression functions (dependent variable = log₁₀ percent initial chlorophyll *a*

remaining) were significant for both time exposed and cumulative PAR (Table 3). Percent biomass remaining did not change with time exposed or cumulative PAR ($r^2 < 0.04$) (Figure 1).

Experiment II

In experiment II and in all subsequent experiments, exposed epilithon started to turn brown within a few days of reinundation. Epilithic chlorophyll *a* declined 40-70% after 24 hours of reinundation, and 65-80% after one week, depending on treatment (Figure 2). The percent of initial chlorophyll *a* remaining on exposed cobble increased about 17% in the second week. The effect of exposure was significant on all sample dates ($P < 0.01$), although at 24 hours after reinundation, only the 48 h exposed and 0 h exposed (control) treatments differed. Mean percent of initial chlorophyll *a* remaining did not differ significantly between the two exposure treatments (24 or 48 h exposed) on any sample date.

Despite a dramatic loss of chlorophyll *a* in exposed epilithon, the gross physical structure appeared intact. The effect of treatment on the percent biomass remaining was significant only after two weeks ($P < 0.05$), when epilithon that had been exposed for 24 hours had 40% less biomass than cobbles not exposed. As with chlorophyll *a*, effects of the 24 and 48h exposure treatments were not significantly different.

Sandstone tiles in the sluiceway were quickly colonized by the chlorophyte *Ulothrix tenuissima* Kutz. Accrual of chlorophyll *a* and biomass was very rapid after the first week (Figure 3). Chlorophyll *a* accrued at a rate of ca. 50 mg m⁻² day⁻¹, and biomass accrued at a mean rate of ca. 8 g AFDM m⁻² day⁻¹ between day 10 and 20 (corresponds to day 5-15 of experiment II reinundation schedule, Figure 2). *U. tenuissima* filaments 1-2 m meters long developed on most tiles; colonization on the plastic boxes and on the bleached filaments of *Cladophora* also was observed. *U. tenuissima* is present in Glen Canyon (D. W. Blinn, personal communication), but is abundant only on the concrete faces of dam spillways.

Experiment III

Experiment III at 14 Mile Bar confirmed the findings of experiment II (sluiceway experiment). Percent decline of chlorophyll *a* was similar to that of experiment II. The effect of exposure was

significant on all sample dates ($P < 0.01$), but there was no difference between the 24 and 48 h exposure treatments (Figure 4). Unlike experiment II, there was no increase in chlorophyll *a* after the first week.

As in experiment II, the effect of treatment on percent biomass remaining was significant only after two weeks, and the effects of the 24 h and 48 h exposure treatments were not different. The reason for the decline in chlorophyll *a* and biomass on unexposed cobbles at 24 h after reinundation is not known, but may be attributable to initial sample collection and repositioning disturbances.

Experiment IV

In experiment IV there was an inverse relationship between time exposed and the amount of chlorophyll *a* remaining (Figure 5). One week after reinundation, the chlorophyll *a* of the epilithon that had been exposed for 8 h had decreased more than that of the epilithon exposed for either 0, 1, or 2 h. After two weeks, the 8 h exposure treatment differed from the 0 and 2 h exposure treatment. After four weeks, there was only a weak treatment effect ($P = 0.08$). There was no effect of exposure duration on percent biomass remaining on any sample date.

Experiment V

In experiment V, there was no effect of exposure duration on percent of chlorophyll *a* remaining after one week. After two weeks, the chlorophyll *a* content of epilithon exposed for 6 and 8 hours was significantly less than that of epilithon exposed for 1 hour (Figure 6). After four weeks the same trend was evident, though not significant ($P = 0.08$). There was no effect of exposure duration on percent biomass remaining on any sample date.

Experiment VI

Mean gross primary productivity (GPP) was higher for unexposed cobbles than for exposed cobbles for both the permanently inundated and fluctuating flow zones ($P < 0.001$, Figure 7). GPP of unexposed cobbles from the permanently inundated zone was about 10 times higher than the GPP of unexposed cobbles from the fluctuating flow zone. However, the GPP of unexposed

cobbles from the fluctuating flow zone approached that of exposed cobbles from the permanently inundated zone.

There was no effect of exposure on the assimilation ratio (AR) of permanently inundated cobbles ($P = 0.26$, Figure 7). When the effect of an outlier was eliminated (Figure 8, plot 2), there was no effect of exposure on the AR of cobbles from the fluctuating flow zone ($P = 0.16$), nor was there an effect of zone on AR for pooled treatments ($P = 0.67$).

Linear regression functions for the relationship between GPP and PAR and between AR and PAR were significant ($P < 0.05$, Table 3) for all treatment and level combinations except for the effect of PAR on the GPP of exposed cobbles ($P = 0.13$, $r^2 = 0.03$). PAR explained more of the variation in GPP and AR in unexposed (34-82%) versus exposed cobbles (9-19%, Table 3), probably because exposed epilithon was light-saturated at a lower PAR level. There was no apparent relationship between epilithon parameters (Appendix) and GPP except that the two samples with the most chlorophyll *a* had the highest GPP; use of AR eliminated this effect.

DISCUSSION

In experiment I the similarity of the time and PAR functions (Table 3) is accounted for by the relatively constant environmental conditions during the experiment (Table 1). Under more variable environmental conditions, for exposures of shorter duration, and for among-site and among-season comparisons, cumulative PAR should be a more reliable predictor of chlorophyll *a* decomposition with exposure.

We do not believe that the apparent recovery of chlorophyll *a* in the second week of experiment II represents restoration of, or recolonization by *Cladophora* or epiphytes, but rather represents colonization by *Ulothrix tenuissima*. Rapid colonization of substrates by *Ulothrix* corresponded with the increase in chlorophyll *a* on the exposed cobbles.

Chlorophyll *a* was much more sensitive to exposure than was biomass (Figures 2-6). This finding is partly an artefact of the duration of the experiments: bleached filaments, although chlorophyll-depleted, retained most of their ash-free biomass. Upon reinundation, these filaments were not immediately sloughed from the epilithon *en masse*, but appeared to fragment

incrementally. Usher and Blinn (1990) were able to demonstrate significant exposure effects after one day using dry weights. However, the initial epilithon biomass in their study was at least four times lower than that which we tested. As in our study, they found chlorophyll *a* to be more sensitive to exposure than biomass.

There is probably a continuous inverse relationship between exposure (time or PAR) and percent of initial chlorophyll *a* remaining, at least in the short term (e.g., functions 3-6, Table 3; Figure 8), but the inherent variability of the epilithon precluded detection of significant effects for exposures of less than about 6 hours or 10-15 moles m⁻² (experiments IV and V, based on June-August conditions). Under the conditions of our experiments, the effects of one versus two days of exposure were similar. However, under less severe conditions (i.e., less PAR, higher humidity) the disturbance threshold could shift from 6-8 hours to 12 daylight hours or longer.

The actual mechanisms of chlorophyll destruction with exposure are uncertain. Usher and Blinn (1990) hypothesized that ultraviolet radiation damages exposed basal holdfasts, which weakens filaments enough for them to break off and become entrained. Citing studies of intertidal macroalgae, they proposed that many holdfasts are protected by overlying filaments, which provide some resistance to UV damage. Our observations corroborate this hypothesis for brief exposures, but we emphasize that under summer conditions of prolonged daytime exposure (\leq 8 h), most of the filaments are bleached, and the productive capacity of the epilithon is largely destroyed.

There is some evidence from our study (experiment V) that epilithon from the fluctuating flow zone was more tolerant of exposure than epilithon from the permanently inundated zone (Figures 5, 6). Relative reduction of chlorophyll *a* and biomass was less and recolonization (measured as increase in chlorophyll *a* after week two) was greater in exposed epilithon from the fluctuating flow zone. The blue-green alga, *Oscillatoria*, is reported to be tolerant of exposure (Blinn et al., 1992), and may be capable of replacing *Cladophora* in the fluctuating flow zone in Glen Canyon. The productivity (e.g., GPP, Figure 7) and surface area (discussed below) of epilithon from the fluctuating flow zone is much lower than that of the intact *Cladophora*-dominated epilithon.

Although epilithon from the permanently inundated zone was as much as ten times more productive, it had an assimilation ratio very similar to that of the epilithon from the fluctuating flow zone. Furthermore, exposure did not greatly alter the assimilation ratios of epilithon. GPP appeared to be a rather constant function of the amount of chlorophyll *a* present. Changes in GPP resulting from exposure can therefore be predicted with a simple model that includes cumulative PAR and initial chlorophyll *a* (Figure 9). The GPP range predicted by the model is in agreement with published studies of production for similar chlorophyll *a* levels (Bott et al., 1985). The response of epilithon to exposure will vary among seasons as the light regime changes, but the form of the model may be general for other regulated rivers where seasonal changes in community composition, temperature, and nutrient availability are small.

The reach-wide loss of GPP resulting from exposure depends on channel morphology and the flow regime. A model incorporating channel morphology and cobble distribution (Figure 9) indicates that changes in reach-wide littoral production are an approximately linear function of minimum daytime flow (especially on weekends when daytime flow are lowest) over the range of normal water releases (140 to >566 cms); loss of reach-wide GPP would increase dramatically at flows < 140 cms. The model overestimates the loss in GPP because it does not include the relatively small amount of GPP by recolonizing algae. In effect, the model predicts GPP immediately after a severe exposure disturbance; the relative magnitude of the overestimation of loss would increase with time since disturbance.

The impact on the Glen Canyon ecosystem of this lost primary production is difficult to evaluate without estimates of secondary production on littoral cobble bars versus secondary production in other habitat, and a better understanding of trophic linkages in the ecosystem. Cobble bars comprise only about 16% of the total littoral habitat in Glen Canyon (Figure 9, caption). Relatively unproductive (10 - 20 mg chlorophyll *a* m⁻², T. Angradi, unpublished data) sandy substrates are predominant. The importance of *Cladophora*-colonized cobble bars is disproportionate to its area, and even relatively moderate losses of epilithon GPP could have a large effect on the Glen Canyon trophic structure.

Effects of exposure disturbance on primary productivity are likely to be protracted. Recolonization of substrates in Glen Canyon is slow; studies of algal colonization of introduced substrates at 14 Mile Bar indicated that accrual of chlorophyll *a* to the levels found on natural

cobbles would take 4-6 months in the permanently inundated zone, and even longer in the fluctuating flow zone (Angradi et al., 1992). These findings suggest that *Cladophora* has low resilience following disturbance. This conclusion is supported by the observations of Dodds (1991) who studied *Cladophora* in an ephemeral channel, and of Fisher et al. (1982) who found that *Cladophora* was a late successional species following flash floods in desert streams.

The available evidence suggests the following scenario: *Cladophora*, once established, thrives in upper Glen Canyon, even on substrates exposed to daily exposure (mostly at night), where it may have a competitive advantage over other taxa (Usher and Blinn, 1990), but is unresistant to protracted daytime exposure, especially in summer. The combination of daily nighttime exposure and low dissolved nutrient concentrations results in low recolonization rates (Steinman and McIntire, 1991; DeAngelis et al., 1990; T. Angradi, unpublished data).

The consequences of a shift to early colonizers and resistant taxa, such as *Oscillatoria*, to ecosystem function (e.g., trophic structure, macroinvertebrate habitat) in Glen Canyon are not known. As is often the case below dams with hypolimnetic discharge, the Glen Canyon phytobenthos lacks the functional redundancy and taxonomic evenness of most unregulated rivers (Ward, 1976; Petts, 1984; Dufford et al., 1987). Filamentous macroalgae other than *Cladophora* are rare (Blinn et al., 1992), and vascular hydrophytes are restricted to depositional areas. The growth form, distribution, and high biomass typical of *Cladophora* are unique to that species in Glen Canyon.

Studies of the ecology of the amphipod *Gammarus lacustris* at 14 Mile Bar indicate a potential higher trophic-level response to disturbance of the epilithon. The macroinvertebrate fauna of Glen Canyon is depauperate (Blinn and Cole, 1991), and a very few taxa, including *Gammarus*, constitute most of the diet of the most abundant fish species in Glen Canyon, the rainbow trout (*Oncorhynchus mykiss*) (Angradi et al., 1992). *Gammarus* were, on average, eight times more abundant in the permanently inundated zone where *Cladophora* biomass was high than in the fluctuating flow zone where *Cladophora* was largely absent (Figure 10). Stable isotope analyses (^{13}C , ^{15}N) revealed that assimilated C and N in *Gammarus* collected at 14 Mile Bar originated from diatoms rather than from *Oscillatoria*, terrestrial detritus, or seston exported from Lake Powell (T. Angradi, unpublished data). Intact *Cladophora* has a very high surface area which supports a dense assemblage of these diatoms (Blinn et al., 1989). The most important

ecosystem-level function of attached *Cladophora* may be as habitat for other organisms (Dodds and Gudder, 1992), and reach-wide disruption of this structural function due to exposure could precipitate higher trophic level effects within the Glen Canyon ecosystem.

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FIGURE CAPTIONS

- Figure 1. Mean (± 1 SE) percent of initial chlorophyll *a* and biomass remaining following exposure (Experiment I). Regression functions for percent chlorophyll *a* remaining are given in Table 3. Initial values (chl *a* [mg m^{-2}], biomass [g AFDM m^{-2}]) are 655 ± 94 and 201 ± 22 .
- Figure 2. Mean (± 1 SE) percent chlorophyll *a* and biomass remaining following exposure and reinundation in a sluiceway at Glen Canyon Dam (Experiment II). Initial values (chl *a* [mg m^{-2}], biomass [gAFDM m^{-2}]) are, exposed 0 h: 634 ± 85 , 221 ± 31 ; exposed 24 h: 877 ± 102 , 253 ± 21 ; exposed 48 h: 784 ± 102 , 356 ± 63 .
- Figure 3. Accrual of chlorophyll *a* and biomass on sandstone tiles placed in the sluiceway at Glen Canyon Dam (Experiment II). Values are means ± 1 SE. Day 5 corresponds to day 0 in Figure 2.
- Figure 4. Mean (± 1 SE) percent chlorophyll *a* and biomass remaining following exposure and reinundation at 14 Mile Bar (Experiment III). Initial values (chl *a* [mg m^{-2}], biomass [gAFDM m^{-2}]) are, exposed 0 h: 573 ± 36 , 459 ± 24 ; exposed 24 h: 781 ± 60 , 535 ± 42 ; exposed 48 h: 610 ± 53 , 591 ± 103 . Symbols are as in Figure 2.
- Figure 5. Percent chlorophyll *a* and biomass remaining following exposure and reinundation of epilithon from the permanently inundated zone at 14 Mile Bar (Experiment IV). Initial values (chl *a* [mg m^{-2}], biomass [gAFDM m^{-2}]) are, exposed 0 h: 767 ± 148 , 121 ± 11 ; exposed 1 h: 876 ± 78 , 134 ± 18 ; exposed 2 h: 647 ± 92 , 109 ± 19 ; exposed 4 h: 801 ± 202 , 120 ± 27 ; exposed 6 h: 1160 ± 403 , 127 ± 32 ; exposed 8 h: 1058 ± 250 , 157 ± 19 .
- Figure 6. Percent chlorophyll *a* and biomass remaining following exposure and reinundation of epilithon from the fluctuating flow zone at 14 Mile Bar (Experiment V). Initial values (chl *a* [mg m^{-2}], biomass [gAFDM m^{-2}]) are, (Experiment V). Initial values (chl *a* [mg m^{-2}], biomass [gAFDM m^{-2}]) are, exposed 0 h: 300 ± 17 , 118 ± 9 ; exposed 1 h: 334 ± 41 , 139 ± 27 ; exposed 2 h: 271 ± 34 , 99 ± 13 ; exposed 4 h: 342 ± 47 , 131 ± 11 ; exposed 6 h: 302 ± 47 , 120 ± 16 ; exposed 8 h: 307 ± 24 , 124 ± 11 . Symbols are as in Figure 5.

- Figure 7. Relationship between GPP and PAR and between AR and PAR for unexposed and exposed epilithon from the permanently inundated and fluctuating flow zones. Regression functions are given in Table 3. Plot numbers refer to experimental parameters given in the Appendix.
- Figure 8. Percent chlorophyll *a* remaining following exposure and reinundation versus hours exposed and cumulative PAR. Values are means \pm 1 SE. Regression functions are given in Table 3.
- Figure 9. Gross primary production (GPP) of epilithon from the permanently inundated zone as a function of exposure duration and initial chlorophyll *a* content (a), and (b) loss of GPP from the first 12 km of littoral cobble habitat downstream from Glen Canyon Dam as a function of flow and chlorophyll *a* of epilithon. Model a was generated using functions 4 and 9 from Table 3. GPP was calculated for a range of chlorophyll *a* values (function 9) with ambient PAR data for 15-17 July 1991. GPP was then recalculated for exposure durations (cumulative PAR) using function 4. An assumption of the model was that AR did not vary with exposure or chlorophyll content (see Figure 7). Flow refers to the lowest level at which a viable *Cladophora*-dominated epilithon is present. Lost GPP is in comparison to summertime littoral production if a *Cladophora*-dominated epilithon is present up to the 566 cms level. Estimates of littoral area were based on channel profiles from a 1990 survey of fixed rangelines (U.S. Bureau of Reclamation, in litt.); distribution of cobble substrates was determined from aerial photographs. Model b was generated using function 9 from Table 3 with ambient PAR data for 15-17 July 1991; the resulting assimilation ratios were used to generate GPP values for a range of chlorophyll *a* values, which were then expressed on a reach-wide basis. Estimates of partial loss due to incomplete destruction of the epilithon without a change in flow regime can be derived by calculating the endmember chlorophyll *a* value using function 4, Table 3. An assumption of the model is that light limitation does not occur in the littoral zone at any flow \leq 566 cms.
- Figure 10. Epilithon biomass and density of *Gammarus lacustris* in the permanently inundated and fluctuating flow zones at 14 Mile Bar in 1992. Epilithon biomass values are means \pm 1 SE ($n = \geq 10$) for samples collected using the same methods as for exposure experiments. *Gammarus lacustris* densities (\pm 1 SE, $n = 8$) are from Hess samples (0.087 m²) collected at 14 mile Bar (D. Parmley, in litt.).

Table 1. Meteorological data for all experiments. Dates and times refer to periods of epilithon exposure. Values are means (SE, except experiments IV and V) based on hourly records. PAR refers to maximum (full sun) photosynthetically active radiation (400 - 700nm) during exposure. Temperature and relative humidity data are from sensors located at Glen Canyon Dam.

Expt.	Date(s)	Temperature (C)		Relative Humidity (%)		Par ($\mu\text{moles s}^{-1}\text{m}^{-2}$)	
		Day	Night	Day	Night		
I	070491-071191	33.1 (0.41)	28.3 (0.33)	23 (1.0)	30 (1.3)	2300	
	071291-071591	34.6 (0.35)	30.0 (0.33)	17 (0.6)	20 (0.7)	2200	
II	071191	na*	28.7 (0.81)	na	25 (1.4)	na	
	071291	34.0 (1.02)	29.4 (0.80)	20 (1.9)	25 (2.1)	2240	
	071391	34.1 (0.91)	na	22 (1.9)	na	2240	
III	082291	33.3 (0.74)	29.0 (0.57)	19 (1.0)	24 (0.8)	2140	
	082391	33.7 (0.97)	28.5 (0.67)	20 (1.3)	33 (2.8)	1920	
		<u>Hours</u>					
IV	062492	10-1100	31.1	na	29	na	1800
		11-1200	32.3	na	23	na	1900
		12-1400	34.2	na	19	na	1460
		14-1600	31.4	na	21	na	720
		16-1800	30.0	na	23	na	900
V	081192	10-1100	32.6	na	28	na	1850
		11-1200	34.4	na	26	na	2075
		12-1400	35.6	na	22	na	2020
		14-1600	35.6	na	20	na	1380
		16-1800	32.0	na	28	na	864
VI	091592	10-1400	25.0 (0.86)	na	53 (4.7)	na	1800
	091792	29.3 (0.90)	25.6 (0.74)	33 (3.4)	31 (1.6)	1760	
	091892	22.3 (0.40)	na	51 (3.3)	na	882	
	092292	10-1800	30.1 (0.80)	na	26 (2.0)	na	1670
	092492	31.3 (0.42)	25.9 (1.14)	25 (1.4)	24 (0.4)	1750	
092592	24.4 (1.03)	na	19 (1.4)	na	1770		

* na, not applicable.

Table 2. Selected water quality parameters for experiments II-VI. Values are means (SE) based on hourly records. Start date is the first day of inundation following experimental exposure. Data are from United States Geological Survey gaging station No. 09379910 located 2 km below Glen Canyon Dam.

Experiment	Start Date (ddmmyy)	Week	Temperature (°C)	Specific Conductance ($\mu\text{S cm}^{-1}$)	pH	Dissolved Oxygen (mg l^{-1})
II	071191	1	8.6 (0.02)	929 (0.8)	8.0 (0.01)	8.1 (0.06)
		2	8.6 (0.02)	928 (1.0)	8.0 (0.01)	7.6 (0.04)
III	082391	1	8.8 (0.01)	914 (0.5)	7.9 (0)	6.5 (0.01)
		2	9.0 (0.04)	906 (0.7)	7.9 (0.01)	6.6 (0.01)
IV	062592	1	7.8 (0.01)	906 (0.9)	7.8 (0.01)	6.2 (0.02)
		2	7.9 (0.02)	905 (0.9)	7.8 (0.01)	6.1 (0.01)
		3	7.9 (0.01)	905 (0.7)	8.0 (0.01)	6.2 (0.02)
		4	8.0 (0.01)	899 (0.7)	7.8 (0.01)	6.4 (0.01)
V	081292	1	8.2 (0.01)	876 (0.9)	7.5 (0.01)	6.1 (0.01)
		2	8.2 (0.02)	884 (0.9)	7.9 (0.01)	6.6 (0.02)
		3	8.3 (0.01)	880 (0.7)	8.0 (0.01)	6.4 (0.01)
		4	8.4 (0.02)	875 (0.8)	7.9 (0.01)	6.3 (0.01)
VI	090192	1	8.5 (0.01)	868 (0.6)	7.6 (0.01)	6.4 (0.04)
		2	8.6 (0.01)	858 (0.5)	7.7 (0.01)	6.4 (0.01)
		3	8.9 (0.02)	848 (0.6)	7.6 (0.01)	6.2 (0.02)

Table 3. Linear regression functions and associated statistics for effects of exposure time and cumulative PAR (moles m⁻²) on the percent of chlorophyll *a* remaining (PCR), and for the relationship between GPP (gO₂ m⁻² h⁻¹) and PAR (μmoles s⁻¹ m⁻²) and between AR (mgO₂ mg chl a⁻¹ h⁻¹) and PAR. All models shown are significant (*P* < 0.05).

Experiment	Function	SE*	r ²	n
I	1. log (PCR) = 2.05 - 0.31 log (hours exposed)	0.06	0.74	30
	2. log (PCR) = 2.08 - 0.27 (cumulative PAR)	0.04	0.66	30
II-IV	<u>After one week</u>			
	3. log (PCR) = 2.07 - 0.43 log (hours exposed)	0.07	0.79	12
II-IV	<u>After two weeks</u>			
	4. log (PCR) = 2.14 - 0.38 log (cumulative PAR)	0.05	0.76	12
II-IV	5. log (PCR) = 1.92 - 0.31 log (hours exposed)	0.06	0.73	12
	6. log (PCR) = 1.99 - 0.30 log (cumulative PAR)	0.06	0.80	12
VI	<u>Permanently inundated zone, unexposed</u>			
	7. log (GPP) = -0.027 + 0.27 log (PAR)	0.06	0.46	25
	8. log (GPP) = 0.013 + 0.23 log (PAR)**	0.02	0.82	20
	9. log (AR) = -0.56 + 0.26 log (PAR)	0.16	0.46	25
	<u>Permanently inundated zone, exposed</u>			
	10. log (AR) = -0.17 + 0.12 log (PAR)	0.05	0.09	51
	<u>Fluctuating flow zone, unexposed</u>			
	11. log (GPP) = -1.19 + 0.19 log (PAR)	0.05	0.38	22
	12. log (AR) = 0.40 + 0.24 log (PAR)	0.07	0.34	22
<u>Fluctuating flow zone, exposed</u>				
13. log (GPP) = -1.44 + 0.19 log (PAR)	0.08	0.18	27	
14. log (AR) = -0.46 + 0.19 log (PAR)	0.07	0.19	27	

* Standard error of the regression coefficient.

** Regression function if incubation 1 omitted (see figure 8).

Appendix. Experimental parameters for estimations of GPP and AR (Experiment VI). Plot numbers refer to Figure 7. Cumulative PAR is the total PAR to which exposed cobbles were subjected. Chlorophyll *a* and biomass values represent the epilithon sample on which incubations were run.

Plot No.	Cumulative PAR (moles/m ²)	Chlorophyll <i>a</i> (mg sample ⁻¹)	Percent Chlorophyll <i>a</i> Remaining*	Biomass (gAFDM sample ⁻¹)
<u>Permanently inundated zone</u>				
1	0	21.5	100	3.7
2	0	13.5	100	2.5
3	0	6.3	100	1.5
4	0	12.7	100	2.1
5	47	7.5	84	2.6
6	64	5.7	30	2.9
7	64	4.4	30	1.1
8	37	4.3	80	1.2
9	37	5.4	80	1.5
10	31	1.6	60	0.5
11	31	5.5	60	1.6
12	47	1.6	65	0.8
<u>Fluctuating flow zone</u>				
1	0	1.2	100	0.5
2	0	0.5	100	0.2
3	47	0.9	36	0.6
4	64	0.9	30	0.7
5	0	0.9	100	0.3
6	0	1.1	100	0.4
7	37	1.1	77	0.6

* Values are based on unreplicated samples; values for exposed material from the fluctuating flow zone overestimate the percent chlorophyll *a* remaining.

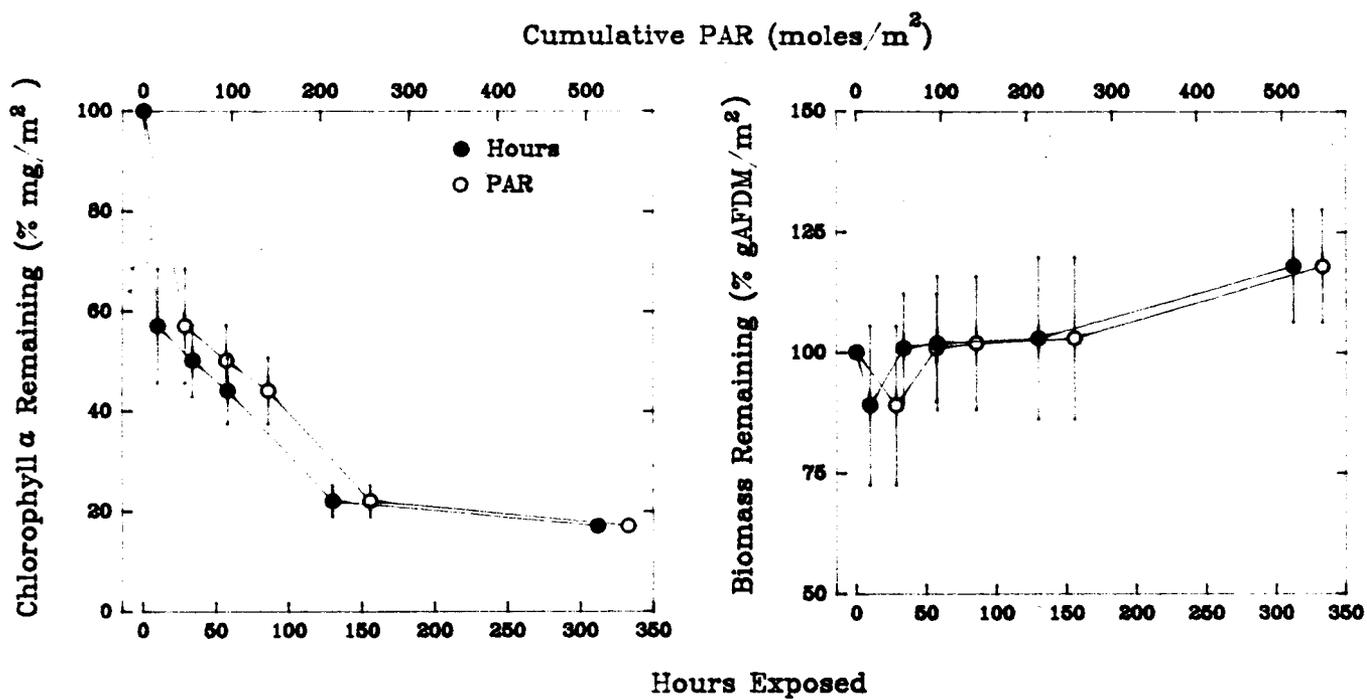


FIGURE 1.

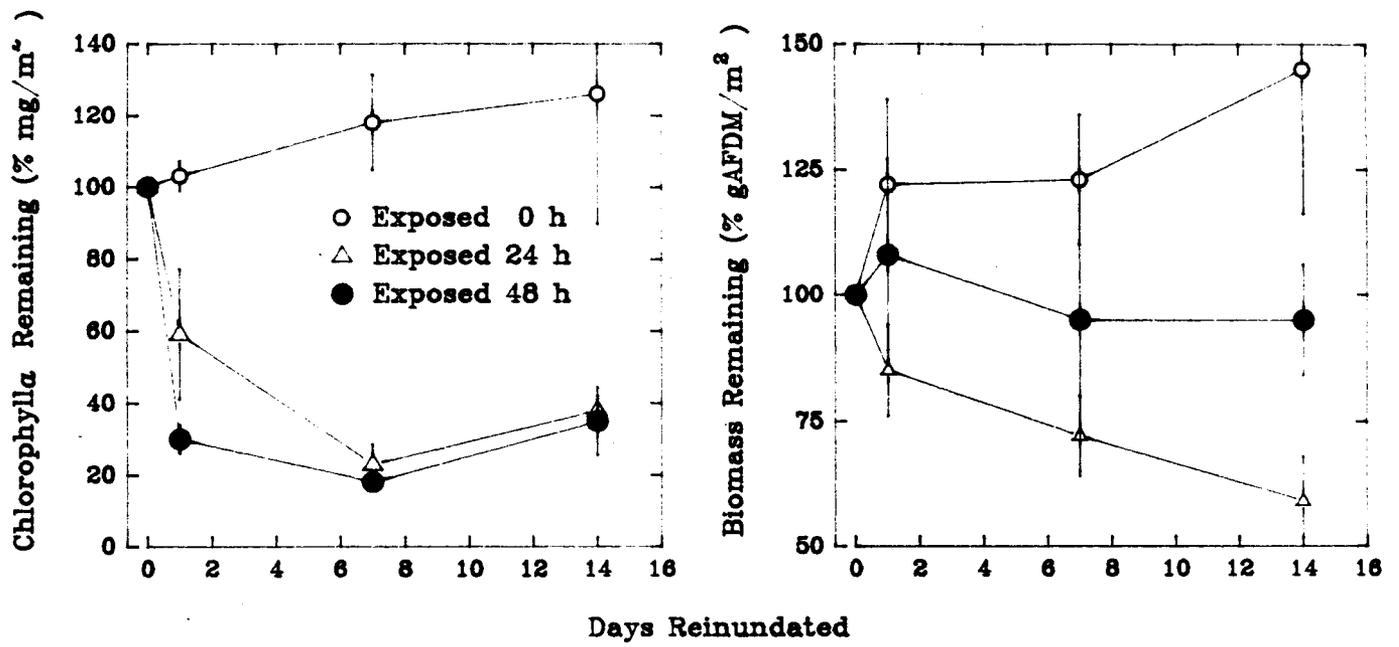


FIGURE 2.

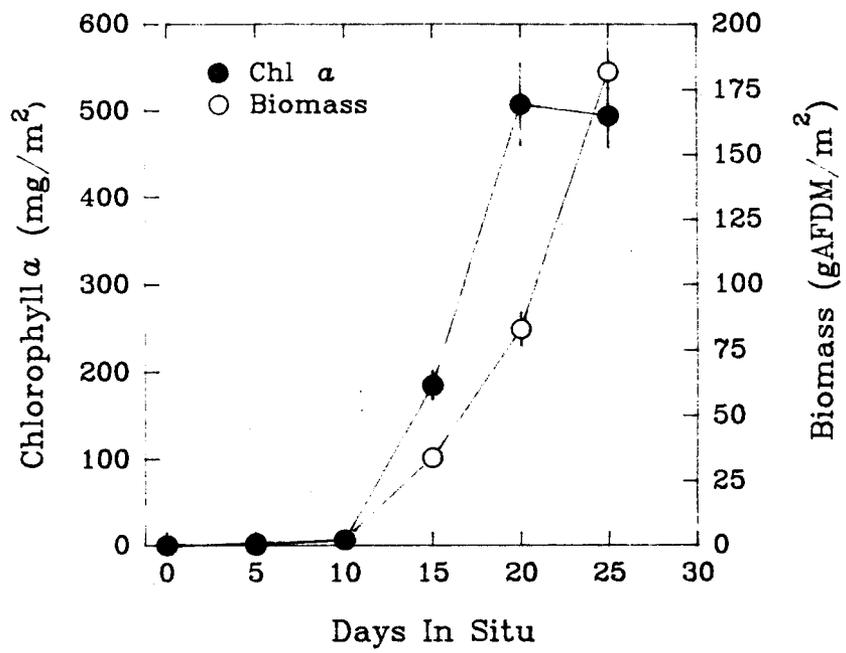


FIGURE 3.

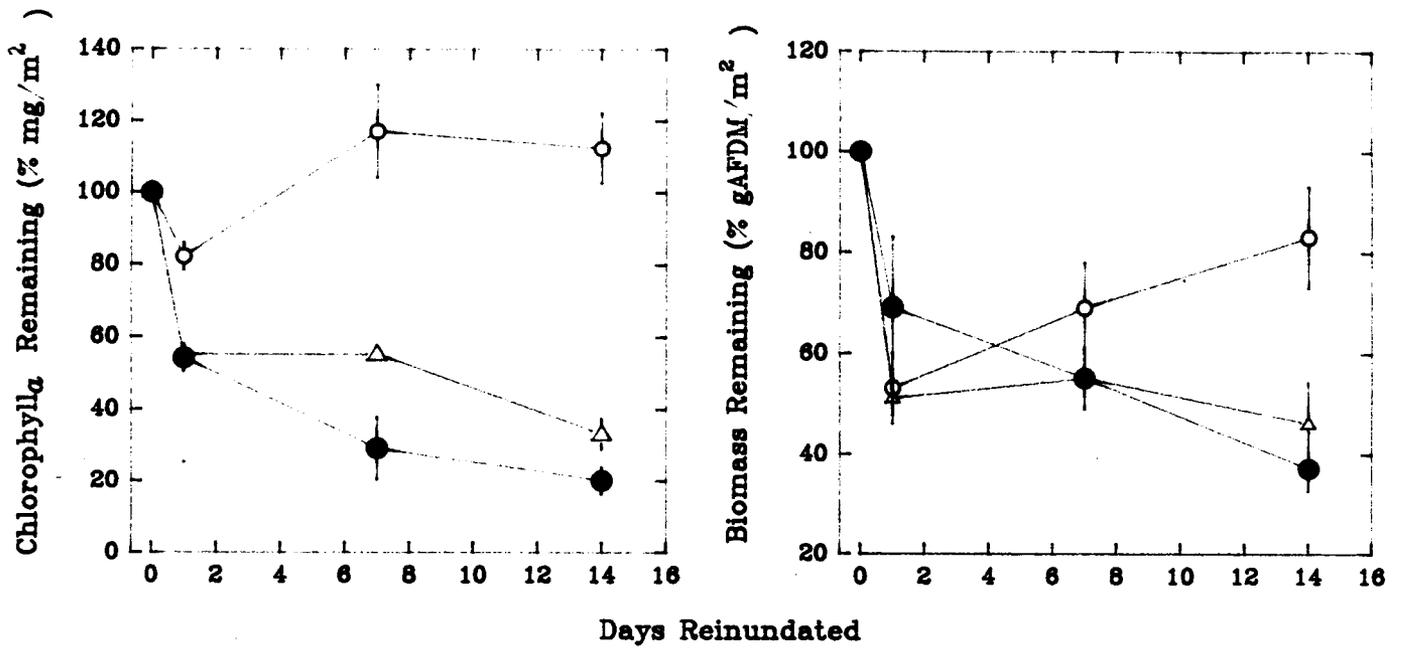


FIGURE 4.

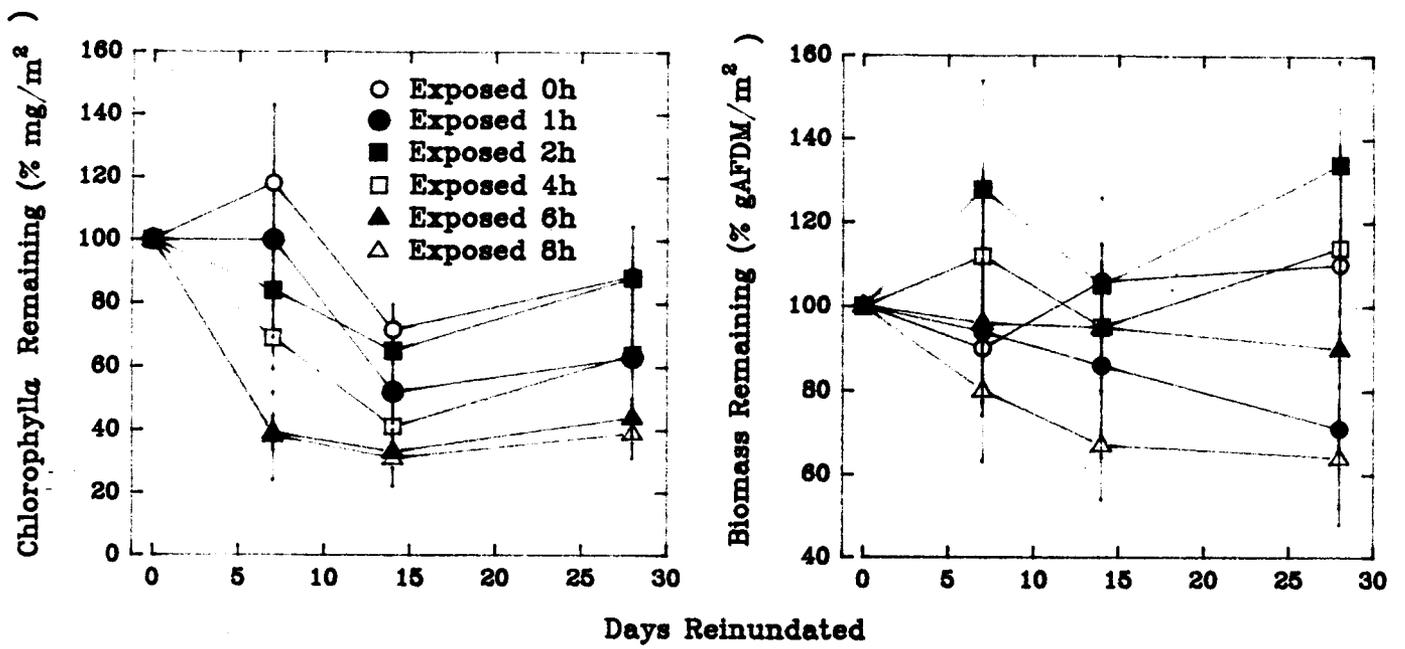


FIGURE 5.

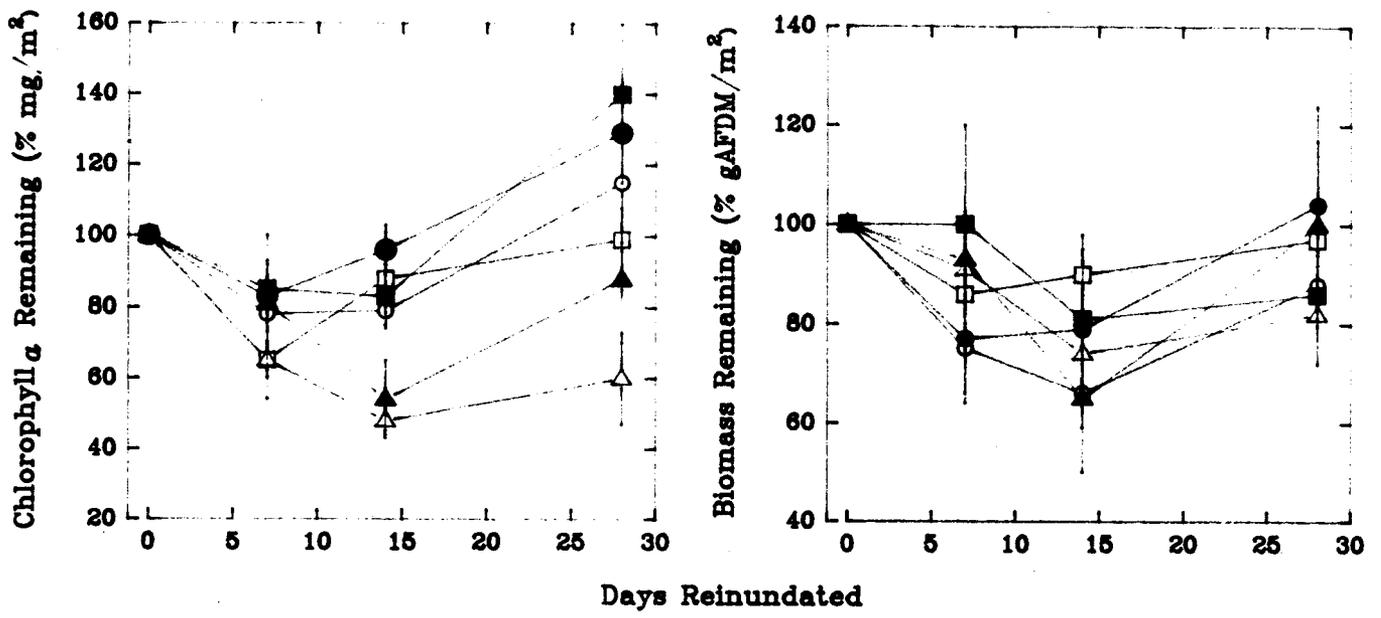


FIGURE 6.

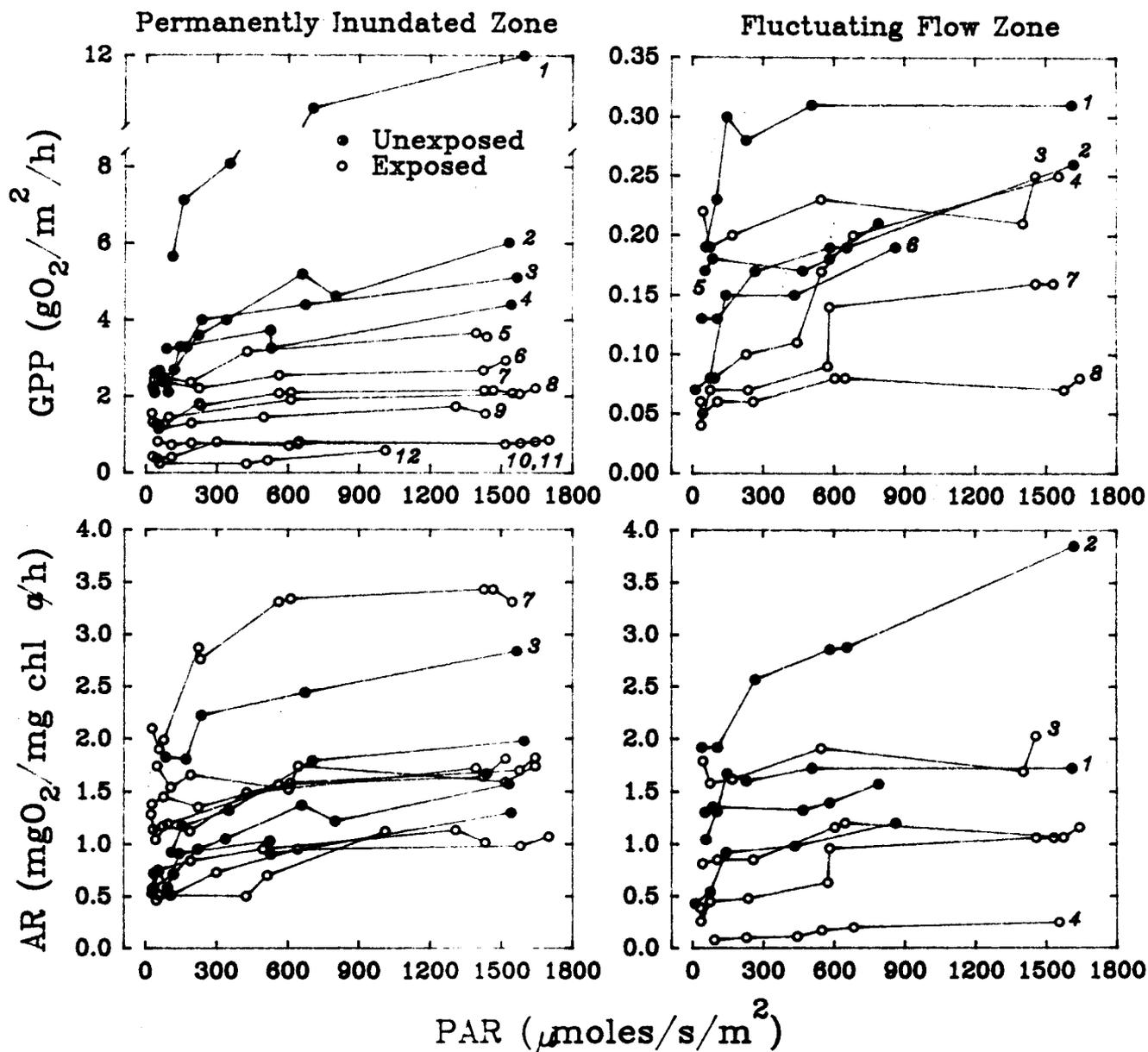


FIGURE 7.

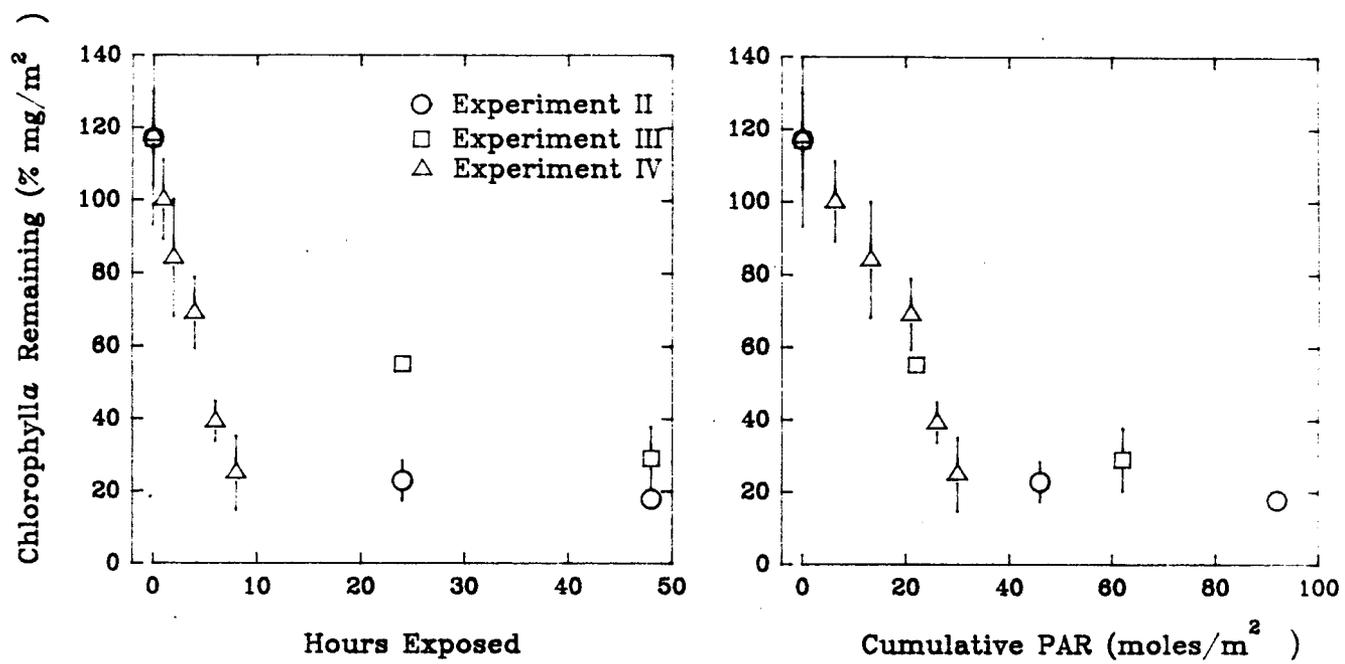


FIGURE 8.

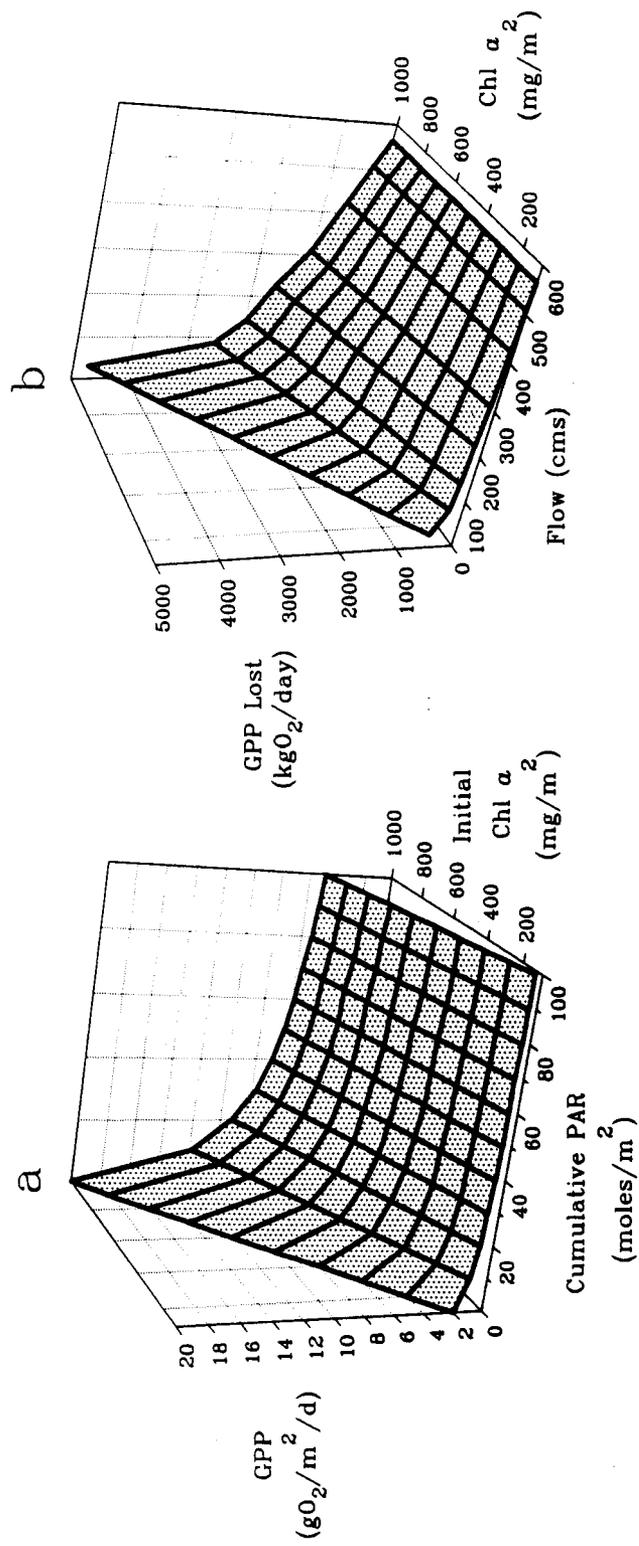


FIGURE 9.

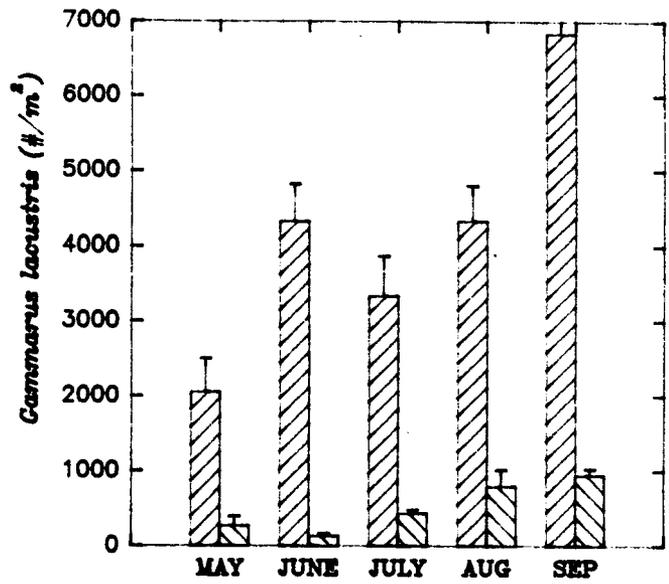
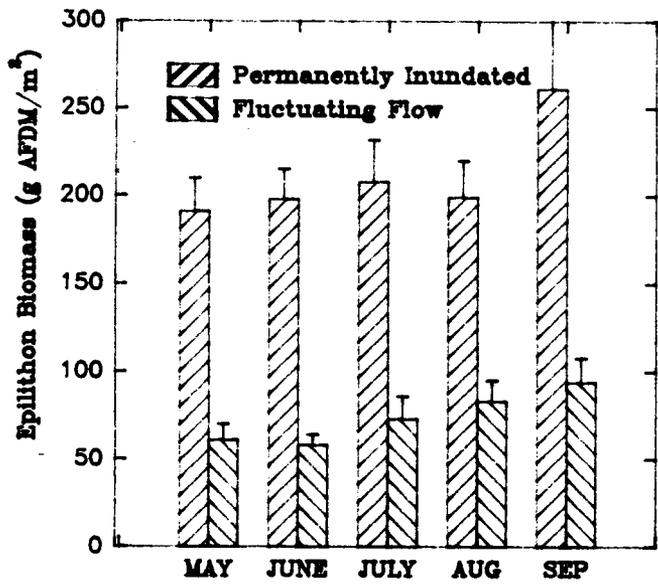


FIGURE 10.

3. Mainstem Colorado River Native Fishes

William R. Persons and D. Alan Kinsolving

The purpose of this chapter is to summarize initial findings of studies of mainstem backwaters and tributary mouth rearing habitats and to review how we plan to fulfill objectives outlined in the 'Cooperative Agreement'. This chapter summarizes information on temperature and water levels in backwaters from DataSondes and presents preliminary fish catch data with emphasis on humpback chub.

Objectives 3.4 and 3.6. Determine the environmental conditions at each tributary mouth and in the mainstem Colorado River. Determine the behavioral responses of larval to juvenile native fishes to changing environmental conditions in rearing habitats.

Methods and Progress

During the period from March 1991 through November 1992, 13 downriver trips took place. Trips utilized three different sampling protocols. Opportunistic sampling was used to obtain a quick, qualitative point-in-time characterization of a site. Intensive sampling (Type A) was more quantitative, but still provided a point-in-time perspective. Type B trips were designed to assess changes in fish abundance and habitat use across varied flow and diel cycles. Multi-day intensive sampling took place on Type B trips. Trip dates and type of samples collected are shown in Table 3.4.1.

Opportunistic sampling

At opportunistically sampled sites, fish were captured by making a single pass through the backwater, mainchannel, or tributary site using either a straight or bag seine. The choice of gear depended on site, size and topography; with bag seines used in larger, less structurally complex habitats. Additionally, dip nets were used to capture fish in areas where it was not practical to seine. Effort was recorded in square meters of water seined, and collected fish were identified, measured and enumerated following each seine haul. Unidentified fishes were preserved in 10% buffered formalin for later identification in the lab. At each site; the habitat type, dominant substrate, water temperature and site dimensions were recorded. Opportunistic sampling was generally used for smaller sites, where it was not feasible to perform intensive sampling.

Type A Sampling

At intensively sampled sites (Type A), fishes were captured by two methods. In the backwater portion of the site, block nets (3.25 mm mesh) were placed near the mouth of the backwater to prevent fish from escaping from the site. The site was then electrofished using one or two hand held probes powered by a Coffelt VVP pulsator and a 5000 watt generator. Following electrofishing, the site was seined, depending on site topography and size, using either straight or bag seines (3-10 m long, 1-1.5 m high). Electrofishing and seining continued until no additional fish were captured. During times of the year when very small (<25 mm) fish were present, the site was also seined using a 0.84 mm mesh larval seine. In the mainstream and mainstream eddy portion of the site, fishes were captured in the same manner as for opportunistic sampling described above.

Because of potential safety hazard and fish health problems associated with electrofishing, it was discontinued during the April 1992 trip, and seines and dip nets were used exclusively for Type A sampling. Normally, each site was seined at least three times to allow the calculation of depletion population estimates. However, it was frequently not possible to complete three seine hauls of the entire site. This was because the first pass would disturb fine sediments and subsequent attempts at seining would result in a large volume of fine sediment becoming entrapped in the net.

Sites were mapped using an alidade and plane table to create an accurate map showing wetted perimeter, contour lines for 25 cm, 50 cm, 100 cm and 150 cm depths, and areas of various substrates.

Water temperature and current speed were recorded at 10 to 30 evenly spaced locations along the long axis of the backwater and at one location in the main river. Water temperature was measured to the nearest tenth of a degree C using a digital type K thermocouple thermometer. Current speed was measured to the nearest hundredth of a m/sec using a Marsh-McBirney meter. Dissolved oxygen (as percent saturation and concentration in mg/l) and water turbidity (in nephelometric turbidity units) were each measured at one location per habitat type. When water turbidity was greater than 100 NTU, it was necessary to dilute water samples prior to measuring turbidity. In those cases, 500 ml of the water to be measured was mixed with 500 ml of filtered water of known turbidity and measured. If turbidity of the dilute sample remained above 100 NTU, it was further diluted until turbidity was below 100 NTU. Actual sample turbidity was then calculated. Prior to using this technique, the formula for calculating turbidity of the actual sample from turbidity of the dilute sample was tested in the lab using a series of solutions of known turbidity.

Prior to shocking and seining the site; benthos, plankton and sediment samples were taken and preserved in 5-10% formalin for later lab identification and analysis. Benthos was

sampled at two locations within each habitat type using a Petite Ponar dredge. Plankton samples were taken in each habitat type by pouring 30 l of water, collected from a single location, through a 45 μm mesh plankton net. Volume of plankton samples was increased to 50 l in February of 1992. Sediment core samples were taken in each habitat type using a 50 cm^3 minicore sampler.

Type B Sampling

At each Type B backwater and tributary sampling locations, from 30 to 50 minnow traps were deployed throughout the site. For backwater locations, traps were located in the mainstream, the mainstream eddy, the return channel eddy and the backwater proper. At each tributary mouth, traps were deployed in the mainstream and up the tributary as far as the estimated high water zone. Traps were checked approximately four to five times a day. Whenever possible trap checks took place during ascending water, stable high water, descending water and stable low water over a three day period. During each trap check, current speed, depth, water temperature and substrate type were recorded for each trap as well as the species and length of fishes captured. Benthos, sediment and plankton samples were collected as described above at five to ten locations along a gradient of flow related influence ranging from locations that were submerged (or perpetually riverine) throughout the three day period to those that were submerged only briefly (or were influenced by the river only briefly). Sites were mapped using an ETM (Leitz or equivalent) supplied by GCES to accurately locate individual minnow traps and benthos sampling sites, and to record topographic conditions. Two DataSondés (Hydrolab Corporation) were set to record Ph, dissolved oxygen, conductivity, water depth and temperature at 15 to 30 minute intervals. They were deployed at each site in the mainstream and also in the tributary or backwater. Some backwaters that were sampled intensively during early trips decreased in size during the period of study; primarily because of the deposition of fine sediments. Therefore, they were replaced by different backwaters during subsequent trips. Clear Creek was also replaced by Crystal Creek because of the unsuitability of the Clear Creek area for camping.

Other Sampling

Qualitative tributary sampling took place during trips six, eight and ten. In general, tributaries were sampled in the area of the confluence (first 100 m of the tributary) and in an area either above a barrier falls (Shinumo Creek and Deer Creek) or approximately 1 km upstream from the confluence. Sampling took place in the manner described above for opportunistic sampling, with approximately 100-200 m^2 of effort devoted to both pool and riffle habitat in both the near confluence and non-confluence zones. Paria River sampling took place

December 14th and March 29th 1992 at ten fixed sites located along the reach from the confluence to 3 km above the confluence. At each site approximately 50 m² of stream was seined using a 1/4" mesh seine.

Larval-drift nets 3 m long, with 750 µm mesh net, 500 µm mesh bucket and 0.25 m² openings were deployed in nearshore mainstream and tributary locations during some trips. Current velocities were taken at the mouth of the net immediately after deployment and prior to retrieval. The mean of the two readings was used to calculate volume of water filtered. Depending on the debris load and current speed, nets were deployed for periods ranging from 10 to 45 minutes. Drift netting effort was increased beginning with trip 9 to approximately six hours per day because almost no larval fish were caught in the mainstream drift. However, because this resulted in such a large number of samples, it was decided that the majority of samples would be examined in the field for larval fish and then discarded.

Chlorophyll samples were collected by filtering 30 l of water through a 0.7 µm glass fiber filter. Following filtration, the filter paper and residue were frozen in liquid nitrogen. Chlorophyll samples were taken during trip seven at six locations along the river above the Little Colorado River (LCR). It was not possible to collect samples below that point, or on subsequent trips, because high sediment loads in the river caused filter paper to clog well before an adequately large sample of water could be filtered.

Results and Discussion

DataSondes

The ability of backwaters to warm has been identified by other workers (Maddux et al. 1987, Angradi et al. 1992) as being important in making backwaters suitable nursery and rearing areas for fishes in Grand Canyon. Therefore, for this report we examined flow, water level and temperature data from several traces in backwaters and nearby mainchannel habitats during periods of steady and fluctuating flows.

Datafiles from Hydrolab DataSonde sets were adjusted by eliminating the first and last recordings when it was evident from temperature and water level data that the sonde was out of the water during these periods. It was common for the instrument to record data when it was first prepared for deployment. Frequently it took up to 30 minutes to deploy the sonde once it was prepared. The sonde also had the capability to record power losses during traces. Records that indicated power losses during traces were removed from the datafiles (all original raw data were retained in the original file). Data from all sonde traces were then compiled into a master datafile for analyses.

Preliminary analyses indicated several problems with the data, especially from early trips. For example, the majority of the traces from Trip 1 (3/28/91 - 4/13/91) were taken with a low

battery level in the sonde (less than 15 volts) and are therefore suspect. Next, the computer used to set up the sondes during Trip 2 (5/8/91 - 5/25/9) defaulted to a "system" date. Therefore the date and time in the datafiles were invalid. To correct this problem starting dates were determined from the "master" dataform. Starting times were also estimated from minnow trap data (Type B) when available. The time field has been corrected for Study 30280, but other Trip 2 traces still need to be corrected. It also appeared that dissolved oxygen levels were incorrect for early trips, probably due to calibration error and use of the wrong membrane on the sonde. This data sanitizing process is currently underway, but it is anticipated that it will take 2-3 months to complete this task.

Table 3.4.2 summarizes mean, minimum, and maximum water temperatures (C) and the range between minimum and maximum water level (m). The sites were coded in the following fashion: site code 1 was either a backwater or tributary mouth deployment, whereas site code 2 was a mainchannel or backwater eddy deployment. The location of site codes 3 and 4 will be determined using plane table and ETM maps and comparison with additional sonde data and Type B habitat data.

Trip 1 traces (Studies 30104-30161) were taken during "normal" fluctuating flows ranging from 2,000 to 28,000 cfs. Trip 1 water level data are invalid, evidently because of low sonde system failure. However, temperature data appear to be valid based on preliminary comparison with Type B temperature data.

Several trip 2 traces were collected during the "D" research flows (3,000-26,000 cfs), but dates and times in the data still need to be corrected. Traces at RM 60.71 (reported as RM 60.66 in Angradi et al 1991a) and RM 60.85 have been previously reported (Angradi et al. 1991a). Several trip 2 traces were also collected during the 5,000 cfs steady flow and the 15,000 cfs steady flow during May 1991.

DataSonde traces from the May 1991 research flows of 5,000 cfs and 15,000 cfs during studies 30255, 30269, and 30270, and 30280 are presented in Figure 3.4.1. River miles and dates of traces are presented in Table 3.4.1. The dashed vertical lines on the figure represent midnight and the dotted vertical lines represent noon. Times shown on the figure are incorrect for studies 30255, 30269, and 30270, and appear to be about 4 hours too early. Times for study 30280 were corrected based on Type B data. The water levels measured by the sonde are also somewhat contradictory. For example, the 'tail' at the end of trace 30255 is probably a result of the sonde being accidentally moved while the 'tail' at the beginning of the trace may represent a 'warm-up' time for the sonde. This trace, taken at river mile 173 was evidently taken during a steady 5,000 cfs discharge period. The water level traces for studies 30269 and 30270 show the rise from 5,000 cfs to 15,000 cfs at river mile 193.91 L and 193.95 R, respectively. The drop in water level measured by trace 30269 is probably the result of the sonde being moved,

perhaps during minnow trap checks. The water level trace for study 30270, taken just across the river from study 30269, also shows the rise in water elevation from 5,000 cfs to 15,000 cfs. Differences in the absolute water elevation change between the two studies can probably be resolved by closer examination of the raw data. The water level trace from study 30280, taken at river mile 201.06 R, also shows changes in water surface elevations that are not reflected in flow release data from Glen Canyon Dam. Examination of stage data from other USGS gauging stations may provide better flow information to relate to observed water elevation data. Inflow from the LCR or other tributaries may account for the discrepancies between sonde data and Glen Canyon Dam releases.

Temperature traces from May 1991 studies (Figure 3.4.2) illustrate the potential for backwater warming during the day, as well as the variability in warming potential between different backwaters. Trace 30255 was probably deployed during early afternoon and pulled the following morning. The trace shows cooling of the backwater at night, even under steady flows. Temperature traces from studies 30269 and 30270 illustrate both diurnal temperature fluctuations during steady flow, and the variability in backwater warming during the same time periods, at approximately the same river mile. The backwater temperature trace from study 30280 warmed from approximately 14 °C to 23 °C during the day, then cooled to approximately 14 °C at night. The mainstem trace (labeled MC) also showed slight warming during the day. Examination of maps; Type A depth data; Type B depth, velocity, and temperature data; and ambient air temperature may help clarify why some backwaters warmed more than others.

Temperature and water level data from Study 31105, RM 201.06R, 8/17/91-8/20/91, were plotted to illustrate changes in water temperature from a typical return eddy channel backwater during 'interim flows' (Figure 3.4.2). This particular study contains data from both backwater (Site 1) and main channel (Site 2) sites. This location was also chosen for analysis because it was mapped with the ETM instrument during at least two trips and because it represented a relatively stable backwater. The data indicated that at flows greater than approximately 15,000 cfs the sonde position in the backwater was inundated by cold mainchannel water. At lower flows (e.g. 12,000 cfs) the backwater sonde position warmed to almost 19 °C during the day.

Figure 3.4.3 displays the effects of varied water levels on temperatures at RM 201.06 R during both interim (Study 31105) and steady flows (Study 30280). It was apparent that steady flows allowed for greater backwater warming at this location. However, the data also showed that in shallow backwaters such as this one, the water cooled to near main channel temperature at night; even under steady flow regimes.

Type A Studies

Fathead minnow and speckled dace comprised approximately 57% of mainchannel and backwater catches by seining and electrofishing during Type A studies (Table 3.4.3). Juvenile flannelmouth sucker (mean length 78 mm) were also common in Type A samples and made up approximately 17% of fishes collected.

Catch per unit effort; fish population depletion estimates; benthos species composition, diversity, and biomass; and sediment data still need to be compiled and analyzed. Benthos samples from trips 1 - 13 have been sorted, identified, counted, and weighed. Identification of some organisms still need to be verified, and the data needs to be analyzed. Analysis of sediment core samples has commenced. Samples have been separated into silt and sand components with a 65 μm sieve, organic matter were burned, and weights have been determined for organic matter, silt and sand.

Plane table maps from Type A studies were digitized and planimeter measurements were taken to estimate total surface area, volume, and depths of backwater habitats. However, the plane table data still needs to be examined, verified, and analyzed. Total station (ETM) maps have been catalogued and maps are being generated for further analysis of sonde and Type B habitat data. It is anticipated that it will take several months to accomplish these tasks.

Type B Studies

Type B studies were conducted to measure key habitat variables (depth, temp., substrate, current velocity) from locations in backwater habitats where small minnow traps were placed. These studies were designed to relate those habitat variables to fish catches.

In the mainstem and backwater habitats only 572 fish were collected in 2,887 trap sets (ca. 0.2 fish/set which is equivalent to about 0.03 fish/hour) (Table 3.4.3). Fathead minnow and speckled dace comprised approximately 79% of mainstem and backwater minnow trap catches. Minnow trap catch rates were almost 3 times higher in tributary streams than in mainstem habitats (2,121 fish collected in 4,127 trap sets, ca. 0.5 fish/set). Speckled dace, plains killifish, and fathead minnow comprised approximately 68%, 15%, and 11% respectively, of trap catches in tributaries. Most killifish were collected during August 1992 in Crystal Creek. Flannelmouth sucker were more common in mainstem than tributary catches and bluehead sucker were more common in tributary catches. Juvenile humpback chub (mean length 71 mm) made up approximately 10% of mainstem and backwater catches, but less than 1% of tributary catches.

Most traps were set in shallow, low velocity areas that were typical of backwaters. A distribution of habitat variables (depth, velocity, temp) was plotted against catch (lines) to estimate the preference of fish for depth, velocity, or temp (Table 3.4.4, Figure 3.4.4). In

general, there appeared to be little preference for velocity or depth. However, there appeared to be a slight preference for warmer temperatures; especially in the tributary habitats. High catch rates of young-of-the-year fishes during August and October, 1992 in warm tributaries (Crystal Creek, Shinumo Creek, Kanab Creek) may account for this apparent preference. Results must be accepted with caution for the depth measurements in the mainstem sites due to a possible sampling artifact. Samples will be reexamined to confirm or correct these data.

Because of the small mesh and mouth opening the traps were obviously size selective. In addition, it is possible that they were also selective for those species that sought refuge in the traps. Further analysis is clearly warranted given the results of the trapping data. However, due to the relatively low catches, difficulty in securing traps to fixed locations, and the large degree of disturbance impacted on backwater habitats while inspecting the traps, we have decided to discontinue their use as a primary sampling technique. Instead, we will partition backwaters into several different habitat types (mouth, center, and foot) and will measure key habitat variables (benthos, plankton, sediment, temperature, velocity, depth, dissolved oxygen) at those locations. Fish caught by seining each partition of the backwater can then be used to estimate habitat preference.

Opportunistic Samples

Opportunistic sampling by seine, minnow trap, angling, kick seine, and dip net collected 3,075 fishes. Speckled dace and fathead minnow comprised approximately 73% of catches in all habitats combined (Table 3.4.3). Juvenile flannelmouth sucker (mean length 92 mm) were more common in mainstem than in tributary habitats and made up 4% and 2% of the catch at those locations, respectively. Juvenile humpback chub (mean length 68 mm) were also more common in mainstem catches than in tributary catches.

Catch of humpback chub

Humpback chub were relatively common in catches in Reach 30 (LCR to Bright Angel Creek) during the fall of 1991 and 1992 (trips 4 and 13). Chub as small as 16 mm caught in Reaches 30 and 40 during June 1992 (Trip 10) were probably flushed from the LCR (Tables 3.4.5, 3.4.6). Other small chub collected during Trips 12 and 13 in Reaches 40 and 50 may be the same cohort that showed slow growth in the mainstem. Species, number of fish measured, mean length, minimum length, and maximum length by Reach code are presented for each trip in Appendix 3.4.2. The three largest catches of humpback chub in the mainstem Colorado River were from Study 30411 (RM 68.01, 9/13/91, n = 55); Study 30413 (RM 72.03, 9/13/91, n = 80); and Study 30901 (RM 68.01, 5/22/92, n = 26). No other single catch of chub exceeded 15 fish. The large catches at RM 68.10 and 72.03 on 13 September 1991 are probably juvenile

and young-of-the-year fishes that were flushed from the LCR during a spate in early September, 1991 (See Angradi et al. 1992, Figure 4.4). Catches at RM 68.10 on 22 May 1992 most likely represent the same group of fishes that exhibited little growth in the cold mainstem water (Figure 3.4.5).

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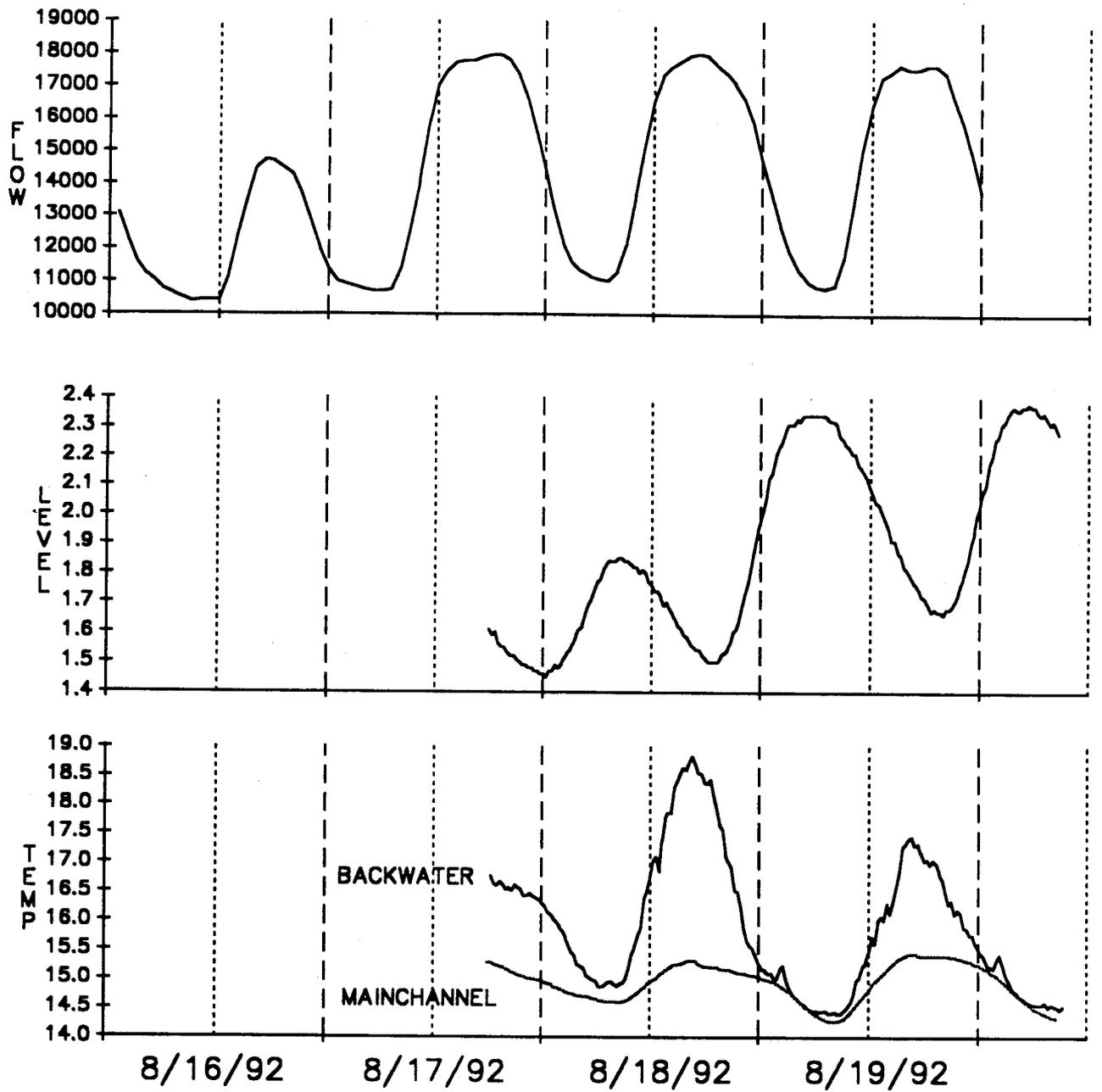


Figure 3.4.1 Releases from Glen Canyon Dam (cfs), relative water elevation (m) from DataSondes, and water temperature from DataSonde, Study 31105, RM 201.06, 8/17/92 - 8/20/92.

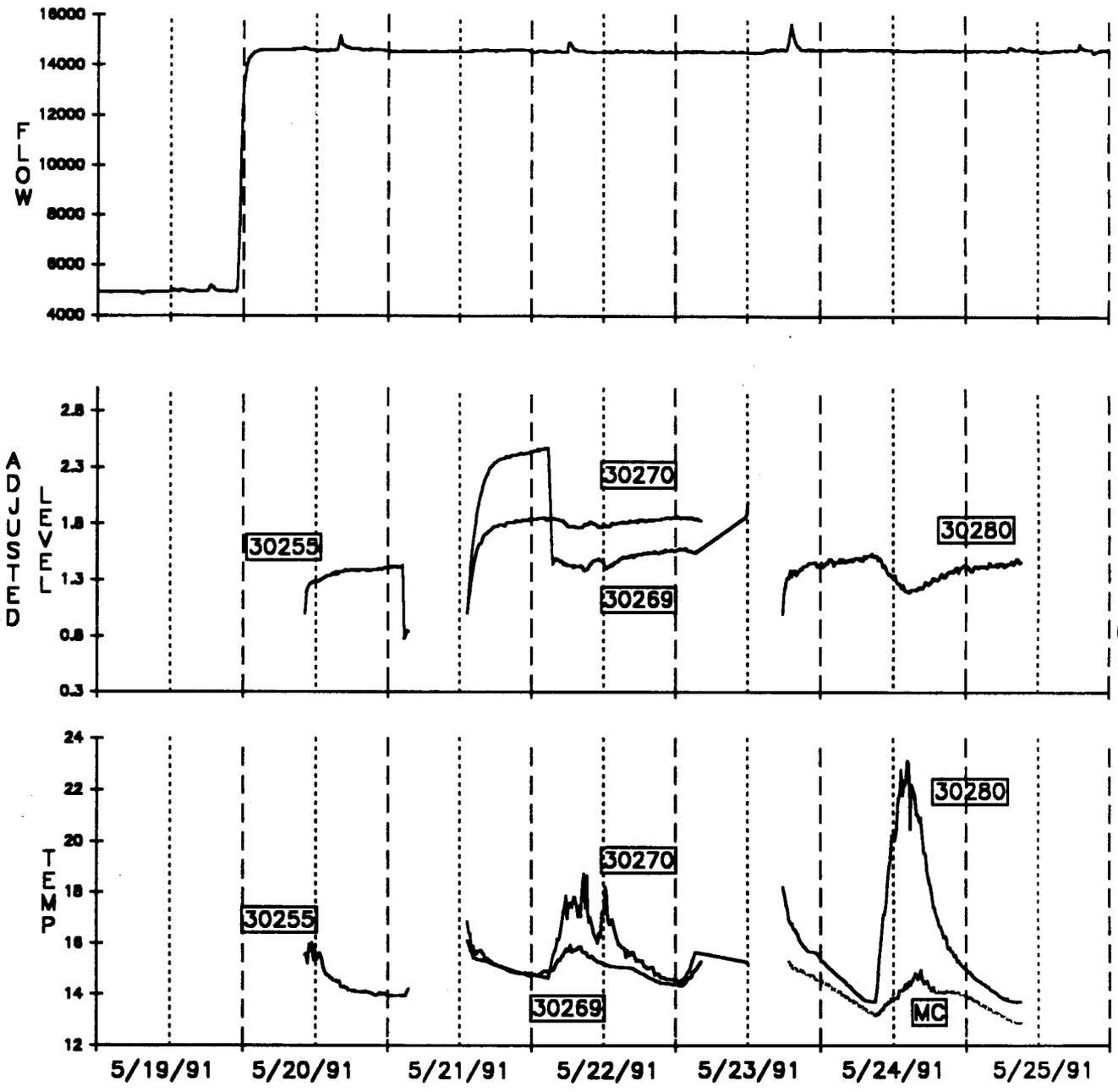


Figure 3.4.2 Releases from Glen Canyon Dam (cfs); relative water elevation (m) and water temperatures($^{\circ}$ C) from DataSondes, Studies 30255,30269,20370, and 30280, 5/19/92 - 5/25/92.

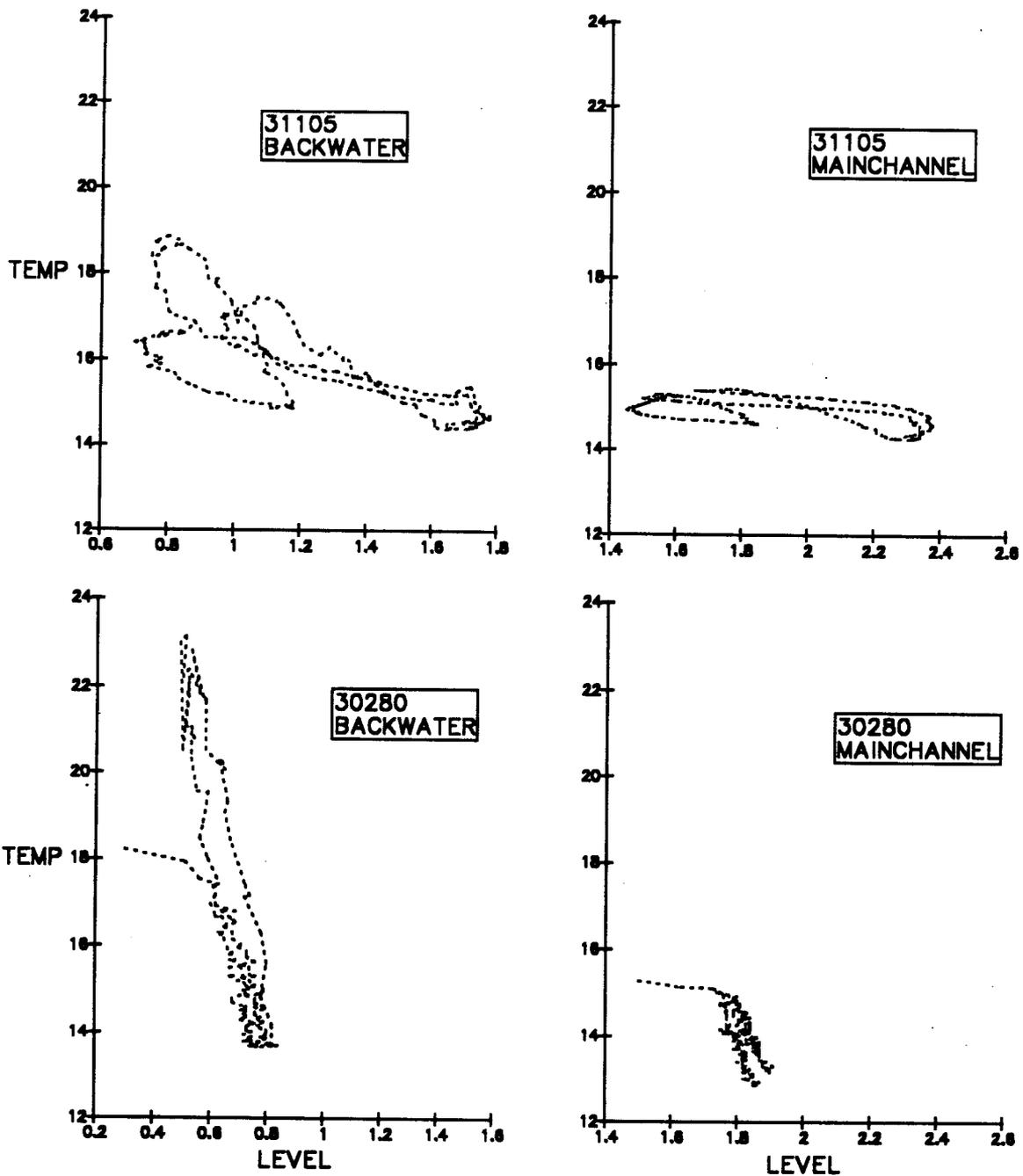


Figure 3.4.3 Relationship between water level (m) and water temperature ($^{\circ}\text{C}$) during studies 30280 (Steady flow) and 31105 (Interim flow) at backwater and mainchannel sites.

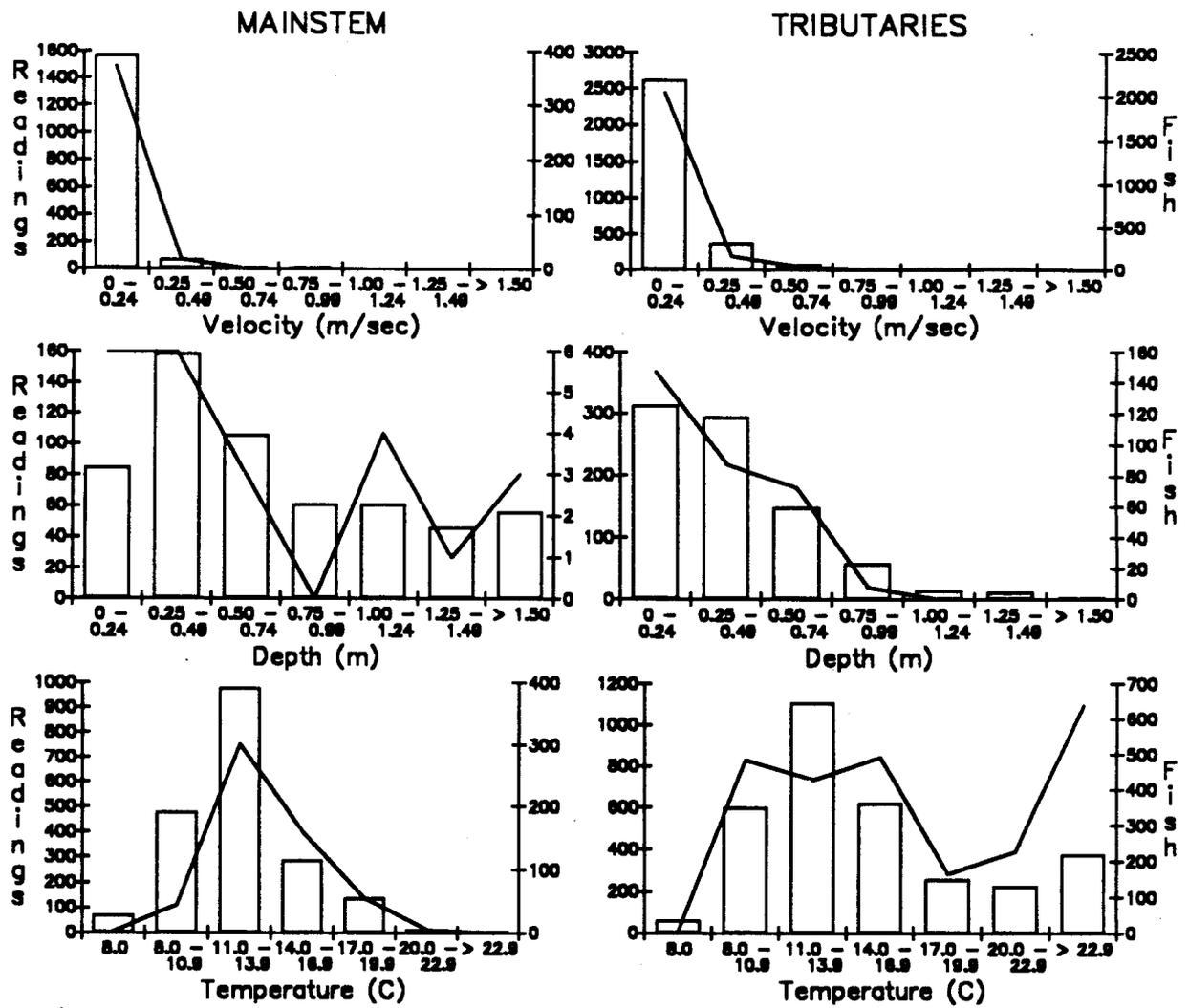


Figure 3.4.4 Frequency distribution of velocity (m/sec), depth (m), and temperature (°C) (open bars, left axis); and catch of fish (line, right axis) at mainstem and tributary minnow traps.

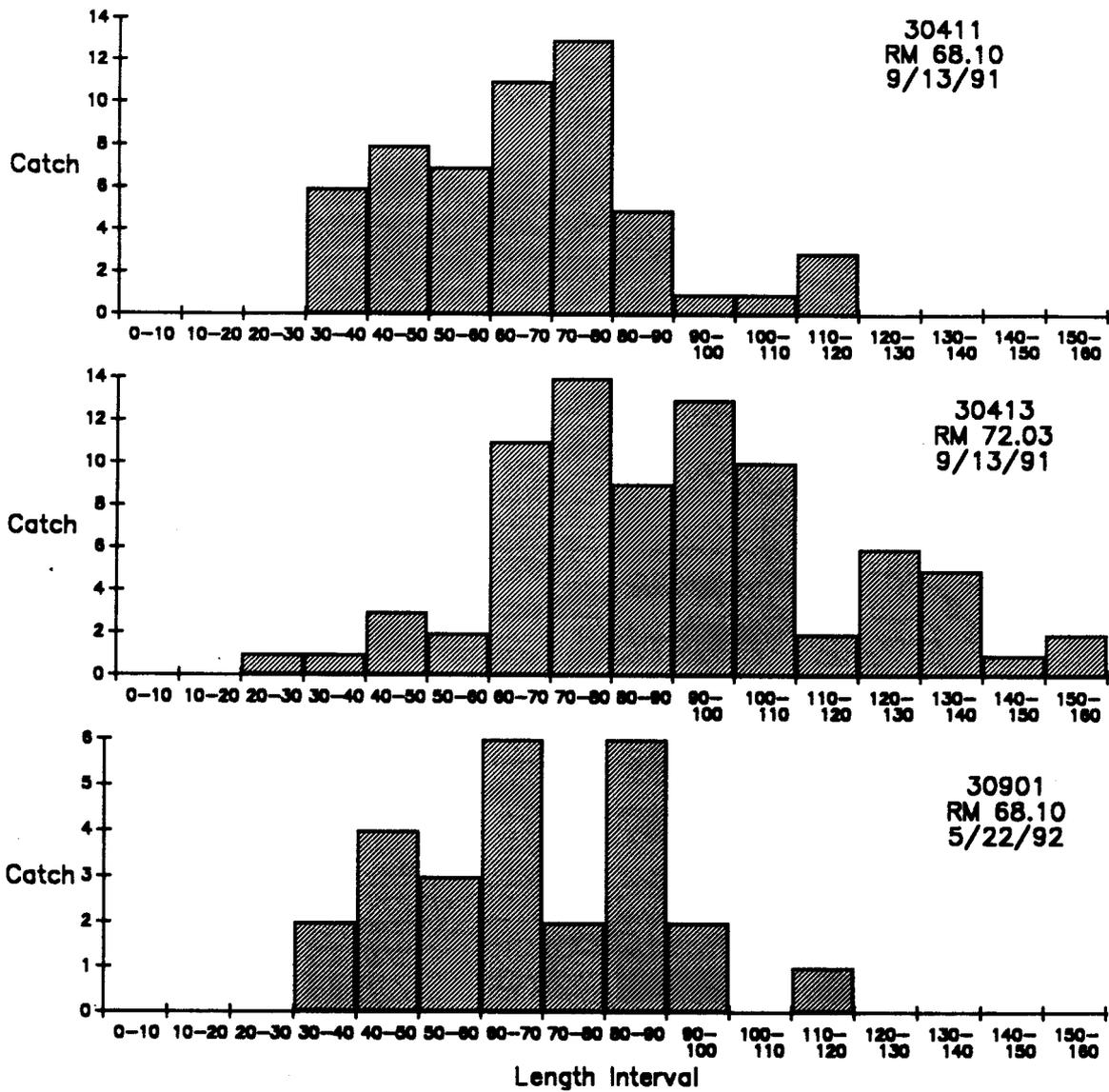


Figure 3.4.5 Length frequency (mm) distributions of humpback chub collected below the Little Colorado River, 9/13/91 and 5/22/92.

TABLE 3.4.1. Trip numbers, type of studies, dates of trips, study numbers, and number of studies, mainstem sampling, March 1991 - November 1992.

Trip Number	Type of Studies ^{1/}	Dates	Study Numbers	Number of Studies
1	B,O	3/28/91- 4/13/91	30101-30172	72
2	B,O	5/08/91- 5/25/91	30201-30204	94
3	A,O	7/07/91- 7/20/91	30301-30324	24
4	A	9/11/91- 9/24/91	30401-30470	70
5	B	11/03/91-11/16/91	30501-30505	5
6	A	1/06/92- 1/18/92	30600-30627	28
7	B	2/19/92- 3/03/92	30701-30705	5
8	A,O	4/13/92- 4/25/92	30801-30842	42
9	B	5/22/92- 6/04/92	30901-30905	5
10	A,O	6/22/92- 7/02/92	31001-31038	38
11	B	8/06/92- 8/17/92	31101-31105	5
12	A,O	9/14/92- 9/25/92	31201-31235	35
13	B,O	10/25/92-11/10/92	31301-31320	20

^{1/} A = Type A

B = Type B

O = Opportunistic

TABLE 3.4.2. DataSonde summary, Trips 1 - 13. Study number, river mile, site code, start time, end time, time interval (Int.), number of data points collected (n), duration of recording (minutes), mean temperature (°C), minimum temperature (°C), maximum temperature (°C), temperature range, and water level range (m). March 1991 - November 1992.

Study	Mile	Site	Start Date	Start Time	End Date	End Time	Int. (min)	n	Min. Covered	Mean Temp °C	Min Temp °C	Max Temp °C	Temp Range °C	Level Range (m)
30104	60.10	2	3/30/91	18:15	3/31/91	18:45	15	99	1,485	9.43	8.0	11.9	3.89	.09
30107	65.50	2	4/02/91	09:35	4/03/91	07:15	20	66	1,320	9.95	9.3	10.3	1.01	.03
30124	165.24	1	3/31/91	11:40	4/02/91	11:15	5	352	1,760	9.46	8.9	10.2	1.21	.23
30161	192.33	1	4/12/91	09:10	4/13/91	07:50	20	69	1,380	11.44	10.6	12.4	1.82	.10
	192.33	2	4/12/91	09:00	4/13/91	08:00	20	70	1,400	11.43	10.5	12.4	1.83	.04
30213	60.71	1	5/09/91	12:25	5/10/91	10:40	15	90	1,350	10.19	9.7	10.9	1.21	3.11
30214	60.85	1	5/09/91	12:25	5/10/91	09:40	15	86	1,290	10.23	9.7	10.9	1.19	2.56
30225	71.12	1	5/13/91	01:50	5/14/91	00:20	15	91	1,365	10.22	9.6	10.6	.97	1.82
30232	122.01	1	5/17/91	07:30	5/18/91	01:45	15	74	1,110	11.63	11.3	11.9	.63	2.51
	122.01	2	5/17/91	02:44	5/17/91	08:59	15	26	390	11.39	11.2	11.7	.43	2.89
30255	173.00	1	5/20/91	10:11	5/21/91	03:26	15	70	1,050	14.42	13.9	16.0	2.11	.65
30269	193.91	1	5/21/91	13:15	5/23/91	12:00	15	153	2,295	15.62	14.5	18.7	4.26	1.47
30270	193.95	1	5/21/91	13:15	5/23/91	04:15	15	157	2,355	15.06	14.3	16.9	2.54	.87
30280	201.06	1	5/23/91	17:45	5/25/91	09:00	15	154	2,310	16.15	13.7	23.2	9.48	.54
	201.06	2	5/23/91	18:45	5/25/91	09:00	15	154	2,310	13.96	12.9	15.3	2.42	.41
30295	87.62	3	5/14/91	07:32	5/15/91	03:47	15	82	1,230	11.86	10.7	14.7	4.01	.46
	87.62	4	5/14/91	08:43	5/14/91	16:43	15	33	495	13.01	11.5	14.4	2.93	.33
30327	143.50	1	7/15/91	16:20	7/17/91	07:35	15	158	2,370	21.34	16.5	28.7	12.19	2.25
	143.50	3	7/15/91	16:20	7/17/91	07:35	15	158	2,370	25.16	22.2	29.8	7.59	.65

(continued)

TABLE 3.4.2. (continued) DataSonde summary, Trips 1 - 13. Study number, river mile, site code, start time, end time, time interval (Int.), number of data points collected (n), duration of recording (minutes), mean temperature (°C), minimum temperature (°C), maximum temperature (°C), temperature range, and water level range (m). March 1991 - November 1992.

Study	Mile	Site	Start Date	Start Time	End Date	End Time	Int. (min)	n	Min. Covered	Mean Temp °C	Min Temp °C	Max Temp °C	Temp Range °C	Level Range (m)
30329	108.60	1	7/12/91	16:30	7/14/91	10:00	15	162	2,430	21.91	19.3	25.7	6.34	.40
	108.60	2	7/12/91	16:30	7/14/91	09:45	15	160	2,400	14.97	11.9	17.9	6.02	1.20
30702	98.04	1	2/22/92	18:30	2/24/92	09:00	30	78	2,340	9.97	6.4	15.8	9.38	.12
	98.04	2	2/22/92	18:30	2/24/92	09:00	30	78	2,340	7.77	3.6	9.6	6.00	.29
30703	108.60	1	2/25/92	15:30	2/27/92	09:00	30	84	2,520	9.94	7.9	13.0	5.11	.45
	108.60	2	2/25/92	15:30	2/27/92	09:00	30	84	2,520	8.40	4.8	9.3	4.46	.51
30704	143.50	1	2/28/92	16:00	3/02/92	07:00	30	127	3,810	11.03	9.2	12.7	3.51	.61
	143.50	2	2/28/92	16:00	3/02/92	06:30	30	126	3,780	9.61	9.4	9.8	.36	.54
30705	201.06	1	3/03/92	11:00	3/05/92	06:00	30	87	2,610	11.02	10.4	11.7	1.27	.54
	201.06	2	3/03/92	11:00	3/05/92	06:00	30	87	2,610	10.49	10.3	10.9	.67	.69
30901	68.10	1	5/22/92	17:10	5/25/92	08:50	20	192	3,840	10.51	10.2	12.0	1.81	.58
	68.10	2	5/22/92	17:30	5/25/92	08:30	20	190	3,800	10.46	10.1	11.0	.81	.46
30902	98.04	1	5/25/92	16:25	5/28/92	08:05	20	192	3,840	21.66	18.1	29.2	11.15	.48
	98.04	2	5/25/92	17:05	5/28/92	08:05	20	190	3,800	12.77	11.7	15.7	3.99	.57
30903	108.60	1	5/28/92	15:00	5/31/92	08:00	20	196	3,920	16.84	14.7	21.2	6.48	.31
	108.60	2	5/28/92	15:00	5/31/92	07:40	20	195	3,900	12.33	11.8	12.9	1.13	.49
30904	143.50	1	5/31/92	19:20	6/03/92	06:20	20	178	3,560	21.79	18.9	29.1	10.24	.09
	143.50	2	5/31/92	19:20	6/03/92	06:40	20	179	3,580	14.00	13.0	15.0	2.02	.55
30905	201.06	1	6/03/92	18:00	6/06/92	05:00	20	178	3,560	17.14	16.2	18.5	2.31	.72
	201.06	2	6/03/92	18:00	6/05/92	16:40	20	141	2,820	16.27	15.6	16.9	1.34	1.69

(continued)

TABLE 3.4.2. (continued) DataSonde summary, Trips 1 - 13. Study number, river mile, site code, start time, end time, time interval (Int.), number of data points collected (n), duration of recording (minutes), mean temperature (°C), minimum temperature (°C), maximum temperature (°C), temperature range, and water level range (m). March 1991 - November 1992.

Study	Mile	Site	Start Date	Start Time	End Date	End Time	Int. (min)	n	Min. Covered	Mean Temp °C	Min Temp °C	Max Temp °C	Temp Range °C	Level Range (m)
31101	68.10	1	8/06/92	18:00	8/08/92	18:40	20	147	2,940	10.93	10.4	11.6	1.19	.70
	68.10	2	8/07/92	17:20	8/08/92	19:20	20	79	1,580	11.04	10.7	11.6	.87	.41
31102	98.04	1	8/09/92	16:20	8/11/92	08:40	20	121	2,420	26.15	23.5	34.7	11.27	.06
	98.04	2	8/09/92	16:20	8/11/92	16:00	20	134	2,680	12.75	12.2	13.3	1.09	1.54
31103	108.60	1	8/11/92	13:20	8/14/92	06:00	20	195	3,900	23.61	20.5	27.0	6.47	.53
	108.60	2	8/11/92	13:00	8/14/92	06:00	20	196	3,920	12.65	12.3	13.2	.81	1.01
31104	143.50	2	8/14/92	17:10	8/17/92	06:10	20	184	3,680	13.40	13.2	13.7	.50	.50
31105	201.06	1	8/17/92	18:20	8/20/92	09:20	20	190	3,800	15.90	14.4	18.9	4.46	1.08
	201.06	2	8/17/92	18:00	8/20/92	08:40	20	189	3,780	14.93	14.3	15.4	1.16	.93
31302	64.60	2	10/25/92	18:20	10/29/92	07:00	20	163	3,260	11.10	10.7	11.7	1.01	.60
31303	64.70	1	10/27/92	10:00	10/29/92	08:20	20	140	2,800	12.97	11.7	14.0	2.26	.31
31310	108.60	1	10/31/92	07:40	11/02/92	07:00	20	142	2,840	12.24	10.8	14.1	3.27	.30
	108.60	2	10/31/92	09:00	11/02/92	07:00	20	138	2,760	11.01	10.4	11.4	1.00	.35
31312	122.01	1	11/02/92	20:30	11/05/92	07:50	20	179	3,580	10.33	9.5	11.4	1.88	.76
	122.01	2	11/02/92	20:30	11/05/92	07:50	20	179	3,580	10.33	9.5	11.4	1.88	.76
31313	143.50	1	11/06/92	08:55	11/09/92	07:35	20	213	4,260	10.69	9.2	12.0	2.83	.60
	143.50	2	11/06/92	09:00	11/09/92	07:40	20	213	4,260	10.00	9.7	10.4	.65	.57

TABLE 3.4.3. Species, number of fish collected, and mean length (mm) collected by Type A, Type B, Opportunistic, and other samples, mainchannel, backwaters, and tributary sites, March 1991 - November 1992.

Type	Species	Mainchannel and Backwaters		Tributaries		Total
		Number of fish	Mean Length	Number of fish	Mean Length	Number of fish
Type A	Bluehead sucker	417	63			417
	Brown trout	3	236			3
	Channel catfish	11	345			11
	Carp	78	404			78
	Fathead minnow	1,734	39			1,734
	Flannelmouth sucker	866	78			866
	Humpback chub	189	75			189
	Plains killifish	26	43			26
	Rainbow trout	116	217			116
	Red shiner	1	38			1
	Speckled dace	1,205	43			1,205
	Striped bass	1	575			1
	Sucker species	357	25			357
	Unidentified	117	34			117
	Subtotal	5,121				5,121
Type B	Bluehead sucker	4	58	77	63	81
	Brown trout	1	97			1
	Channel catfish			1	71	1
	Fathead minnow	342	48	229	43	571
	Flannelmouth sucker	47	66	15	76	62
	Humpback chub	60	71	2	76	62
	Plains killifish			313	43	313
	Rainbow trout	1	220	25	56	26
	Speckled dace	111	46	1,448	47	1,559
	Sucker species	3	23	2	30	5
Unidentified	3	42	9	15	12	
	Subtotal	572		2,121		2,693

(continued)

TABLE 3.4.3 CONTINUED

Type	Species	Mainchannel and Backwaters		Tributaries		Total
		Number of fish	Mean Length	Number of fish	Mean Length	Number of fish
Opportunistic	Black bullhead	1	50			1
	Bluehead sucker	60	56	65	57	125
	Brown trout			5	185	5
	Channel catfish			23	540	23
	Carp	13	444	2	47	15
	Fathead minnow	824	45	73	46	897
	Flannelmouth sucker	105	92	16	100	121
	Humpback chub	68	73	8	107	76
	Plains killifish	29	46	16	34	45
	Rainbow trout	73	183	97	69	170
	Speckled dace	1,036	46	296	64	1,332
	Sucker species	150	24	9	41	159
	Unidentified	65	21	41	18	106
	Subtotal	2,424		651		3,075
Other	Bluehead sucker	3	71			3
	Brook trout			1	123	1
	Brown trout			2	134	2
	Channel catfish			6	474	6
	Carp	2	321			2
	Fathead minnow	32	41	24	46	56
	Flannelmouth sucker	17	54	11	68	28
	Plains killifish	9	47	117	44	126
	Rainbow trout			21	35	21
	Speckled dace	9	29	488	52	497
Sucker species	15	27			15	
	Subtotal	87		670		757
Total		8,204		3,442		11,646

TABLE 3.4.4. Number of minnow trap sets and total number of fish caught by minnow trap at various depths, velocities, and temps, Colorado River mainstem sites and tributary sites, March 1991 - November 1992.

	Colorado River		Tributaries	
	Number of Fish Caught	Number of Trap Sets	Number of Fish Caught	Number of Trap Sets
Current Velocity (m/sec)				
0.00 - 0.24	371	1,576	2,036	2,629
0.25 - 0.49	17	75	158	385
0.50 - 0.74		14	38	77
0.75 - 0.99		1	3	18
1.00 - 1.24			3	2
1.25 - 1.49			2	3
> 1.49				1
Total	388	1,666	2,240	3,115
Depth (m)				
0.00 - 0.24	6	85	147	313
0.25 - 0.49	6	159	87	295
0.50 - 0.74	3	106	72	149
0.75 - 0.99		61	8	59
1.00 - 1.24	4	61		16
1.25 - 1.49	1	46		13
> 1.50	3	56		1
Total	23	574	314	846
Temperature (C)				
< 8.0	3	72	6	64
8.0 - 10.9	45	481	483	601
11.0 - 13.9	301	981	426	1112
14.0 - 16.9	161	290	493	622
17.0 - 19.9	55	141	166	259
20.0 - 22.9	5	13	228	228
> 22.9	1	3	639	379
Total	571	1,981	2,441	3,265

TABLE 3.4.5. Humpback chub length frequencies (mm) by reach and trip, all gear combined.

REACH 30												
Trip:	1	2	3	4	5	8	9	10	11	12	13	Total
Length												
10 -19								4				4
20 -29	1		1	1	1			3			2	9
30 -39				7	1	2	2	3			1	16
40 -49		2		15	6	4	4	2				33
50 -59	4	2		12		2	3		3		1	27
60 -69				23		1	6	1	2		8	41
70 -79				27		6	2			2	6	43
80 -89				14		2	6		2	1	8	33
90 -99	1			14		2	2				2	21
100 -109				11		2			3	1	1	18
110 -119				6			1		2	1	1	11
120 -129				8					3		1	12
130 -139				5							1	6
140 -149				1		1						2
150 -159				2						1	2	5
160 -169										1		1
170 -179												
350 -359		1										1
360 -369												
Total	6	5	1	146	8	22	26	13	15	7	34	283

(CONTINUED)

TABLE 3.4.5 Continued

REACH 40												
Trip:	1	2	3	4	5	8	9	10	11	12	13	Total
Length												
10 -19								1				1
20 -29			1	1						1		3
30 -39	2							1		2	1	6
40 -49	1			1								2
50 -59		1				1				1		3
60 -69			1	1				1	1	1		4
70 -79			2					2				4
80 -89				1							1	2
90 -99												
100 -109												
110 -119												
120 -129				1								1
130 -139												
140 -149		2										2
150 -159												
160 -169								1				1
170 -179												
350 -359												
360 -369												
Total	3	3	4	5		1		6		5	2	29

(CONTINUED)

TABLE 3.4.5 Continued

	SHINUMO			KANAB	HAVASU		REACH 50			Total
Trip:	3	4	11	13	10	2	4	11	12	
Length										
10 -19										
20 -29									2	2
30 -39				1			1			2
40 -49	1							1		2
50 -59										
60 -69		1				1				2
70 -79	2		2							4
80 -89		1								1
90 -99										
100 -109										
110 -119										
120 -129										
130 -139										
140 -149										
150 -159										
160 -169										
170 -179										
350 -359										
360 -369					1					1
Total	3	2	2	1	1	1	1	1	2	14

Trip Numbers and Dates:

Trip	Dates
1	3/28/91- 4/13/91
2	5/08/91- 5/25/91
3	7/07/91- 7/20/91
4	9/11/91- 9/24/91
5	11/03/91-11/16/91
6	1/06/92- 1/18/92
7	2/19/92- 3/03/92
8	4/13/92- 4/25/92
9	5/22/92- 6/04/92
10	6/22/92- 7/02/92
11	8/06/92- 8/17/92
12	9/14/92- 9/25/92
13	10/25/92-11/10/92

TABLE 3.4.6. Mean, minimum, maximum, standard deviation, and number measured (Valid n), humpback chub, mainstem and tributaries, March 1991 - November 1992.

TRIP	Reach 30	Reach 40	Shirumo	Kanab	Haveau	Reach 50
(01):03/28/91-04/13/91:						
Mean	57	39
Minimum	28	37
Maximum	94	41
Standard Deviation	21	2
Valid N	6	3
(02):05/08/91-05/24/91:						
Mean	110	115	.	.	.	62
Minimum	44	58	.	.	.	62
Maximum	350	147	.	.	.	62
Standard Deviation	134	49
Valid N	5	3	.	.	.	1
(03):07/07/91-07/20/91:						
Mean	25	59	67	.	.	.
Minimum	25	22	49	.	.	.
Maximum	25	74	79	.	.	.
Standard Deviation	.	25	16	.	.	.
Valid N	1	4	3	.	.	.
(04):09/11/91-09/24/91:						
Mean	79	70	74	.	.	36
Minimum	29	27	63	.	.	36
Maximum	155	127	85	.	.	36
Standard Deviation	28	38	16	.	.	.
Valid N	146	5	2	.	.	1
(05):11/03/91-11/16/91:						
Mean	40
Minimum	26
Maximum	46
Standard Deviation	8
Valid N	8
(08):04/13/92-04/25/92:						
Mean	71	55
Minimum	33	55
Maximum	142	55
Standard Deviation	27
Valid N	22	1
(09):05/22/92-06/04/92:						
Mean	68
Minimum	35
Maximum	111
Standard Deviation	20
Valid N	26
(10):06/22/92-07/02/92:						
Mean	30	72	.	.	365	.
Minimum	16	18	.	.	365	.
Maximum	63	163	.	.	365	.
Standard Deviation	13	50
Valid N	13	6	.	.	1	.
(11):08/06/92-08/17/92:						
Mean	92	.	76	.	.	47
Minimum	50	.	76	.	.	47
Maximum	128	.	76	.	.	47
Standard Deviation	28
Valid N	15	.	2	.	.	1
(12):09/14/92-09/25/92:						
Mean	110	43	.	.	.	25
Minimum	73	28	.	.	.	24
Maximum	162	62	.	.	.	26
Standard Deviation	36	14	.	.	.	1
Valid N	7	5	.	.	.	2
(13):10/25/92-11/10/92:						
Mean	81	61	.	34	.	.
Minimum	28	34	.	34	.	.
Maximum	157	87	.	34	.	.
Standard Deviation	29	37
Valid N	34	2	.	1	.	.

APPENDIX 3.1.

Appendix 3.1 is a catalogue of samples collected, March 1991 - November 1992. Table values should indicate number of each type of sample collected. Column headings are abbreviated as:

Rch	Reach code (Maddux et al. 1987).
Flo Cod	Flow code estimated on the river: SH = steady high SL = steady low DC = descending AC = ascending
Flow CFS	Estimated flow in cfs
Typ A	Type A studies
Typ B	Type B studies
Ang lng	Angling effort
Opp	Opportunistic studies
Son de	DataSonde deployments
Ben ths	Benthos samples
Sed	Sediment core samples
Chl	Chlorophyll samples
Pkn	Plankton samples
Tot Map	ETM total station maps
Pla Map	Plane table maps
Vis cer	Viscera collections
Drift	Drift samples
A -2nd-	Modified Type A studies
Fsh Coll	Fish collections

APPENDIX 3.1

Trip Study	Sites	Date--Time	Mile	Flo Rch	Flow Cod	Typ A	Typ B	Ang lng	Son Opp	Ben de	Sed	Chl	Pkn	Tot Map	Pla Map	Vis cer	Dri ft	-A- 2nd	Fsh Coll
1 30101	3	03/28/91 15:43	45.00	L	20	0	0	0	0	3	0	0	0	0	0	0	0	0	0
30102	3	03/28/91 16:53	47.00	R	20	0	0	0	0	3	0	0	0	0	0	0	0	0	0
30103	4	03/29/91 11:56	51.50	L	20	0	0	0	0	4	0	0	0	0	0	0	0	0	0
30104	21	03/31/91 09:43	60.10	R	20	0	0	1	0	0	0	0	0	0	0	0	0	0	0
30107	16	04/02/91 08:15	65.50	L	30	0	0	1	0	0	0	0	0	0	0	0	0	0	0
30106	3	04/02/91 10:55	64.56	R	30	0	0	0	0	3	0	0	0	0	0	0	0	0	0
30105	2	04/02/91 11:25	63.45	L	30	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30108	2	04/02/91 15:05	66.80	L	30	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30109	3	04/02/91 15:40	67.90	L	30	0	0	0	0	3	0	0	0	0	0	0	0	0	1
30110	3	04/02/91 16:20	68.10	L	30	0	0	0	0	3	0	0	0	0	0	0	0	0	2
30112	2	04/04/91 11:08	86.98	R	30	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30114	4	04/04/91 14:34	88.52	L	40	0	0	0	0	4	0	0	0	4	0	0	0	0	1
30115	5	04/06/91 09:22	110.80	R	40	0	0	0	0	5	0	5	5	0	0	0	0	0	0
30116	2	04/06/91 12:10	115.40	L	40	0	0	0	0	2	0	0	0	0	0	0	0	0	0
30117	3	04/06/91 14:38	122.01	R	40	0	0	0	0	3	0	0	0	0	0	0	0	0	1
30118	3	04/06/91 15:05	122.55	L	40	0	0	0	0	3	0	0	0	0	0	0	0	0	1
30119	1	04/08/91 14:33	147.80	L	40	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30120	1	04/09/91 10:11	164.90	R	40	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30124	29	04/09/91 13:50	165.24	R	40	0	0	2	0	0	0	0	0	0	0	0	0	0	1
30122	4	04/09/91 15:00	165.00	L	40	0	0	0	0	4	0	4	4	0	4	0	0	0	1
30125	1	04/09/91 16:30	166.40	R	40	0	0	0	0	1	0	0	0	0	0	0	0	0	2
30134	1	04/09/91 17:00	167.00	L	50	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30123	2	04/10/91 08:35	165.24	R	40	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30121	1	04/10/91 09:25	165.00	L	40	0	0	0	0	1	0	0	0	0	0	0	0	0	1
30129	4	04/10/91 10:42	165.88	R	40	0	0	0	0	4	0	4	4	0	4	0	0	0	1
30127	1	04/10/91 16:20	165.49	R	40	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30128	1	04/10/91 16:30	165.67	R	40	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30130	1	04/10/91 16:40	166.00	R	40	0	0	0	0	1	0	0	0	0	0	0	0	0	1
30131	1	04/10/91 17:00	166.20	R	40	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30132	1	04/10/91 17:05	166.40	R	40	0	0	0	0	1	0	0	0	0	0	0	0	0	1
30126	1	04/10/91 17:40	165.41	R	40	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30133	2	04/11/91 08:45	166.85	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	0
30135	2	04/11/91 09:30	167.21	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30136	2	04/11/91 09:45	167.53	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	2
30137	2	04/11/91 09:55	167.58	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30138	2	04/11/91 10:17	168.15	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30139	1	04/11/91 10:30	170.30	R	50	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30140	2	04/11/91 10:40	170.57	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30141	2	04/11/91 10:55	171.56	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30142	2	04/11/91 11:30	172.80	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30143	1	04/11/91 11:52	173.50	R	50	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30144	2	04/11/91 12:10	174.10	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	0
30145	2	04/11/91 12:10	175.20	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30147	2	04/11/91 13:10	177.43	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30146	2	04/11/91 13:22	176.52	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	3
30148	2	04/11/91 15:10	183.80	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30149	2	04/11/91 15:20	184.04	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30151	2	04/11/91 15:30	186.00	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30150	2	04/11/91 15:39	185.55	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	0
30152	2	04/11/91 16:00	187.43	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30153	1	04/11/91 16:45	189.54	R	50	0	0	0	0	1	0	0	0	0	0	0	0	0	1
30154	1	04/12/91 08:55	191.20	R	50	0	0	0	0	1	0	0	0	0	0	0	0	0	0
30161	16	04/12/91 08:55	192.33	R	50	0	0	1	0	0	1	3	3	0	3	0	0	0	3
30155	2	04/12/91 09:30	191.60	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	0
30156	2	04/12/91 09:45	191.80	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30157	2	04/12/91 10:05	192.00	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30158	2	04/12/91 10:40	192.10	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30159	2	04/12/91 11:15	192.20	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	0
30160	1	04/12/91 11:35	192.50	L	50	0	0	0	0	1	0	0	0	0	0	0	0	0	1
30162	4	04/12/91 13:50	193.91	L	50	0	0	0	0	4	0	3	4	0	4	0	0	0	1
30163	2	04/12/91 15:05	193.85	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	2
30164	1	04/12/91 16:00	194.50	L	50	0	0	0	0	1	0	0	0	0	0	0	0	0	1
30165	2	04/13/91 08:50	196.00	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1
30166	2	04/13/91 09:20	196.60	L	50	0	0	0	0	2	0	0	0	0	0	0	0	0	5
30167	1	04/13/91 11:03	209.00	R	50	0	0	0	0	1	0	0	0	0	0	0	0	0	2
30168	2	04/13/91 11:40	209.50	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	0
30169	2	04/13/91 11:55	212.60	R	50	0	0	0	0	2	0	0	0	0	0	0	0	0	1

APPENDIX 3.1

Trip Study	Sites	Date--Time	Mile	Rch	Flo Cod	Flow CFS	Typ A	Typ B	Ang lng	Son Opp	Ben ths	Sed	Chl	Pkn	Tot Map	Pla Map	Vis cer	Dri ft	-A- 2nd	Fsh Coll
30261	2	05/21/91 11:50	177.50	R	50 SL	5000	0	0	0	2	0	0	0	0	0	0	0	0	0	0
30262	2	05/21/91 13:35	180.00	R	50 SL	5000	0	0	0	2	0	0	0	0	0	0	0	0	0	0
30263	2	05/21/91 14:17	182.52	R	50 SL	5000	0	0	0	2	0	0	0	0	0	0	0	0	0	0
30264	2	05/21/91 14:50	182.83	R	50 SL	5000	0	0	0	2	0	0	0	0	0	0	0	0	0	0
30267	2	05/21/91 15:45	189.00	L	50 SL	5000	0	0	0	2	0	0	0	0	0	0	0	0	0	0
30272	2	05/21/91 16:21	194.02	L	50 SL	5000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30269	23	05/22/91 08:20	193.91	L	50 SH	15000	0	1	0	1	1	3	3	0	3	1	0	0	0	4
30270	20	05/22/91 09:37	193.95	R	50 SH	15000	0	1	0	1	1	3	3	0	3	1	0	0	0	2
30268	2	05/22/91 14:42	192.00	R	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30266	2	05/22/91 15:40	188.73	L	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30265	2	05/22/91 16:06	188.40	R	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30271	2	05/23/91 11:17	193.85	R	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	4
30281	1	05/23/91 12:00	202.30		50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	2
30274	2	05/23/91 13:55	195.57	R	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	0
30273	3	05/23/91 14:00	196.50	R	50 SH	15000	0	0	0	3	0	3	3	0	3	0	0	0	0	3
30275	1	05/23/91 14:11	195.70	R	50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	0
30277	1	05/23/91 14:32	198.10	R	50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30276	1	05/23/91 14:49	198.00	R	50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30278	1	05/23/91 15:17	199.40	R	50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30279	1	05/23/91 15:32	200.20	R	50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	2
30282	1	05/23/91 15:57	202.40	R	50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	3
30280	38	05/23/91 17:00	201.06	R	50 SH	15000	0	2	0	0	2	2	2	0	2	1	0	0	0	3
30283	2	05/24/91 09:50	202.90	R	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	2
30284	2	05/24/91 10:13	203.00	L	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	2
30285	3	05/24/91 10:46	204.00	R	50 SH	15000	0	0	0	3	0	0	0	0	0	0	0	0	0	2
30286	2	05/24/91 11:17	204.30	L	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30287	2	05/24/91 12:09	204.50	L	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30288	2	05/24/91 12:32	204.70	R	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30289	2	05/25/91 10:05	207.80	L	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30290	2	05/25/91 10:55	210.80	L	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	0
30292	1	05/25/91 11:11	213.50	L	50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	2
30291	2	05/25/91 11:15	211.40	R	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30293	1	05/25/91 13:00	216.60	R	50 SH	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30294	2	05/25/91 14:15	219.40	R	50 SH	15000	0	0	0	2	0	0	0	0	0	0	0	0	0	2
Sum	436						0	15	0	188	9	42	42	0	41	8	0	0	0	78
3 30336	1	07/06/91 19:30	18.00	L	30	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30301	2	07/07/91 10:09	26.03	L	20 SL	10000	1	0	0	0	0	1	1	0	1	0	1	0	0	1
30302	2	07/07/91 10:30	26.03	L	20 SL	10000	1	0	0	0	0	2	2	0	2	0	1	0	0	1
30303	2	07/08/91 08:15	39.24	R	20 SL	10000	1	0	0	0	0	2	2	0	2	0	2	0	0	0
30304	2	07/08/91 10:01	41.50	R	20 SL	10000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30305	2	07/08/91 13:29	44.00	L	20 SL	10000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30306	2	07/08/91 13:29	44.00	L	20 SL	10000	1	0	0	0	0	1	1	0	1	0	2	0	0	1
30307	2	07/09/91 08:48	51.14	L	20 DC	22000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30308	2	07/09/91 11:30	55.00	L	20 DC	20000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30309	2	07/09/91 14:00	55.00	R	20 DC	15000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30338	1	07/09/91 17:15	61.50	L	22	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
30337	1	07/10/91 09:20	61.50	L	22	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
30328	1	07/10/91 11:45	64.30	L	20	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
30310	2	07/10/91 12:20	66.70	R	30 DC	20000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30311	2	07/10/91 14:30	68.50	L	30 DC	15000	1	0	0	0	0	1	1	0	2	0	2	0	0	1
30325	1	07/11/91 19:00	71.12	L	30	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30331	1	07/12/91 19:00	108.60	R	42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30335	2	07/13/91 00:00	108.60	R	42	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1
30332	1	07/13/91 08:05	108.60	R	42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30334	1	07/13/91 17:00	108.60	R	42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30330	1	07/13/91 18:00	108.60	R	42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30333	1	07/13/91 19:00	108.60	R	42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30329	1	07/14/91 08:00	108.60	R	42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
30312	2	07/14/91 14:42	118.50	R	40 SL	5000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30313	2	07/14/91 16:30	119.40	R	40 SL	5000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30314	2	07/15/91 08:38	120.30	R	40 SL	5000	1	0	0	0	0	2	2	0	2	0	2	0	0	1
30327	4	07/16/91 08:55	143.50	R	45	0	0	0	0	4	0	0	0	0	0	0	0	0	0	2
30326	1	07/16/91 15:00	156.93	L	46 AC	10000	0	0	0	1	0	0	0	0	0	0	0	0	0	0
30315	2	07/18/91 08:26	167.53	R	50 SL	10000	1	0	0	0	0	2	2	0	2	0	2	0	0	1

APPENDIX 3.1

Trip Study	Sites	Date--Time	Mile	Flo Rch	Flow Cod	Typ CFS	Typ A	Ang B	Opp Lng	Son de	Ben ths	Sed	Chl	Pkn	Tot Map	Pla Map	Vis cer	Dri ft	-A- 2nd	Fsh Coll
30316	2	07/18/91 09:30	169.00	R	50 SL	10000	1	0	0	0	2	2	0	2	0	1	0	0	1	2
30317	2	07/18/91 11:40	176.08	L	50 SL	10000	1	0	0	0	2	2	0	2	0	1	0	0	1	0
30318	2	07/18/91 14:43	179.00	L	50 SL	10000	1	0	0	0	2	2	0	2	0	2	0	0	1	0
30319	2	07/19/91 08:32	186.00	L	50 DC	11000	1	0	0	0	2	2	0	2	0	1	0	0	1	1
30320	2	07/19/91 10:40	193.85	R	50 SL	10000	1	0	0	0	2	2	0	2	0	0	0	0	1	2
30321	2	07/19/91 11:40	193.95	R	50 SL	10000	1	0	0	0	2	2	0	2	0	2	0	0	1	3
30322	2	07/20/91 07:45	193.91	L	50 DC	22000	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30323	2	07/20/91 11:30	196.50	R	50 DC	18000	1	0	0	0	2	2	0	2	0	2	0	0	1	2
30324	2	07/20/91 13:51	201.06	R	50 DC	18000	1	0	0	0	2	2	0	2	0	2	0	0	1	1
Sum	66						24	0	0	18	0	45	45	0	46	0	41	0	24	43
4 30401	2	09/11/91 08:25	33.27	L	20 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	0
30402	2	09/11/91 10:40	37.32	R	20 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30403	2	09/11/91 13:50	41.13	R	20 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30404	3	09/11/91 16:00	44.27	L	20 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30405	3	09/12/91 08:30	54.80	R	20 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30406	3	09/12/91 10:25	55.50	R	20 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	2
30407	2	09/12/91 13:00	55.60	R	20 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30408	1	09/12/91 18:33	61.50	L	22	0	0	0	1	0	0	0	0	0	0	0	6	0	0	1
30409	1	09/13/91 09:12	64.30	R	30 DC	0	0	0	0	1	0	0	0	0	0	0	2	0	1	1
30410	1	09/13/91 09:38	64.80	R	30 DC	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
30411	2	09/13/91 10:25	68.10	L	30 DC	0	1	0	0	0	2	2	0	2	0	2	3	0	1	5
30412	1	09/13/91 13:09	70.19	L	30 DC	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
30413	2	09/13/91 14:27	72.03	R	30 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	5
30414	1	09/14/91 13:03	92.62	R	30 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30415	1	09/14/91 14:30	98.04	R	41 DC	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2
30416	1	09/14/91 17:00	108.50	R	42 DC	17000	0	0	0	1	0	0	0	0	0	0	0	0	1	2
30417	2	09/15/91 10:36	117.40	R	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30418	2	09/15/91 11:50	118.10	R	40 AC	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
30419	2	09/15/91 13:00	119.13	R	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30420	2	09/15/91 14:33	120.30	L	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30421	2	09/16/91 07:56	122.01	R	40 SL	10000	1	0	0	0	2	2	0	2	0	2	0	0	0	2
30422	3	09/16/91 09:51	122.55	L	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30423	2	09/16/91 11:10	123.42	R	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30424	2	09/16/91 12:10	124.20	R	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30425	3	09/16/91 13:40	125.61	R	40 AC	15000	1	0	0	0	2	2	0	2	0	1	0	0	0	1
30426	2	09/16/91 14:27	127.00	R	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30427	1	09/17/91 08:40	133.70	R	43	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30428	1	09/17/91 10:40	136.30	R	44	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
30429	2	09/17/91 11:37	137.30	R	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30430	2	09/17/91 14:36	145.00	L	40 AC	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
30431	2	09/17/91 14:55	145.60	L	40 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30432	2	09/18/91 10:40	160.70	L	40 SL	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
30433	2	09/18/91 11:35	164.70	L	40 SL	0	1	0	0	0	2	2	0	2	0	2	0	0	0	0
30434	2	09/18/91 13:20	166.85	L	50 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30435	2	09/18/91 14:10	166.86	R	50 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30436	2	09/18/91 15:40	167.40	R	50 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30437	3	09/19/91 09:14	170.30	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30438	2	09/19/91 12:36	172.39	L	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30439	3	09/19/91 13:24	173.63	L	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30440	3	09/19/91 14:20	174.10	L	50 DC	0	1	0	0	0	2	2	0	2	0	4	0	0	0	1
30441	2	09/19/91 15:29	174.90	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30442	2	09/19/91 17:00	177.90	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30443	1	09/20/91 10:00	181.18	L	50 DC	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
30444	2	09/20/91 10:35	181.51	L	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30445	2	09/20/91 13:05	182.37	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	1	0	0	2
30446	2	09/20/91 14:07	182.52	R	50 SL	0	1	0	0	0	2	2	0	2	0	2	0	0	0	0
30447	3	09/20/91 14:57	182.82	L	50 SL	0	1	0	0	0	2	2	0	2	0	2	2	0	0	1
30448	1	09/20/91 14:57	182.83	L	50 SL	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
30449	2	09/20/91 16:30	182.83	R	50 SL	0	1	0	0	0	2	2	0	2	0	2	0	0	0	1
30450	2	09/21/91 09:00	185.55	L	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30451	2	09/21/91 10:10	187.12	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	3
30452	2	09/21/91 13:15	189.04	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	3
30453	2	09/21/91 14:45	190.25	L	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1	1
30454	2	09/21/91 16:30	191.95	L	50 SL	0	1	0	0	0	2	2	0	2	0	2	3	0	1	1

APPENDIX 3.1

Trip Study	Sites	Date--Time	Mile	Flo Rch	Flow Cod	Typ CFS	Typ A	Ang B	Son Opp	Ben de	Sed ths	Chl	Pkn	Tot Map	Pla Map	Vis cer	Dri ft	-A- 2nd	Fsh Coll			
30455	1	09/21/91 18:17	191.76	L	50 SL	0	0	0	0	0	0	0	0	0	0	3	0	0	0			
30456	2	09/22/91 08:31	193.91	L	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	1	1			
30457	2	09/22/91 09:40	193.95	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	1	2			
30458	2	09/22/91 11:14	193.85	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	1	2			
30459	2	09/22/91 13:50	195.37	L	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	1	1			
30460	2	09/22/91 14:50	195.57	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	1	1			
30461	2	09/23/91 08:27	199.58	R	50 SH	16000	0	0	0	1	0	0	0	0	0	0	0	2	1			
30462	2	09/23/91 09:07	201.06	R	50 DC	0	1	0	0	0	2	2	0	2	0	2	0	0	1			
30463	2	09/23/91 11:00	204.30	L	50 DC	15000	1	0	0	0	2	2	0	2	0	2	0	1	1			
30464	2	09/23/91 11:57	208.40	L	50 DC	12000	1	0	0	0	2	2	0	2	0	2	0	1	1			
30465	2	09/23/91 15:25	212.73	R	50 DC	10000	1	0	0	0	2	2	0	2	0	2	0	1	1			
30466	2	09/24/91 08:10	214.13	R	50 SL	8000	1	0	0	0	2	2	0	2	0	2	0	1	1			
30467	2	09/24/91 10:13	215.50	L	50 AC	8000	1	0	0	0	2	2	0	2	0	2	0	0	1			
30468	2	09/24/91 11:22	216.15	L	50 AC	10000	1	0	0	0	2	2	0	2	0	2	0	0	1			
30469	2	09/24/91 13:00	218.10	L	50 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	1			
30470	2	09/24/91 14:10	218.95	L	50 AC	0	1	0	0	0	2	2	0	2	0	2	0	0	1			
Sum	137							55	0	1	13	0	110	110	0	110	0	111	20	0	39	83
5	30501	440	11/03/91 15:05	64.60	R	30	0	0	1	0	0	10	10	0	10	1	0	0	0	1		
	30502	236	11/07/91 10:45	84.03	R	31	0	0	1	0	0	3	3	0	8	1	0	0	0	0		
	30503	410	11/09/91 18:00	108.60	R	42	0	0	1	0	0	6	10	0	10	1	0	0	0	6		
	30504	408	11/13/91 16:00	143.50	R	45	0	0	1	0	0	10	10	0	10	1	0	0	0	3		
	30505	419	11/16/91 16:30	193.95	R	50	0	0	1	0	0	10	10	0	10	1	0	0	0	1		
Sum	1913							0	5	0	0	0	39	43	0	48	5	0	0	0	0	11
6	30600	1	01/06/92 12:00	31.65	R	20 DC	10000	0	0	0	0	0	0	0	0	0	0	0	0	0		
	30601	3	01/07/92 10:00	52.20	R	21 DC	10000	0	0	0	0	0	0	0	0	0	0	0	0	0		
	30602	2	01/07/92 14:41	54.60	R	20 SL	8000	0	0	0	0	4	0	2	0	0	0	0	1	0		
	30603	2	01/08/92 12:14	68.10	L	30 SH	13000	0	0	0	0	4	0	2	0	0	0	0	1	1		
	30604	2	01/08/92 14:35	71.12	L	30 SH	13000	0	0	0	0	0	0	0	0	0	0	0	1	0		
	30605	2	01/09/92 10:50	72.03	R	30 SH	10000	0	0	0	0	4	0	2	0	0	0	0	1	1		
	30608	0	01/09/92 13:30	84.03	R	31	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
	30606	3	01/10/92 13:00	87.62	R	32 SH	11000	0	0	0	0	0	0	0	0	0	0	0	0	0		
	30607	5	01/11/92 10:10	88.95	L	401 AC	10000	0	0	0	0	0	0	0	0	0	0	0	0	1		
	30609	3	01/11/92 14:11	95.00	L	40 SH	10000	0	0	0	0	0	0	0	0	0	0	0	0	1		
	30610	3	01/12/92 09:30	108.60	R	42 AC	10000	0	0	0	0	0	0	0	0	0	0	0	0	1		
	30611	3	01/12/92 13:45	116.50	L	402 SH	12000	0	0	0	0	0	0	0	0	0	0	0	0	0		
	30612	3	01/13/92 10:55	131.80	R	403 DC	8000	0	0	0	0	0	0	0	0	0	0	0	0	0		
	30613	2	01/13/92 13:26	133.83	R	43 SL	7500	0	0	0	0	0	0	0	0	0	0	0	0	1		
	30614	4	01/14/92 09:40	136.25	R	44 DC	8000	0	0	0	0	0	0	0	0	0	0	0	0	1		
	30615	2	01/14/92 14:16	143.50	R	45 AC	10000	0	0	0	0	0	0	0	0	0	0	0	0	0		
	30616	3	01/15/92 10:00	147.80	L	40 DC	12000	0	0	0	0	0	0	0	0	0	0	0	0	1		
	30617	2	01/15/92 13:15	153.17	L	40 AC	13000	0	0	0	0	2	4	0	2	0	2	0	1	1		
	30618	2	01/16/92 10:30	166.62	L	50 AC	10000	0	0	0	0	2	4	0	2	0	2	0	1	0		
	30619	2	01/16/92 11:30	167.21	R	50 AC	11000	0	0	0	0	2	4	0	2	0	2	0	1	1		
	30620	2	01/16/92 13:15	168.71	R	50 DC	10000	0	0	0	0	2	4	0	2	0	2	0	1	1		
	30621	3	01/17/92 10:00	182.63	L	50 AC	11000	0	0	0	0	2	6	0	3	0	2	0	2	1		
	30622	2	01/17/92 11:35	187.53	R	50 DC	10000	0	0	0	0	2	4	0	2	0	2	0	1	2		
	30623	2	01/17/92 13:30	191.41	L	50 DC	10000	0	0	0	0	2	4	0	2	0	2	0	1	2		
	30624	2	01/17/92 14:35	192.40	R	50 DC	9000	0	0	0	0	2	4	0	2	0	2	0	1	1		
	30625	2	01/18/92 09:40	204.30	L	50 SH	15000	0	0	0	0	2	4	0	2	0	2	0	1	1		
	30626	1	01/18/92 11:00	207.70	R	50 SH	15000	0	0	0	0	1	2	0	1	0	2	0	0	1		
	30627	1	01/18/92 13:00	211.53	L	50 DC	15000	0	0	0	0	2	4	0	2	0	2	0	1	0		
Sum	64							0	0	0	0	0	33	44	6	22	0	22	0	0	15	20

APPENDIX 3.1

Trip Study	Sites	Date--Time	Mile	Flo Rch	Cod	Flow CFS	Typ A	Typ B	Ang lng	Son Opp	Ben de	Sed ths	Chl	Pkn	Tot Map	Pla Map	Vis cer	Dri ft	-A- 2nd	Fsh Coll	
7	30701	328 02/19/92 15:00	68.10	L	30 DC	10000	0	0	0	0	0	10	10	0	10	0	0	0	0	0	0
	30702	419 02/22/92 17:30	98.04	R	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	30703	321 02/25/92 16:00	108.60	R	42	0	0	0	0	0	0	5	3	0	0	0	0	0	0	0	0
	30704	371 02/28/92 15:00	143.50	R	45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	30705	138 03/03/92 18:00	201.06	R	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sum		1577					0	0	0	0	0	15	13	0	10	0	0	0	0	0	0
8	30801	2 04/13/92 10:05	38.95	L	20 SL	8000	1	0	0	0	0	2	2	1	2	0	2	0	0	1	1
	30802	2 04/13/92 13:55	39.88	L	20 SL	8000	1	0	0	0	0	2	2	1	2	0	2	0	0	1	1
	30803	9 04/14/92 08:00	52.20	R	21 SL	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
	30804	2 04/14/92 10:48	54.40	R	20 SH	10000	1	0	0	0	0	2	2	1	2	0	2	0	0	1	1
	30805	2 04/14/92 12:29	55.50	R	20 SH	10000	1	0	0	0	0	2	2	1	2	0	2	0	0	1	1
	30800	1 04/14/92 18:20	61.50	L	22 DC	2000	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1
	30806	2 04/15/92 08:57	64.50	L	30 AC	10000	1	0	0	0	0	2	2	1	2	0	2	0	0	1	6
	30807	2 04/15/92 11:06	68.10	L	30 AC	10000	1	0	0	0	0	2	2	1	2	0	2	0	0	1	2
	30808	1 04/15/92 14:05	72.25	L	30 AC	10000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
	30809	1 04/15/92 15:25	76.65	L	30 DC	10000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
	30810	8 04/16/92 10:05	84.03	R	31 SH	12	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
	30811	1 04/16/92 13:36	87.62	R	32 SH	20000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	30812	5 04/17/92 14:25	98.04	R	41 SH	12000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	30813	3 04/18/92 08:30	108.60	L	42	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	30814	2 04/18/92 13:00	122.01	R	40 AC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30815	2 04/18/92 16:50	133.83	R	43 SH	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	30816	2 04/19/92 08:30	136.25	R	44 SL	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	30817	2 04/19/92 11:15	138.50	L	40 SL	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30818	2 04/20/92 08:30	161.50	R	40 DC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30819	2 04/20/92 12:00	163.86	L	40 DC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30820	2 04/20/92 12:00	166.85	L	50 SL	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30821	2 04/20/92 12:00	166.85	L	50 SL	0	1	0	0	0	0	1	1	0	2	0	2	0	0	1	1
	30822	2 04/20/92 13:00	167.20	R	50 SL	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30823	2 04/20/92 14:50	168.70	R	50 SL	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30824	2 04/20/92 16:37	172.70	L	50 SL	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30825	2 04/21/92 09:45	181.30	L	50 AC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30826	2 04/21/92 11:15	182.83	R	50 AC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30827	2 04/21/92 12:45	183.20	L	50 AC	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
	30828	2 04/21/92 14:00	187.20	R	50 AC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30829	2 04/22/92 09:00	189.40	R	50 SH	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30830	2 04/22/92 09:00	189.40	R	50 SH	0	1	0	0	0	0	1	1	0	1	0	2	0	0	1	1
	30831	2 04/22/92 13:30	191.55	R	50 DC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30832	2 04/22/92 14:45	192.00	L	50 DC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30833	2 04/22/92 15:40	192.45	R	50 DC	0	1	0	0	0	0	2	2	0	2	0	2	0	0	1	1
	30834	2 04/23/92 08:45	196.75	R	50 SH	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	30835	2 04/23/92 10:00	200.48	L	50 SH	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
	30836	2 04/23/92 11:20	201.06	R	50 SH	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
	30837	2 04/23/92 14:00	202.75	L	50 SH	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
	30838	2 04/23/92 16:15	204.12	R	50 SH	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
	30839	2 04/23/92 17:10	204.11	R	50 SH	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
	30840	2 04/24/92 08:45	207.40	L	50 SH	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
	30841	2 04/24/92 10:30	210.80	L	50 SH	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
	30842	2 04/25/92 10:00	225.00	R	50 AC	0	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
Sum		99					32	0	1	11	0	62	62	6	63	0	55	0	0	32	46
9	30901	405 05/22/92 15:00	68.10	L	30 DC	10000	0	18	0	0	2	7	7	0	7	0	0	17	0	0	2
	30902	399 05/25/92 16:41	98.04	R	41 SL	8000	0	18	0	0	2	3	3	0	0	2	0	8	0	0	4
	30903	385 05/28/92 14:30	108.60	R	42 AC	10000	0	17	0	0	2	2	2	0	1	0	0	2	0	0	12
	30904	349 05/31/92 16:00	143.50	R	45 SL	7000	0	16	0	0	2	6	6	0	1	0	0	1	0	0	11
	30905	204 06/04/92 18:00	201.06	R	50 AC	7000	0	9	0	0	2	6	6	0	0	1	0	4	0	0	1
Sum		1742					0	78	0	0	10	24	24	0	7	5	0	0	32	0	30

APPENDIX 3.1

Trip Study	Sites	Date--Time	Mile	Flo Rch Cod	Flow CFS	Typ A	Typ B	Ang lng	Opp	Son de	Ben ths	Sed	Chl	Pkn	Tot Map	Pla Map	Vis cer	Dri ft	-A- 2nd	Fsh Coll
10 31001	1	06/22/92 12:00	29.02	R 20 SL	6000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
31002	2	06/22/92 13:13	30.40	R 20 AC	6000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
31003	2	06/22/92 15:36	32.90	L 20 AC	7000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	11
31004	1	06/22/92 15:36	32.90	L 20 AC	7000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6
31005	2	06/23/92 10:53	44.27	L 20 DC	10000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	9
31006	2	06/23/92 14:36	54.60	R 20 DC	9000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	9
31007	2	06/24/92 09:15	64.50	L 30 AC	12000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	65
31008	2	06/24/92 12:22	68.10	L 30 AC	17000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	57
31009	2	06/24/92 14:39	72.25	L 30 SH	17000	1	0	0	0	0	0	0	0	0	0	0	0	0	0	60
31010	1	06/25/92 07:50	88.95	L 401 SL	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	50
31011	1	06/25/92 08:50	87.62	R 32 SL	20	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1
31012	2	06/25/92 12:00	95.00	L 40 SL	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	23
31013	1	06/25/92 12:55	98.04	R 41 SL	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7
31014	1	06/25/92 15:00	108.60	R 42 SL	10	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
31015	2	06/26/92 09:00	117.40	R 40 AC	10000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	54
31016	2	06/26/92 10:40	119.13	R 40 AC	11000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	43
31017	2	06/26/92 13:24	122.01	R 40 AC	12000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	.
31018	1	06/26/92 14:55	122.55	L 40 AC	14000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	12
31019	2	06/27/92 10:35	138.50	L 40 AC	10000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
31020	2	06/27/92 13:12	143.50	R 45 AC	13000	0	0	0	2	0	0	0	0	0	0	0	0	0	0	3
31026	1	06/27/92 19:00	156.93	L 46 AC	15000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	3
31021	2	06/28/92 09:20	163.86	L 40 DC	11000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	.
31022	2	06/28/92 11:40	166.23	L 40 DC	10000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	78
31023	2	06/28/92 14:08	167.21	R 50 DC	9000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	74
31024	2	06/28/92 15:24	167.40	L 50 DC	8000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	21
31025	2	06/28/92 16:40	167.40	R 50 AC	9000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	20
31027	2	06/29/92 08:33	171.12	R 50 DC	13000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	23
31028	1	06/29/92 10:00	176.45	R 50 DC	13000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	9
31029	3	06/29/92 13:00	182.82	L 50 DC	10000	1	0	0	0	0	2	2	0	2	0	1	0	0	2	30
31030	2	06/29/92 15:09	187.53	R 50 DC	8500	1	0	0	0	0	2	2	0	2	0	1	0	0	1	80
31031	1	06/30/92 09:30	190.10	L 50 DC	12000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
31032	2	06/30/92 10:15	189.04	R 50 DC	12000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	11
31033	2	06/30/92 13:06	190.76	R 50 DC	11000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	52
31034	2	06/30/92 15:12	192.33	R 50 DC	10000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	.
31035	2	07/01/92 08:41	193.85	R 50 SH	16000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	.
31036	2	07/01/92 10:50	197.69	L 50 DC	15000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	.
31037	2	07/01/92 13:27	201.06	R 50 DC	14000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	.
31038	2	07/02/92 10:06	211.22	L 50 SH	16000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	26
Sum	67					26	0	0	14	0	50	50	0	50	0	25	0	0	27	841

Trip Study	Sites	Date--Time	Mile	Flo Rch Cod	Flow CFS	Typ A	Typ B	Ang lng	Opp	Son de	Ben ths	Sed	Chl	Pkn	Tot Map	Pla Map	Vis cer	Dri ft	-A- 2nd	Fsh Coll
11 31101	193	08/06/92 17:00	68.10	L 30 dc	11000	0	8	0	0	2	4	4	0	5	1	0	0	4	0	3
31102	134	08/09/92 16:00	98.04	R 41 DC	19000	0	6	0	0	2	1	1	0	2	1	0	0	2	0	13
31103	263	08/11/92 13:00	108.60	R 42 SH	19000	0	12	0	0	2	3	3	0	4	2	0	0	2	0	10
31104	147	08/14/92 17:00	143.50	R 45 DC	18000	0	7	0	0	2	3	4	0	4	1	0	0	0	0	3
31105	239	08/17/92 17:00	201.06	R 50 DC	11000	0	11	0	0	2	5	5	0	5	1	0	0	0	0	3
Sum	976					0	44	0	0	10	16	17	0	20	6	0	0	8	0	32

12 31201	2	09/14/92 13:00	2.41	L 20 AC	15000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
31202	2	09/15/92 13:15	44.27	L 20 DC	9000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
31203	2	09/16/92 09:00	50.70	L 20 SL	15000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
31204	2	09/16/92 11:12	54.60	R 20 SL	15000	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
31205	2	09/16/92 13:10	55.40	R 20 SL	15000	0	0	0	2	0	0	0	0	0	0	1	0	0	0	1
31206	2	09/17/92 08:25	58.30	R 20 DC	14000	1	0	0	0	0	2	2	0	2	0	1	0	0	0	1
31207	2	09/17/92 10:08	58.68	L 20 DC	14000	1	0	0	0	0	2	2	0	2	0	1	0	0	0	1
31208	2	09/17/92 12:50	62.12	R 30 DC	12000	1	0	0	0	0	2	2	0	2	0	1	0	0	0	3
31209	2	09/19/92 09:30	119.13	R 40 DC	12000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	2
31210	2	09/19/92 13:00	122.01	R 40 DC	14000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1
31211	1	09/19/92 14:30	122.00	R 40 AC	14000	1	0	0	0	0	1	1	0	1	0	1	0	0	1	1
31212	2	09/19/92 16:09	117.40	R 40 DC	17000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	1

APPENDIX 3.1

Trip Study	Sites	Date--Time	Mile	Flo Rch	Flow Cod	Typ CFS	Typ A	Ang B	Opp	Son de	Ben ths	Sed	Chl	Pkn	Tot Map	Pla Map	Vis cer	Dri ft	-A- 2nd	Fsh Coll	
31213	1	09/20/92 09:30	121.20	L	40 SL	9000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31214	1	09/20/92 10:30	121.70	L	40 SL	9000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31215	1	09/20/92 10:30	122.01	R	40 SL	9000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31216	1	09/20/92 11:15	122.80	R	40 SL	9000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31217	1	09/20/92 12:02	125.78	L	40 SL	9000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31218	1	09/21/92 13:30	137.16	L	40 SL	8000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31219	1	09/21/92 15:30	140.70	L	40 SL	7000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31220	2	09/22/92 11:30	161.63	L	40 SL	7000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31221	2	09/22/92 13:50	164.76	L	40 SL	7000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31222	2	09/23/92 09:00	168.75	R	50 SL	7000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31223	2	09/23/92 11:05	172.15	L	50 SL	7000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31224	2	09/23/92 13:35	176.68	L	50 SL	7000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31225	2	09/23/92 15:00	176.80	R	50 SL	7000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31226	2	09/24/92 09:00	182.83	L	50 DC	17000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31227	2	09/24/92 11:00	186.00	R	50 DC	15000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31228	2	09/24/92 11:55	187.85	R	50 DC	15000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31229	2	09/24/92 14:00	190.76	R	50 DC	14000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31230	1	09/24/92 15:50	192.33	R	50 DC	14000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31231	2	09/25/92 08:25	193.85	R	50 DC	14000	1	0	0	1	0	2	2	0	2	0	1	0	0	1	
31232	1	09/25/92 08:25	198.03	L	50 DC	14000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31233	1	09/25/92 10:00	200.48	L	50 DC	14000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31234	2	09/25/92 11:00	200.80	R	50 DC	14000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
31235	2	09/25/92 13:00	201.06	R	50 DC	13000	1	0	0	0	0	2	2	0	2	0	1	0	0	1	
Sum	59						26	0	0	11	0	49	49	0	49	0	26	0	0	23	38
13 31301	4	10/25/92 11:00	55.40	R	20 AC	6500	0	0	0	0	0	12	12	0	4	0	0	0	0	0	
31302	78	10/25/92 16:00	64.60	R	30 DC	9000	0	3	0	0	1	0	0	0	0	0	0	0	0	1	
31304	1	10/26/92 16:00	64.70	L	30 DC	8000	0	0	0	1	0	0	0	0	0	0	0	0	0	3	
31303	60	10/27/92 11:00	64.70	L	30 AC	11000	0	3	0	0	1	0	0	0	0	0	0	0	0	5	
31305	1	10/27/92 17:00	64.70	L	30 DC	9000	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
31306	1	10/28/92 16:00	64.60	R	30 DC	8000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31307	1	10/28/92 16:30	64.70	L	30 DC	7000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31308	1	10/28/92 16:45	64.70	L	30 DC	6500	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31309	1	10/28/92 17:00	64.70	L	30 DC	6500	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31310	163	10/30/92 17:50	108.60	R	42 SH	9000	0	8	0	0	2	0	0	0	0	1	0	0	0	5	
31311	9	11/02/92 13:00	119.10	R	40 SL	5000	0	0	0	1	0	9	9	0	6	0	0	0	0	1	
31312	139	11/03/92 17:00	122.01	R	40 AC	6000	0	6	0	0	2	0	0	0	0	1	0	0	0	1	
31315	1	11/04/92 17:00	122.01	R	40 AC	10000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31314	1	11/05/92 17:00	143.50	L	45 AC	9000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31313	174	11/06/92 09:00	143.50	L	45 DC	7000	0	8	0	0	2	0	0	0	0	1	0	0	0	2	
31316	1	11/08/92 15:00	143.50	L	45 AC	6000	0	0	0	1	0	0	0	0	0	0	0	0	0	2	
31317	1	11/08/92 15:30	143.50	L	45 AC	6000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31318	1	11/08/92 16:00	143.50	R	45 AC	6000	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31319	1	11/09/92 12:00	156.93	L	46 SL	25	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
31320	3	11/10/92 08:00	201.06	R	50 DC	7000	0	0	0	0	0	9	9	0	3	0	0	0	0	0	
Sum	642						0	28	0	13	8	30	30	0	13	0	3	0	0	29	
Sum	7993						163	175	2	401	38	534	549	12	498	24	283	20	40	160	1310

APPENDIX 3.4.2

Number of each species measured (Valid n), mean, maximum, and minimum total length (mm) by Reach code and trip.

Species codes are:

BBH	Black bullhead
BHS	Bluehead sucker
BKT	Brook trout
BNT	Brown trout
CCF	Channel catfish
CRP	Common carp
FHM	Fathead minnow
FMS	Flannelmouth sucker
HBC	Humpback chum
PKF	Plains killifish
RBT	Rainbow trout
RSH	Red shiner
SPD	Speckled dace
STB	Striped bass
SUC	Sucker species
UID	Unidentified in the field

Reach Codes are:

10	Glen Canyon Dam to Lees Ferry
20	Lees Ferry to Little Colorado River
30	Little Colorado River to Bright Angel Creek
40	Bright Angel Creek to National Canyon
50	National Canyon to Diamond Creek

APPENDIX 3.2

	REACH														
	Reach 20					Nankoweap			LCR			Reach 30			
	TRIP					TRIP			TRIP			TRIP			
	2	3	4	8	10	12	6	8	3	4	8	1	2	3	4
BBH															
Valid N															
Mean	
Maximum	
Minimum	
BHS															
Valid N			1		1						5	1		24	
Mean	.	.	52	.	18	82	64	.	59	
Maximum	.	.	52	.	18	99	64	.	109	
Minimum	.	.	52	.	18	75	64	.	40	
BKT															
Valid N															
Mean	
Maximum	
Minimum	
BNT															
Valid N					1									1	
Mean	33	374	
Maximum	33	374	
Minimum	33	374	
CCF															
Valid N								23	6	1					
Mean	559	474	540	
Maximum	710	620	540	
Minimum	350	333	540	
CRP															
Valid N		1													
Mean	.	490	
Maximum	.	490	
Minimum	.	490	
FHM															
Valid N	13										26	26	1	22	
Mean	49	54	49	36	32	
Maximum	68	73	73	36	62	
Minimum	27	39	32	36	20	
FMS															
Valid N			51	4	4	15		1			2		1	18	
Mean	.	.	57	76	37	97	.	80	.	.	104	.	35	59	
Maximum	.	.	88	83	51	191	.	80	.	.	149	.	35	85	
Minimum	.	.	26	70	32	19	.	80	.	.	58	.	35	32	
HBC															
Valid N											6	5	1	146	
Mean	57	110	25	79	
Maximum	94	350	25	155	
Minimum	28	44	25	29	
PKF															
Valid N											6	5		2	
Mean	44	49	.	41	
Maximum	50	57	.	63	
Minimum	34	31	.	19	

(continued)

APPENDIX 3.2

	REACH														
	Reach 20				Nankoweap				LCR			Reach 30			
	TRIP				TRIP				TRIP			TRIP			
	2	3	4	8	10	12	6	8	3	4	8	1	2	3	4
RBT															
Valid N	6	13	21	3	12	18		2	1			3	5	1	5
Mean	139	359	279	101	43	186	.	384	405	.	.	387	149	402	333
Maximum	432	525	455	222	85	846	.	400	405	.	.	397	420	402	364
Minimum	25	38	37	34	28	38	.	368	405	.	.	379	35	402	297
RSH															
Valid N															
Mean	
Maximum	
Minimum	
SPD															
Valid N	32				17	57		15				7	8		
Mean	56	.	.	.	30	43	.	92	.	.	.	51	43	.	.
Maximum	96	.	.	.	57	71	.	120	.	.	.	75	57	.	.
Minimum	36	.	.	.	15	17	.	69	.	.	.	38	24	.	.
STB															
Valid N															
Mean	
Maximum	
Minimum	
SUC															
Valid N			3		1									1	13
Mean	.	.	27	.	23	17	26
Maximum	.	.	32	.	23	17	33
Minimum	.	.	19	.	23	17	21
UID															
Valid N					1									1	
Mean	17	21	.
Maximum	17	21	.
Minimum	17	21	.

(continued)

APPENDIX 3.2

	REACH														
	Reach 30										Clear		Bright		
	Reach 40										Creek		Angel		
	TRIP										TRIP	TRIP		TRIP	
	5	6	7	8	9	10	11	12	13	8	8	10	1	2	3
BBH															
Valid N															
Mean															
Maximum
Minimum
BHS															
Valid N		2		7		9			4						2
Mean	.	56	.	61	.	48	.	.	14	88
Maximum	.	70	.	115	.	79	.	.	15	109
Minimum	.	41	.	39	.	35	.	.	12	66
BKT															
Valid N															
Mean															
Maximum															
Minimum															
BNT															
Valid N															
Mean															
Maximum															
Minimum															
CCF															
Valid N															
Mean															
Maximum															
Minimum															
CRP															
Valid N															
Mean															
Maximum															
Minimum															
FHM															
Valid N	5	3	10	139	15	39	41	54	115				17	2	
Mean	44	40	48	45	62	46	54	40	42	.	.	.	41	55	.
Maximum	63	50	65	68	70	66	77	65	72	.	.	.	58	57	.
Minimum	37	34	29	22	48	10	24	24	21	.	.	.	29	52	.
FMS															
Valid N		1		17		11		4						3	3
Mean	.	59	.	70	.	50	.	56	222	179
Maximum	.	59	.	108	.	88	.	61	309	189
Minimum	.	59	.	32	.	20	.	52	107	160
HBC															
Valid N	8			22	26	13	15	7	34				3	3	4
Mean	40	.	.	71	68	30	92	110	81	.	.	.	39	115	59
Maximum	46	.	.	142	111	63	128	162	157	.	.	.	41	147	74
Minimum	26	.	.	33	35	16	50	73	28	.	.	.	37	58	22

(continued)

APPENDIX 3.2

REACH															
	Reach 40			Reach 30						Clear		Bright			
										Creek		Angel			
	TRIP											TRIP			
	5	6	7	8	9	10	11	12	13	8	8	10	1	2	3
PKF															
Valid N		4	4	17		1			1				2	1	
Mean	.	50	44	48	.	34	.	.	44	.	.	.	50	48	.
Maximum	.	56	55	61	.	34	.	.	44	.	.	.	53	48	.
Minimum	.	38	37	27	.	34	.	.	44	.	.	.	47	48	.
RBT															
Valid N									5	14	7		13		1
Mean	316	26	32	.	157	.	330
Maximum	336	32	40	.	350	.	330
Minimum	305	26	21	.	28	.	330
RSH															
Valid N															
Mean
Maximum
Minimum
SPD															
Valid N	2	1		6	1	20	2		7	4	1		5	2	
Mean	88	27	.	40	67	39	60	.	17	49	41	.	37	48	.
Maximum	90	27	.	52	67	87	79	.	33	70	41	.	44	55	.
Minimum	85	27	.	26	67	17	40	.	9	35	41	.	34	41	.
STB															
Valid N															
Mean
Maximum
Minimum
SUC															
Valid N													2		
Mean	45	.	.
Maximum	50	.	.
Minimum	39	.	.
UID															
Valid N	1			1		1									7
Mean	48	.	.	36	.	49	16
Maximum	48	.	.	36	.	49	18
Minimum	48	.	.	36	.	49	14

(continued)

APPENDIX 3.2

	REACH														
	Reach 40					Crystal					Shinumo				
	TRIP					TRIP					TRIP				
	4	6	8	10	12	13	4	7	8	9	10	11	3	4	5
BBH															
Valid N															
Mean
Maximum
Minimum
BHS															
Valid N	13		3	99	5					2			1	8	
Mean	54	.	76	86	79	80	.	.	113	73	.
Maximum	73	.	95	200	150	89	.	.	113	120	.
Minimum	28	.	60	20	38	71	.	.	113	58	.
BKT															
Valid N															
Mean	123
Maximum	123
Minimum	123
BNT															
Valid N	1					1		2					1		
Mean	301	97	.	134	350	.	.
Maximum	301	97	.	158	350	.	.
Minimum	301	97	.	110	350	.	.
CCF															
Valid N															
Mean
Maximum
Minimum
CRP															
Valid N		1	2	2										1	
Mean	.	560	546	488	47	.
Maximum	.	560	582	515	47	.
Minimum	.	560	510	460	47	.
FHM															
Valid N	3		2	64	127	13				8		66			
Mean	32	.	58	34	36	42	.	.	.	47	.	40	.	.	.
Maximum	37	.	60	59	62	65	.	.	.	52	.	60	.	.	.
Minimum	30	.	55	14	21	23	.	.	.	35	.	29	.	.	.
FMS															
Valid N	4		16	74	4								2	3	1
Mean	105	.	154	86	222	266	64	66
Maximum	195	.	340	354	370	320	72	66
Minimum	37	.	43	16	125	212	54	66
HBC															
Valid N	5		1	6	5	2							3	2	
Mean	70	.	55	72	43	61	67	74	.
Maximum	127	.	55	163	62	87	79	85	.
Minimum	27	.	55	18	28	34	49	63	.
PKF															
Valid N		1		2			16	60		22		106			1
Mean	.	45	.	44	.	.	34	42	.	54	.	39	.	.	30
Maximum	.	45	.	44	.	.	46	64	.	83	.	70	.	.	30
Minimum	.	45	.	44	.	.	21	26	.	40	.	24	.	.	30

(continued)

APPENDIX 3.2

	REACH														
	Reach 40					Crystal						Shinumo			
	TRIP					TRIP						TRIP			
	4	6	8	10	12	13	4	7	8	9	10	11	3	4	5
RBT															
Valid N	23		4		26	6			2	5			3	1	
Mean	264	.	71	.	221	214	.	.	29	54	.	.	141	212	.
Maximum	365	.	178	.	335	350	.	.	30	70	.	.	280	212	.
Minimum	104	.	25	.	70	107	.	.	28	40	.	.	64	212	.
RSH															
Valid N					1										
Mean	.	.	.		38
Maximum	.	.	.		38
Minimum	.	.	.		38
SPD															
Valid N	1		8	80	20	2		12	3	50	5	36	1		12
Mean	44	.	46	49	39	37	.	84	79	66	39	52	12	.	50
Maximum	44	.	62	99	63	40	.	109	88	98	62	88	12	.	53
Minimum	44	.	31	21	26	34	.	55	60	18	27	32	12	.	46
STB															
Valid N															
Mean
Maximum
Minimum
SUC															
Valid N					59								9		
Mean	.	.	.		24	41	.	.
Maximum	.	.	.		38	119	.	.
Minimum	.	.	.		16	26	.	.
UID															
Valid N			1	5									39		
Mean	.	.	45	45	18	.	.
Maximum	.	.	45	60	32	.	.
Minimum	.	.	45	13	7	.	.

(continued)

APPENDIX 3.2

	REACH														
	Shinumo					Tapeats			Deer			Kanab			
	TRIP					TRIP			TRIP			TRIP			
	6	7	8	9	11	13	4	6	8	4	6	8	3	5	7
BBH															
Valid N															
Mean
Maximum
Minimum
BHS															
Valid N				16	3							30	2		
Mean	.	.	.	75	82	51	69	.	.
Maximum	.	.	.	110	110	68	77	.	.
Minimum	.	.	.	35	62	37	61	.	.
BKT															
Valid N															
Mean
Maximum
Minimum
BNT															
Valid N															
Mean
Maximum
Minimum
CCF															
Valid N															
Mean
Maximum
Minimum
CRP															
Valid N															
Mean
Maximum
Minimum
FHM															
Valid N				3	27	6							20	4	
Mean	.	.	.	53	40	48	43	46	.
Maximum	.	.	.	55	55	64	57	50	.
Minimum	.	.	.	50	23	32	26	40	.
FMS															
Valid N		2			2			2				4	1	7	
Mean	.	58	.	.	77	.	.	38	.	.	.	58	72	80	.
Maximum	.	65	.	.	111	.	.	38	.	.	.	68	72	105	.
Minimum	.	51	.	.	43	.	.	37	.	.	.	47	72	65	.
HBC															
Valid N					2										
Mean	76
Maximum	76
Minimum	76
PKF															
Valid N													15	43	
Mean	46	47	.
Maximum	53	68	.
Minimum	36	30	.

(continued)

APPENDIX 3.2

	REACH														
	Shinumo					Tapeats			Deer			Kanab			
	TRIP					TRIP			TRIP			TRIP			
	6	7	8	9	11	13	4	6	8	4	6	8	3	5	7
RBT															
Valid N			1	14	2	2			11			5			
Mean	.	.	31	41	90	86	.	.	31	.	.	28	.	.	.
Maximum	.	.	31	77	98	92	.	.	58	.	.	32	.	.	.
Minimum	.	.	31	28	81	80	.	.	22	.	.	25	.	.	.
RSH															
Valid N															
Mean
Maximum
Minimum
SPD															
Valid N		22	12	213	148	84								10	33
Mean	.	52	61	50	41	49	41	40
Maximum	.	80	79	116	85	93	60	95
Minimum	.	42	45	24	26	34	28	27
STB															
Valid N															
Mean
Maximum
Minimum
SUC															
Valid N															
Mean
Maximum
Minimum
UID															
Valid N														2	
Mean	23	.
Maximum	27	.
Minimum	19	.

(continued)

APPENDIX 3.2

	REACH														
	Kanab				Havasu		Reach 50								
	TRIP				TRIP		TRIP								
	9	10	11	13	10	13	1	2	3	4	5	6	7	8	9
BBH															
Valid N							1								
Mean	50
Maximum	50
Minimum	50
BHS															
Valid N	22		1	23		2	9	24	16	24		1		97	
Mean	50	.	57	44	.	188	48	57	45	49	.	102	.	54	.
Maximum	105	.	57	260	.	213	65	83	59	71	.	102	.	260	.
Minimum	18	.	57	11	.	163	37	33	20	31	.	102	.	25	.
BKT															
Valid N															
Mean
Maximum
Minimum
BNT															
Valid N				1											
Mean	.	.	.	132
Maximum	.	.	.	132
Minimum	.	.	.	132
CCF															
Valid N				2						2				3	
Mean	.	.	.	87	442	.	.	.	355	.
Maximum	.	.	.	103	500	.	.	.	414	.
Minimum	.	.	.	71	383	.	.	.	306	.
CRP															
Valid N							2	2	10	19		1		26	
Mean	284	476	435	446	.	81	.	434	.
Maximum	420	484	490	605	.	81	.	557	.
Minimum	148	468	370	298	.	81	.	150	.
FHM															
Valid N	20		21	87			87	88	10	57	2	19		164	7
Mean	49	.	50	45	.	.	43	47	51	40	55	38	.	42	62
Maximum	60	.	69	269	.	.	67	79	63	69	67	60	.	72	69
Minimum	13	.	36	26	.	.	27	29	30	16	43	24	.	25	52
FMS															
Valid N	10	3	1	4			22	40	1	88		16		234	18
Mean	80	81	49	104	.	.	69	89	34	59	.	53	.	73	72
Maximum	105	147	49	264	.	.	92	434	34	400	.	91	.	495	107
Minimum	43	43	49	33	.	.	35	46	34	26	.	23	.	24	30
HBC															
Valid N				1	1			1		1					
Mean	.	.	.	34	365	.	.	62	.	36
Maximum	.	.	.	34	365	.	.	62	.	36
Minimum	.	.	.	34	365	.	.	62	.	36
PKF															
Valid N	6		1	2			5	2		2				7	
Mean	52	.	60	56	.	.	42	45	.	61	.	.	.	36	.
Maximum	60	.	60	61	.	.	45	54	.	62	.	.	.	60	.
Minimum	30	.	60	51	.	.	38	35	.	60	.	.	.	21	.

(continued)

APPENDIX 3.2

	REACH														
	Kanab				Havasu		Reach 50								
	TRIP				TRIP		TRIP								
	9	10	11	13	10	13	1	2	3	4	5	6	7	8	9
RBT															
Valid N				3			11	2							10
Mean	.	.	.	205	.	.	105	42	55	.
Maximum	.	.	.	405	.	.	357	45	260	.
Minimum	.	.	.	103	.	.	33	39	26	.
RSH															
Valid N															
Mean
Maximum
Minimum
SPD															
Valid N	135		33	18			139	354	3		1	1		268	1
Mean	37	.	48	40	.	.	41	48	36	.	45	30	.	42	35
Maximum	65	.	63	84	.	.	65	78	67	.	45	30	.	68	35
Minimum	15	.	27	12	.	.	31	20	11	.	45	30	.	21	35
STB															
Valid N											1				
Mean	575
Maximum	575
Minimum	575
SUC															
Valid N	2						14	77	12	16		15			
Mean	30	40	20	39	24	.	27	.	.	.
Maximum	32	51	28	60	34	.	35	.	.	.
Minimum	28	29	13	25	15	.	20	.	.	.
UID															
Valid N	2						3	26	38	3	1			4	
Mean	8	32	18	16	255	35	.	.	38	.
Maximum	10	49	33	28	420	35	.	.	78	.
Minimum	5	21	12	10	16	35	.	.	17	.

(continued)

APPENDIX 3.2

	REACH					Tot.
	Reach 50			Pipe Ck		
	TRIP			TRIP		
	10	11	12	6	10	
BBH						
Valid N						1
Mean	50
Maximum	50
Minimum	50
BHS						
Valid N	90	3	19			569
Mean	60	49	58	.	.	62
Maximum	147	65	203	.	.	260
Minimum	14	37	32	.	.	11
BKT						
Valid N						1
Mean	123
Maximum	123
Minimum	123
BNT						
Valid N						9
Mean	181
Maximum	374
Minimum	33
CCF						
Valid N			5			43
Mean	.	.	355	.	.	470
Maximum	.	.	395	.	.	710
Minimum	.	.	301	.	.	71
CRP						
Valid N	4		14			93
Mean	361	.	244	.	.	404
Maximum	460	.	476	.	.	605
Minimum	74	.	62	.	.	47
FHM						
Valid N	128	6	188			1755
Mean	35	48	38	.	.	42
Maximum	72	54	71	.	.	269
Minimum	12	39	17	.	.	10
FMS						
Valid N	153	16	95			958
Mean	97	48	74	.	.	78
Maximum	500	80	290	.	.	500
Minimum	34	21	22	.	.	16
HBC						
Valid N		1	2			326
Mean	.	47	25	.	.	75
Maximum	.	47	26	.	.	365
Minimum	.	47	24	.	.	16
PKF						
Valid N			1			335
Mean	.	.	29	.	.	43
Maximum	.	.	29	.	.	83
Minimum	.	.	29	.	.	19

(continued)

APPENDIX 3.2

	REACH					Tot.
	Reach 50			Pipe Ck		
	TRIP			TRIP		
	10	11	12	6	10	
RBT						
Valid N	1		1	1	6	270
Mean	54	.	69	35	61	163
Maximum	54	.	69	35	86	846
Minimum	54	.	69	35	47	21
RSH						
Valid N						1
Mean	38
Maximum	38
Minimum	38
SPD						
Valid N	137	32	126		23	2210
Mean	50	37	35	.	68	46
Maximum	111	65	90	.	112	120
Minimum	14	23	17	.	52	9
STB						
Valid N						1
Mean	575
Maximum	575
Minimum	575
SUC						
Valid N	115	3	2			344
Mean	25	23	13	.	.	25
Maximum	36	28	14	.	.	119
Minimum	14	18	12	.	.	12
UID						
Valid N	6					142
Mean	49	26
Maximum	84	420
Minimum	7	5

4. Little Colorado River Native Fishes

Robert W. Clarkson and Anthony T. Robinson

Spawning sites of many southwestern native fishes are found in riverine habitats associated with relatively swift currents (Minckley 1973). However, these sites are usually poor producers of zooplankton (Hynes 1970), a major food item of many larval fishes (Minckley 1973; Snyder 1990), and larvae have difficulty contending with the swift currents (Harvey 1987). Thus larvae must disperse to slow-flowing refuges to satisfy their energetic needs (Corbett and Powles 1986; Tyus and Haines 1991). One avenue of dispersal, the downstream transport of native fish larvae via drift, is a common phenomenon in the LCR and is significant to the ecology of this life stage (Angradi et al. 1992).

In 1991, observations of larval fish distributions in the shoreline areas of the LCR indicated that many suitable habitats were not occupied, despite the physical similarity to occupied sites. The impetus for larvae to migrate to suitable rearing habitats once they have hatched is not clear. Since larval movements are usually limited by current velocity, hydraulic variables may dictate whether a given habitat is accessible from the mainstream (Floyd et al. 1984; Harvey 1987, 1991). Other features such as algal or zooplankton densities, substrate types, cover attributes, presence or absence of predators, or physical-chemical variables such as temperature, may ultimately determine the suitability of accessible habitats.

Recent AGFD studies have attempted to define the nearshore availability of larval habitats and habitat utilization patterns. For example, if spawning sites are localized, then the spatial distributions of larvae in nearshore habitats immediately following spawning may identify major spawning reaches. For future studies of reproduction, if there is fidelity to spawning sites across years, then such information could be used to more precisely define sites of egg deposition. AGFD studies from 1992 have attempted to establish the relationships of the temporal and spatial occurrence of larvae in nearshore habitats with adult spawning activity.

The dispersal mechanisms of larvae may include drifting as an energy-conserving strategy, or active swimming along shorelines. Techniques that monitor movements of larval fishes between nearshore habitats may provide further insight into dispersal mechanisms (Brown and Armstrong 1985; Harvey 1991). Recent AGFD research has attempted to identify such mechanisms by quantifying the passive transport and migration of larvae in nearshore and mainstem habitats using drift nets and larval fish traps.

Little is known about behavior patterns of YOY native fishes in the Grand Canyon region. Consequently, knowledge of temporal and spatial segregation of species among habitat types and among age classes within species, schooling, agonistic behavior, selection for cover,

foraging strategy, etc., is important for conservation purposes. AGFD research in 1992 has continued to document behavior patterns in terms of time activity budgets, microhabitat utilization, and food habits.

This chapter updates AGFD research on humpback chub (*Gila cypha*) and other native fishes in the Little Colorado River (LCR) for the period December 1991 through December 1992. This research continued to track the growth and population status of the 1991 cohort of native fishes through their first year of life. The focus of the research was amended to more fully chronicle the early life histories of native fish species, especially their larval stages. New research activities also commenced on the 1992 year class of native fishes. Standardized hoop net monitoring of adult and subadult humpback chub was completed during May and June of 1992. Certain aspects of research conducted between May and October 1991 not reported by Angradi et al. (1991) are also presented.

Objective 3.1. Continue the monitoring program on the native and endangered fishes of the Colorado River and its tributaries in the Grand Canyon that was initiated by AGFD in 1987.

Methods and Progress

The methods used to fulfill this objective were presented in detail by Hendrickson and Kubly (1990). Hoop nets (2-3 m long, 6.4 mm mesh, 1.0 m diameter of the largest hoop) were deployed at 13 standardized locations in the lower 1200 m of the LCR during the May-June annual monitoring period. Nets were run daily, and lengths and weights of captured fishes were recorded to ± 1 mm total length and ± 1 g, respectively. Native species longer than 150 mm were injected with passive integrated transponders (PIT tags) prior to release. A limited amount of seining and dip netting was also conducted within this time period. Spring 1992 monitoring of humpback chubs in the LCR was completed and the bulk of the data have been analyzed.

Results and Discussion

Nine species of fish were captured during the 1992 spring monitoring period, four of which were native (Robinson and Clarkson 1992). All of these species were captured by hoop nets, however, only natives were captured by seines and dip nets. The relative abundances of species by gear type are presented in Table 4.1. The mean catch per unit effort (CPE) of humpback chub collected by hoop net in 1992 was 0.8 individuals per net per 12 hours. Although the 1992 hoop net CPE was greater than the rate in 1991 (0.6), it was lower than had been observed in 1987-1990 (Robinson and Clarkson 1992). Catch rates from 1991 and 1992 reported by Robinson and Clarkson (1992) were in error.

Using the modified Schnaebel method (Ricker 1975), a population estimate at the end of June, 1992, of 571 humpback chub > 150 mm TL (95% C.I. = 426-809) was calculated from AGFD marks and recaptures in May and June. To compare populations across years, estimates were calculated only for the first month of monitoring from the lower 1200 m of the LCR. Analysis revealed the lowest population estimate in 1992 (Figure 4.1). The correlation of population size with study year was negative ($r=-0.88$; $p=0.011$), that is the humpback chub population estimate for the spawning period has significantly decreased since monitoring began in 1987. This result suggests that there has been a decrease in the humpback chub population in the LCR since monitoring began. However, at least one of the assumptions of the modified Schnaebel census method---no recruitment to the sample population---was probably violated. Monitoring was conducted during the spawning season when it has been documented that adult humpback chub migrate to the LCR from the Colorado River (Valdez et al. 1992). Therefore, the results must be accepted with caution. The use of open population models may produce more accurate results (Ricker 1975).

Humpback chub appears to be a predominantly sedentary species as evidenced by movements of relatively short distances between captures (Table 4.2; Kaeding and Zimmerman 1983; Maddux et al 1987; Valdez et al. 1992). For example, the mean absolute distance moved between captures in the LCR in 1992 was 167 m. This is the shortest mean distance calculated since monitoring began in 1987 (Table 4.2). Greater mean distances moved in 1988-1991 may be explained by the fact that the sample area extended beyond 8 km in those years. The mean number of days at large between captures for each year were: 3.18, 3.01, 3.20, 7.26, 8.89, and 7.61 for 1987-1992, respectively. A graphical representation of distances moved for recaptured individuals in 1992 is presented in Figure 4.2.

Flows in the LCR likely affected humpback chub activity patterns. Catch rates increased with decreasing flows in four of the six years of monitoring. CPE was negatively correlated with discharge in 1987, 1988, and 1991 at $p < 0.05$ (Robinson and Clarkson 1992), and in 1992 at $p < 0.1$. In 1989, the LCR was at base flow during the entire monitoring period; consequently a comparison between flows and catch rates could not be made. In 1990 there was no significant relationship between flows and catch per unit effort.

In contrast, rate of discharge does not have an obvious impact on mean distances traveled between recaptures of humpback chub. The distance traveled in 1992 was not significantly correlated with daily flow (this analysis has not yet been made for earlier years).

Objective 3.2. Determine if the reproductive activity of native fishes is temporally or spatially segregated. Determine the timing and duration of reproductive activity for different species as related to physical conditions. Determine if early life stages segregate

themselves within habitats. Determine if early life stages drift in the tributaries. Determine if early life stages feed selectively on available drift and/or benthic sources.

Methods and Progress

Larval Fish Longitudinal Surveys

Quantification of the temporal and spatial distributions of larval native fishes in the LCR was accomplished by conducting longitudinal surveys of nearshore habitats between Atomizer Falls (14.5 km above mouth) and the LCR mouth during the reproductive season. Shorelines (both banks) were surveyed once or twice weekly beginning in April, and the presence or absence of larval fishes in nearshore slackwater habitats within contiguous 100 m reaches was recorded. At base flows, LCR nearshore waters were shallow and clear enough to allow visual observation of small fishes. When turbid conditions were present, sweeps with fine-meshed aquarium nets and seines were performed. A total of twelve longitudinal surveys were completed in 1992 between May and September.

When possible, fishes were identified in the field with the aid of portable 45X stereo dissecting microscopes. Some samples were preserved in 10% formalin for taxonomic identifications and examination of stomach contents, and others were preserved in 95% ethanol for otolith analyses. Larval collections were made from 100 m reaches at 0.5 km intervals in an effort to avoid oversampling, unless distribution patterns dictated otherwise.

Larval Fish Habitat Availability

U.S. Fish and Wildlife Service (FWS) transects located within every fifth 100 m reach (both banks), beginning at river kilometer 0 (mouth), were measured perpendicular to the flow for current velocity, depth, substrate and habitat complexity features to assess the river-wide availability of larval fish habitats. Depths were recorded to ± 1 cm. Current velocity in areas exceeding 5 cm in depth were measured at 0.6 depth to ± 0.01 m/s using a Marsh-McBirney electromagnetic flow meter. In shallower areas, neutral-bouyancy beads were drifted and timed over a known distance. Substrates were classified to categories listed in Table 4.3. Habitat complexity features were depths > 0.5 m, surface turbulence, turbidity, ledges, substrates larger than gravel (> 64 mm), undercut banks, overhanging vegetation, instream vegetation, and woody debris.

Measurements were taken at 10 cm and 25 cm from shore, and at 25 cm intervals from shore thereafter until a current velocity was recorded that exceeded 0.2 m/sec. Previous AGFD observations of larval habitat use indicated that this velocity should be sufficient to include all nearshore larval habitats. The habitat availability procedure was performed at both base and higher flows in 1992.

Habitats at each transect were subjectively categorized to peripheral pools (shoreline invaginations), vegetated shoreline margins (e.g. *Typha*, *Scirpus*, or *Phragmites*), non-vegetated shoreline margins, or springflow channels. Physical measurement data of these habitat types will be compared to groupings generated from Principal Components Analysis or other multivariate techniques.

An additional four 100 m study reaches were to have been established for more intensive larval habitat availability measurements, but scarcity of larvae precluded implementation of this procedure in 1992. If possible in the future, depth, current velocity, substrate, and habitat complexity features (as described above) will be recorded along 2 m spaced perpendicular-to-flow transects at 10 cm intervals beginning 5 cm from shore and extending out to a point in the mainchannel where flow velocities exceed 0.2 m/s. This procedure will yield a total of 400 transects (50 per each of four reaches, both banks).

Larval Fish Habitat Use

Within each fifth 100 m reach (both banks) along the river, a series of up to three perpendicular-to-flow transects were established for the purpose of taking habitat use measurements (depth, substrate, current velocity, habitat features; as described above) of YOY fishes. These transects were spaced a minimum of 10 cm apart, and extended through the area inhabited by the fish(es). Measurement intervals along each transect were 10 cm. If the area inhabited by the fish was less than 20 cm wide, two transects were established; if the area was 20 cm wide or more, three transects were established. The transects were evenly spaced in larger habitats so that the area of use was adequately sampled. A relatively small series of habitat use measurements were made in 1992 but have not yet been analyzed.

All nearshore habitat types occupied by larvae within the four reaches identified for intensive habitat availability (above) will be measured for depth, current velocity and substrate at cell midpoints using a 20 cm square grid system (400 cm² grids) of 6 grids. Four peripheral pools (two occupied, two unoccupied) and two shoreline margin habitats (one occupied, one unoccupied; lengths not to exceed 3 m) within each of the four reaches (both banks) will be randomly selected. Fish abundance and distribution, water temperature, and algal and zooplankton densities will be estimated using the gridded sampling regime. Habitat features will be enumerated. Habitat cover features will be ranked at each sampling point, and water temperatures taken during crepuscular hours using a hand-held thermometer to estimate thermal maxima/minima. Mean zooplankton abundance within the habitat will be estimated by pumping a measured volume (typically 8 l) of water through an 80 μ m mesh plankton net. Algal abundance (as chlorophyll *a*) will be estimated in each grid using a mini-core sediment sampler and freezing the sample on dry ice for later laboratory spectrophotometry. 35 mm photographs

of these gridded habitats will be taken to determine microhabitat use patterns. Frequency of observation will be once per hour for 24 h using a programmable camera with flash, mounted on a tripod directly above the habitat. Species identification, especially early larval stages, is problematic with this technique. Larval collections will be made immediately following observation periods in an attempt to resolve this problem. Data from occupied habitats and grids will be compared to unoccupied habitats and grids, and to habitat availability data using the Manly (1974) selectivity index and graphical techniques (e.g. Thomas and Taylor 1990). Frequency distributions and discriminant analysis will be used to compare habitat parameters between used and unused habitats (Christensen 1985). Turbidity levels during the reproductive and post-reproductive seasons in 1992 precluded implementation of these procedures on other than a trial basis.

Habitat suitability index curves (Bovee 1981) will be generated for the seven parameters quantified above. The relationships between mean frequency-of-use of cells and physical-biological parameters will be evaluated using multiple linear regression or discriminant function analysis.

Direct observations of habitat use of YOY fishes will be supplemented with collections from larval seines, fine-meshed dip nets, and other collection methods. In this manner, larval fishes and other unidentifiable life stages can be sorted in the lab and species associations determined.

Larval Fish Movements

In order to determine the mechanism(s) of longitudinal dispersal of larval fishes among nearshore habitats, larval traps similar to the design of Culp and Glozier (1989) were emplaced at inflow (upstream) and outflow (downstream) points of a subsample of occupied peripheral pools and shoreline margins. Traps were made from transparent plastic, 500-1000 ml wide-mouth bottles, with the central portion of the bottom and screw cap cut out, and each fitted with a 500 μ m-mesh screen funnel in the cap and a flat screen on the bottom.

Numbers of fishes present in each habitat at the start of each sampling period during the reproductive and post-reproductive seasons will be visually estimated at base flows. Four 100 m reaches (two in the vicinity of each camp where larvae are present) were selected for these and other detailed analyses. A minimum of two shoreline margins and two peripheral pool habitats were sampled within each of the four reaches (on both banks), staggered so that each reach was sampled once a week. Traps were deployed and run at 6-h intervals encompassing a 24-h period. When possible following enumeration, trapped fishes were released alive immediately above or below the trap site, depending on their direction of travel at the time of capture. Therefore, emmigration rates may be only determinable from initial trap sets. Escape

rates from traps will be estimated by placing a known number of larvae within traps and monitoring losses over time. Larval trap procedures were implemented on a limited basis in 1992.

Two standard larval drift nets (3 m long, 0.25 m² opening, 750 μ m mesh net, 500 μ m mesh bucket) were placed in deeper habitats, one nearshore adjacent to trap locations, and the other midchannel. Drift nets were run at the same intervals as larval traps. Water volumes filtered were estimated by measuring current velocities at the mouths of drift nets at the beginning and ending of each sampling period. Depths of the water column sampled were recorded. This procedure was accomplished with at least one 24-h sampling period per month in 1992. All 1991 and approximately one third of the 1992 samples have been inspected for fish eggs and invertebrates. Drying and ashing of samples to obtain biomass values are in progress.

Fish Behavioral Analyses

Time bound focal animal behavioral analyses (Altman 1974) were to have been continued in 1992 until sufficient sample sizes (~ 50 for each category) were obtained to characterize both species and species size class activities (general behaviors and vertical positioning in the water column). Turbidities precluded application of this technique in 1992. When turbidities allow, an individual fish will be observed for a period of 5 min and behavior patterns recorded on audio tape. Behavioral categories will include feeding, swimming, schooling, chasing, being chased, hiding, and other. Cumulative time spent in each category will be transcribed from the tape recordings.

Vertical occupation of the water column will be similarly evaluated by recording movements among five zones: 1) in contact with the bottom (benthic); 2) lower one-third of the water column but not in contact with bottom (lower pelagic); 3) middle one-third of the water column (mid-pelagic); 4) upper one-third of the water column but not at surface (upper pelagic), and; 5) at surface (surface). Observation periods will include early morning, mid-day, and early evening. If not visually identifiable to species, the observed fish will be collected for identification.

Fishes will be assigned to one of five groups based on their ontological development (Snyder 1981; Snyder and Muth 1990) and habitat use for among-group comparisons: 1) protolarvae (larvae characterized by undeveloped spines or rays associated with future median fins); 2) mesolarvae (larvae characterized by morphogenesis of distinct principle rays in the median fins; 3) metalarvae (larvae characterized by presence of the full adult compliment of principle fin rays in the median fins and presence of pelvic fins or fin buds); 4) post-larvae in nearshore slackwater habitats, and; 5) post-larvae in mainstem habitats.

Food Selectivity

To determine if the early life stages of fishes in the LCR feed selectively on available drift and/or benthic sources the following methods were used. Fishes were collected and stomachs were analyzed for diet in the laboratory according to procedures in Objective 4.5. Drift samples (above) taken as close to the time of fish capture as possible were analyzed for invertebrates. Similarity indices (Eckblad 1986) were calculated between composition (frequency of occurrence) of the diet and composition (frequency of occurrence) of the drift, and compared with a Mann-Whitney U test. Results from 1991 were reported by Robinson (1992), a summary of which is presented here.

Results and Discussion

Larval Fish Longitudinal Surveys

Twelve complete surveys of the entire river below RKM 14.3 were completed between April 28 and September 3, 1992. In 1992, larval humpback chub were first encountered on April 30 as mesolarvae (Figure 4.3). Humpback chub protolarvae were found only in May. Humpback chub larvae were only found in the lower 43 hectometers in the first survey, but by mid-May they were distributed throughout the river up to 112 hm. Only one larval humpback chub was found in June, but in July and August larvae were in the lower half of the study area. Based on appearance of larvae, humpback chub had a concentrated period of spawning from late April to early May, and again in July.

The 1992 longitudinal surveys first observed speckled dace larvae on May 3 as mesolarvae in the vicinity of Salt Trail Canyon (Figure 4.3). They were found thereafter only in lower reaches of the LCR, and were not observed throughout the river until July. Based on larval fish occupancy data, speckled dace probably spawned over a broader spectrum of time compared with the other native fish species. Limited spawning of dace apparently occurred primarily in lower reaches in May and early June, followed by a more widespread spawn in July and August.

Bluehead sucker larvae were first encountered in 1992 on May 7 as proto- and mesolarvae, and were primarily observed only in the lower 7 km of the river (Figure 4.3). Bluehead sucker spawning occurred synchronous with the early humpback chub spawn. Flannelmouth sucker larvae were only collected on May 10 at hectometer 38 and on May 15 at hectometer 61.

Larval Fish Movements

No larval fishes were captured in larval fish traps, but several juvenile chub and dace were collected. The lack of larval fish captures may be reflective of the scarcity of larval fishes during this time period.

Analyses of drift net samples in 1992 have not been completely analyzed, but those examined thus far (below) did not contain larval fishes. However, high discharges during the early reproductive period typically prevented sets longer than several minutes in duration (due to large volumes of materials collected). This revelation and those previously discussed makes it unlikely that many larvae were captured by this method during these conditions.

Fish Behavioral Analyses

Foraging time budgets of the four native species from the LCR (humpback chub, speckled dace, bluehead sucker, and flannelmouth sucker; total lengths 11-55 mm) are presented in Figure 4.4. The four species differed in the amount of time spent foraging in the water column (Kruskal-Wallis, $p=0.042$) and on the surface ($p<0.001$). However, sample sizes for speckled dace and flannelmouth sucker are low. When the analysis was conducted with only chub and bluehead sucker, chub fed on the bottom less ($p=0.005$), on plants less ($p=0.023$), and on the surface more ($p=0.005$) than bluehead sucker. Size (length) of the fish was not an important factor in determining where they foraged. In addition, chub, dace, and flannelmouth sucker utilized the upper pelagic zones more than expected and under-utilized the middle and lower pelagic and benthic zones (G-test, $p<0.001$). Bluehead suckers utilized the middle pelagic and benthic zones more than expected and under-utilized the lower pelagic zones ($p<0.001$). Angradi et al. (1992) reported similar results.

Food Selectivity

Young-of-year native fishes that inhabit the LCR have diets (Objective 4.5) that are comprised of foods relatively dissimilar to proportions found in the drift (Table 4.4). Robinson (1992) compared the composition of the diets of 1991 YOY native fishes with composition of seven drift samples collected in 1991. YOY humpback ($n=27$) had a diet that was 45% similar to the composition of the drift, the diet of speckled dace ($n=39$) was 37% similar and the diet of bluehead sucker ($n=66$) was 29% similar to the composition of drift. A more detailed analysis of food selectivity has yet to be done on 1991 data and no analysis has yet been conducted on 1992 data.

Objective 3.3. Provide for the propagation of native fishes of the Colorado River in Grand Canyon for use in laboratory or hatchery based studies necessary to satisfy the needs of the Section 7 Conservation Measures.

Methods and Progress

Some studies on native fishes of the Grand Canyon cannot be completed in the field and must be conducted under controlled laboratory conditions. Two attempts at field-fertilization of humpback chub eggs were made in the LCR in late March and late April in 1992 following the methods of Hamman (1982; pers. comm.). Detailed methods of the April trip are presented here, summarized from Hines (1992).

Adult fish were collected in hoop nets, weighed, measured and PIT-tagged, with males and females held separately in live cars. Ripe females were manually stripped of eggs into a shaded plastic spawning bowl and milt from two or three males were added. Sperm diluent was then added, followed by a bentonite solution. After 60 seconds, eggs were washed, and total egg volumes (± 1 ml) and weights (± 0.01 g) were recorded. Two sample counts were made to provide an estimate of the number of eggs/g and ml.

Unripe females were injected intraperitoneally up to three times at 24-h intervals with a 1 mg/ml concentrate of carp pituitary extract at a dosage of 4 mg/kg body weight. When eggs from these fish were readily expressible, the above procedures were applied.

Eggs were then transferred to one of four hatching groups. One group of naturally ripe eggs was placed in a covered floating Heath incubator tray in the mainstem LCR, and the other group placed in a covered cradle-shaped floating egg basket in Salt Trail Canyon outflow. Eggs from pituitary-injected fish were split into similar hatching treatments.

Eggs were held in these trays for up to three days prior to transport by helicopter and truck in oxygenated bags to AGFD Bubbling Ponds Hatchery at Page Springs, Arizona. Eggs were then ionically and thermally acclimated over a 24-h period and placed in Heath incubators and hatching jars at Bubbling Ponds. Egg samples were taken from all treatments at 12-24 h intervals and preserved in 5% formalin.

Results and Discussion

Ten pituitary-injected female humpback chub collected in the lower LCR in late March failed to produce eggs following up to four injections. It is likely that gonadal maturation had not progressed to a point where the pituitary injections were effective in inducing ovulation. No naturally ripe females were observed.

As reported by Hines (1992), approximately 27,000 eggs were collected from eight naturally ripe and four pituitary-injected humpback chub females (five pituitary-injected fish did

not produce eggs) caught near the vicinity of Salt Trail Canyon from the April culture trip. These eggs were split in equal batches between the LCR and Salt Trail Canyon outflow treatments. Temperatures at the LCR incubation site were 19.0-22.0 C, mean flow 0.03 m/s, conductivity 3400 μ S/cm, dissolved oxygen near 8.0 mg/l, pH 7.8, and secchi depth 4 cm. Salt Trail Canyon outflow temperatures were 21.5-23.0 C, mean flow 0.05 m/s, conductivity 7500 μ S, dissolved oxygen near 6.0 mg/l, pH 6.9, and secchi depth > 1 m.

Although initially all eggs appeared healthy in the hatching trays, within a day the eggs from the naturally ripe females (no injected females had yet been stripped) in Salt Trail Canyon were smaller in size, exhibited more clumping, and had a higher proportion of white (dead) eggs than those held in the LCR. The difference in egg size was possibly due to osmotic differences between the two sites. By the third day, eggs from both the natural spawn and earlier injected females incubated at both sites appeared to be dead or decaying. The remaining early-spawned eggs and later-spawned eggs from injected fish were transported to Bubbling Ponds, but all had perished within a few days.

Preserved egg samples were microscopically examined, and no evidence of cell division was observed. Either fertilization never occurred or eggs died soon after fertilization. The cause(s) of this failure is not specifically known at this time. Strongly suspected, however, was the quality of the sperm diluent used, which was obtained from Dexter National Fish Hatchery. No knowledge of its age or expiration date was available. Eggs immediately began clumping after addition of this agent.

Assuming the eggs were fertilized, water quality could also have been a factor. For example, high levels of silt in the LCR and high conductivity in Salt Trail Canyon could have suffocated eggs or created osmotic imbalances, respectively. However, chub larvae were collected from the LCR in late April and early May, indicating that a successful natural spawn had occurred. Chub also have spawned successfully during periods of base flow when conductivities approached those found in Salt Trail Canyon (AGFD, unpublished data).

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

Methods and Progress

Analysis of Digestive Tracts

Samples of larval and juvenile native and introduced fishes were collected on a monthly basis for analysis of digestive tract contents. Relatively large collections were made of larval specimens unidentifiable in the field to ensure that an adequate sample size for each species was

obtained. Monthly collections of 10 specimens of YOY humpback chub >30 mm TL were taken for these analyses. Attempts were made to obtain 20 specimens of the other native species. Collections were made by seine or dipnet, and specimens were preserved in 10% formalin. Heads of specimens identified to species in the field were preserved separately for use in otolith analyses (Objective 3.7).

Due to the small stomach volumes of YOY fishes, relative volumes of stomach content categories were estimated using a modified point system (Hynes 1950), where percent volume of each category was estimated visually. For catostomids with undifferentiated digestive tracts, the intestine anterior to the first loop towards the head was arbitrarily delimited as the "stomach." Volume of food occupying this portion of the gut relative to its potential volume was subjectively estimated and assigned a percentage value from 0 (empty) to 100 (full). Hynes (1950) and Corbet (1961) both reported that estimation of relative volumes does not significantly differ from direct methods of quantification. Numbers of identifiable taxa in stomachs were enumerated. Frequency of occurrence data have been analyzed for 1991 collections and some 1992 samples. Volumetric analysis is complete for the 1992 samples analyzed for frequency of occurrence; this analysis has not been completed for 1991 specimens.

Algal and Invertebrate Standing Crops

Measurement of invertebrate standing crop in the LCR is incomplete to date. AGFD intends to use techniques comparable to those employed on the mainstem Colorado river (Angradi et al. 1992) in 1993.

Results and Discussion

Table 4.5 provides frequency of occurrence of selected materials in stomachs of larvae, early post-larvae, and juvenile speckled dace, bluehead sucker, and humpback chub from the LCR in 1991. Chironomidae was an important food item for all three species, with the two cyprinids reducing their utilization of this component with age, and bluehead sucker increasing its use of this component with age. Ostracods were used most often by larval and early post-larval dace, and by juvenile chub (note the small sample size for juvenile bluehead sucker). Vascular plant material was noteworthy in stomachs of younger dace and chub, while bluehead sucker frequently contained inorganic materials. The latter observation is undoubtedly an artifact of the bottom-feeding habits of this fish, reflected by its highly specialized mouth morphology (Smith 1966). In general, the number of taxonomic categories found in stomachs increased with increasing size (age). The few flannelmouth sucker larva (n=6) and juvenile (n=5) stomachs examined contained chironomid larvae (67 and 100%), chironomid pupae (0 and 40%), ostracods (0 and 40%), and vascular plant material (0 and 20%).

Analyses of stomach contents of early life stage native fishes collected in 1992 were similar in some respects and different in others compared with results from 1991. These contrasts may partially reflect the differences in hydrology between those years (Angradi et al. 1992). With the exception of unidentified organic materials, dipterans (primarily Chironomidae) were the most frequently-occurring food group in humpback chub stomachs in 1992 (as in 1991), and also comprised the greatest relative volume of items in chub stomachs (Table 4.6). The proportion of chub stomachs that contained plant materials (seeds, detritus and algae) was similar between 1991 and 1992, indicating perhaps that they do not necessarily rely more on these materials for sustenance during extended periods of flood. Moderate utilization by humpback chub of ostracods in 1991 was contrasted with a lack of use of that taxonomic group in 1992, an observation also noted for speckled dace and bluehead sucker (Table 4.6). Foods of humpback chub analyzed from 1989 and 1990 from the LCR (Angradi et al. 1992) were for the most part similar to 1991 and 1992 analyses.

The small sample of YOY bluehead sucker collected in 1992 (Table 4.6) revealed a similar pattern of food use to that observed in 1991. This pattern generally held for speckled dace as well, with the exception of a greater frequency of occurrence of inorganic materials in stomachs from 1992. Few YOY flannelmouth sucker were collected in 1992 (Table 4.6), and diet for the most part did not diverge substantially from that observed in 1991.

Of particular note regarding stomach contents of LCR native fishes was the incidence of exotic Asian tapeworm (*Bothriocephalus acheilognathi*) in stomachs of speckled dace and humpback chub (Table 4.7), partial results of which were earlier reported by Angradi et al. (1992) and Clarkson (1992). Cyclopoid copepods are the intermediate hosts for this cestode (Pool 1984; Marcogliese and Esch 1989). The absence of copepods in stomachs of humpback chub and the high levels of tapeworm infestation is paradoxical. This observation is seemingly a result of the infrequent availability of copepods to humpback chub, since it was unlikely that the copepods were digested in chub stomachs prior to preservation (collections were by seine and dip net).

Also of note is the history of infestation patterns in humpback chub (Table 4.7). Three larvae, 11 early post-larvae, and 47 adult and sub-adult chub examined from 1989 did not contain tapeworms, while 92% of 24 larvae, 100% of 13 early post-larvae and 2 juveniles, and 44% of 18 adults (the latter collected from both the LCR and Colorado River mainstem) examined from 1990 were infested. Chub from the 1991 year class were not infested until they exceeded 50 mm in length (September), and as post-larvae and older in the 1992 year class. Marcogliese and Esch (1989) studied the complex seasonal and annual interactions between *B. acheilognathi*, copepod, and mosquitofish (*Gambusia affinis*) populations. Intrapopulation dynamics of the parasite may be related to temperature, temperature-dependent rejection

responses, immune responses, density-dependent factors, or other poorly studied phenomena (Granath and Esch 1983a).

The high incidence of infestation of adult chub in 1990, the first year the tapeworm appeared in stomachs, ostensibly indicates that adult chub also occasionally ingest cyclopoid copepods, perhaps incidentally during ingestion of *Cladophora*. It is also possible that infestation may be achieved by consuming other infested fishes. Piscivory by adult humpback chub was noted by Kaeding and Zimmerman (1983) and Kubly (1990). We have not found other references to this avenue of *B. acheilognathi* infestation, however. Clearly, further research in this area is needed.

Asian tapeworm also infested speckled dace collected from the LCR in 1991 and 1992 (Table 4.7). The infestation rate for dace was higher in 1992 than 1991, although in total it was lower than the average infestation rate for humpback chub.

No tapeworms have been found in flannelmouth sucker stomachs. Heckman et al. (1987) did not find this parasite in guts of flannelmouth sucker from the Virgin River in Utah, although five cyprinid species from that locality and Beaver Dam Wash in the Virgin River drainage in Arizona were infested. Although copepods were identified in stomachs of bluehead sucker (Angradi et al. 1992), we did not find tapeworms in that species either.

Effects of the tapeworm on its hosts are not well studied, but may include reduced growth, depressed swimming ability via elevated muscle fatigue, other debilitating effects, and elevated mortality (Granath and Esch 1983b). The latter effect perhaps would be most apparent to YOY fishes during their first winter as a result of a reduced ability to build fat reserves.

Objective 3.7. Determine the age structure and growth rates of native fishes of the Colorado River in Grand Canyon. Relate these life history features to hydrologic and thermal conditions experienced by the fishes during their growth to present size.

Methods and Progress

Otolith Analyses

Larval and post-larval specimens of native fishes were collected and preserved in 95% ethanol. A minimum of 10 larvae or post-larvae (<30 mm TL) of each species were collected on a weekly basis when present. For YOY specimens >30 mm TL, heads were removed and preserved separately from 10 humpback chub and 20 of the other native species on a monthly basis. Posterior segments of those specimens were preserved in 10% formalin for stomach analyses (Objective 3.5). A subcontract to the University of Texas at Austin has been awarded for preliminary analyses of otolith daily growth rings in humpback chub from Grand Canyon. Otolith analyses of other native species have been subcontracted with the Hawaii Institute of

Geophysics at the University of Hawaii in Manoa, and an initial sample of 79 speckled dace, 69 bluehead sucker, and 47 flannelmouth sucker collected from the LCR and Colorado River has been shipped there for analyses by Dr. Dean Radtke.

Length-Frequency Analyses

Frequency distributions of total lengths of humpback chub and speckled dace caught by seine and dip net were constructed for all months of collection. Sample sizes of flannelmouth sucker were too small for this analysis in 1991 and 1992, as were those for bluehead sucker in 1992. For the most part, length-frequency distributions of putative YOY humpback chubs were completely segregated from larger size classes, and thus mean lengths could be accurately compared among months and years.

Results and Discussion

Otolith Analyses

See Appendix 4.1 for a preliminary report by Dr. Dean Hendrickson of the University of Texas, Austin, on the utility of otoliths for aging humpback chub.

Length-Frequency Analyses

Growth of the 1991 humpback chub cohort between November and May was nearly static according to seine and dip net captures (Figure 4.5). Mean length of this cohort in November was 82 ± 2.0 mm (SE), increased to 85 ± 2.6 mm in December, and remained nearly constant at $86-88 \pm 0.9-1.6$ mm thereafter through the end of their first year of life in May.

Collections of putative specimens from the 1992 humpback chub cohort first appeared in May (Figure 4.5), but ceased following August (Figure 4.6). Mean length of 49 chub larvae collected in May 1992 was 12 ± 0.3 mm. Twelve larvae and early post-larvae collected in July (no YOY were taken in June) had a mean length of 18 ± 1.7 mm.

Figure 4.7 presents length-frequency histograms for mixed-age speckled dace seine and dip net collections for November 1991 through May 1992. Figure 4.8 presents similar data for June 1992 through December 1992. The occasional appearance of larvae in colder months indicates that some spawning occurs throughout the year, perhaps in thermally-constant tributary springs to the LCR.

Captures of age-0 bluehead and flannelmouth suckers between December 1991 and December 1992 were rare, especially for the latter species. Bluehead lengths in December 1991 ranged between 26 and 135 mm ($n=11$), and were thought to represent age-0 fish produced from an extended spawn in May-July of 1991 and a secondary spawn in October following summer floods (Angradi et al. 1992). By May of 1992, the range in length of possibly age-0 blueheads

spanned 39-176 mm (n=3). The paucity of putative YOY bluehead in catches between November 1991 and May 1992 following what was the most numerous of YOY species in summer 1991 may indicate movements out of the LCR, habitat use shifts away from nearshore habitats less susceptible to seining, or high levels of post-larvae mortality. As occurred with humpback chub, collections of 1992 YOY bluehead sucker were rare compared to catches in 1991, and occurrence in seine and dip net collections ceased after July.

A total of 12 flannelmouth suckers were captured in seines and dipnets between December 1991 and May 1992. Lengths ranged from 21-157 mm. The scarcity of juvenile flannelmouth catches likely reflects their low absolute abundance in the LCR. Only small numbers of larvae of this species were encountered in the LCR in 1991 (Angradi et al. 1992) and 1992. The presence of larvae in December, however, indicates that autumn spawning of this species also occurs.

The disparity of captures of larval and post-larval fishes between 1992 and 1991 (Angradi et al. 1992) may be partly attributable to the inefficiency of sampling created by high discharges and turbidity in 1992, but it was more likely due to a scarcity of larvae. It is probable that flooding had deleterious impacts on the survival of YOY native fishes in the LCR in 1992. After flooding at the end of May and early June, very few bluehead sucker or humpback chub larvae were found (Figure 4.3). Speckled dace meso- and metalarvae were found at various locations along the river after the May-June flood, but in low numbers. Dace metalarvae were widespread after an even larger flood in July, but again in low densities. Floods are known to flush larvae downstream (Harvey 1987). In addition, because larvae are primarily sight feeders (Braun 1978), sustained turbidity associated with elevated flows may result in starvation. The physical rigors created by high current velocities and high levels of turbidity may also cause mortality through physiological stress.

Objective 3.8. Compare otolith edge chemistry of native fishes collect in tributary and mainstem habitats for use in growth and movement analysis.

See Appendix 4.1 for a preliminary report by Dr. Dean Hendrickson of the University of Texas, Austin, on the utility of otolith edge chemistry for use in growth and movement analyses.

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.

Methods and Progress

An inflatable kayak trip from Blue Spring (21 km above the mouth) to the LCR mouth was taken in January to characterize longitudinal variations in water chemistry. Water temperature, conductivity, pH, and dissolved oxygen were measured with a Hydrolab Surveyor 3 datalogger and H2O transmitter. A Hach Model AL-36 digital-titrator kit was used to measure alkalinity (brom-cresol green-methyl red endpoint, sulfuric acid titrant) and carbon dioxide (phenolphthalein endpoint, sodium hydroxide titrant). Turbidity measurements were taken using a Milton Roy Spectronic Mini-20 nephelometer. Nitrate-nitrite nitrogen (cadmium reduction method) and soluble reactive phosphate (ascorbic acid method) were measured in the field using a Hach Model DREL 2000 spectrophotometer.

Results and Discussion

Longitudinal patterns of selected water quality parameters in January 1992 (Figure 4.9) were similar to those observed in October (Angradi et al. 1992). January pH was nearly identical to the pattern and levels observed in October, ranging from 6.0 in the Blue Spring outflow 21 km above the mouth to 7.6 near the confluence. Conductivity levels exhibited a trend identical to that observed in October, but at slightly lower levels. This presumably was due to dilution by upper basin runoff. In addition, above-base discharges during the January sampling period also may have reduced overall levels of alkalinity below Blue Spring compared with its October levels.

Conversely, dissolved oxygen and carbon dioxide levels were generally higher in January, which was probably attributable to the greater solubility of these gases at lower temperature. It is not known the presumptive cause(s) of elevated carbon dioxide levels. Turbidity levels below the Blue Spring outflow exceeded 100 NTU's at all sampling sites.

Work Task 3.10. Performance of the thermal tolerance tests on the young-of-the-year humpback chub.

Objective 3.3 summarized the problems experienced collecting viable propagules from humpback chub in the LCR in 1992. A draft study design for planned egg collections in 1993 has been sent for review to Aquatic Coordination Team members. A study plan for conducting thermal tolerance tests on chub larvae obtained from this effort is currently in preparation.

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TABLE 4.1. Relative abundances (percent) and sample size (in parentheses) of species caught by three gear types in the Little Colorado River, May-June 1992.

SPECIES	HOOP NETS	SEINES	DIP NETS
Rainbow trout	<0.1 (1)	---	---
Common carp	<0.1 (1)	---	---
Fathead minnow	0.3 (8)	---	---
Humpback chub	36.9 (862)	64.2 (34)	16.7 (1)
Speckled dace	52.6 (1227)	22.6 (12)	33.3 (2)
Bluehead sucker	3.9 (91)	3.8 (2)	50.0 (3)
Flannelmouth sucker	5.3 (124)	7.5 (4)	---
Channel catfish	0.8 (18)	---	---
Plains killifish	<0.1 (1)	---	---
Unidentified	<0.1 (1)	1.9 (1)	---

TABLE 4.2. Movements (in meters; sample sizes in parentheses) of humpback chub based on recaptures in the Little Colorado River, 1987-1992.

YEAR	MEAN DOWNSTREAM DISTANCE	MEAN UPSTREAM DISTANCE	MEAN ABSOLUTE DISTANCE
1987	316 (16)	334 (26)	286 (48)
1988	737 (33)	320 (46)	376 (164)
1989	1289 (20)	467 (38)	573 (76)
1990	697 (17)	765 (7)	307 (56)
1991	282 (17)	918 (15)	387 (48)
1992	208 (11)	193 (15)	167 (31)

TABLE 4.3. Substrate categories used in AGFD habitat studies in the Little Colorado River. Size designations are based on grouped substrate classes of Lane (1947). Other categories were developed to account for unique substrates of the LCR.

CATEGORY	DEFINITION
Boulders	4.096-0.256 m dia
Cobbles (rubble)	256-64 mm dia
Gravel	64-2 mm dia
Sand	2-0.062 mm dia
Silt	62-4 μ m dia
Clay	4-0.24 μ m dia
Bedrock	>4.096 m dia
Calcium Carbonate	Unconsolidated fine floc
Tufa	Consolidated calcium carbonate
Detritus	Decomposing organic material

TABLE 4.4. Monthly mean densities of invertebrates in drift samples from 1991 and 1992. Densities are mean numbers of individuals per 1000 m³.

CATEGORY	1992														
	MAY (n=11)	JUN (n=30)	JUL (n=10)	AUG (n=3)	SEP (n=2)*	OCT (n=6)*	NOV (n=9)	DEC (n=10)	JAN (n=4)	APR (n=7)	MAY (n=28)	JUN (n=11)	JUL (n=4)	AUG (n=1)*	SEP (n=1)*
Diptera	38.4	190.3	136.8	7.1	283.1	2346.8	5.5	27.3	0.4	50.6	60.7	58.2	68.5	2.9	40.2
Homoptera	7.0	22.9	5.1	3.4	60.7	2921.6	5.1	6.1	---	17.7	15.5	112.7	4.4	---	---
Ephemeroptera	2.8	5.9	2.3	---	---	983.4	1.3	299.0	4.5	0.2	1.2	15.8	32.2	---	---
Hymenoptera	2.7	7.2	5.1	0.2	20.2	74.0	0.1	0.3	0.4	6.6	12.1	10.0	7.8	---	---
Hemiptera	0.4	3.6	0.8	0.1	20.2	35.7	0.1	0.3	---	---	4.2	12.4	1.8	---	---
Tricoptera	2.6	2.8	1.3	<0.1	20.2	5.1	0.2	0.7	1.4	---	2.3	0.3	2.2	8.7	80.4
Neuroptera	---	0.3	---	<0.1	---	35.3	---	---	---	---	16.3	---	1.7	---	---
Thysanoptera	---	1.5	7.6	0.3	---	0.4	---	---	---	---	29.2	0.6	---	---	---
Coloptera	1.3	2.5	0.1	0.1	20.2	2.7	---	0.1	0.1	---	3.4	14.5	0.2	---	---
Mollusca	0.1	4.0	<0.1	<0.1	---	---	0.1	---	---	---	---	---	---	---	---
Nematoda	0.2	<0.1	---	---	40.4	---	---	---	---	---	---	---	---	---	---
Arachnida	1.0	0.9	<0.1	---	---	1.1	<0.1	---	---	---	10.4	2.2	1.7	---	40.2
Annelida	<0.1	0.1	---	---	20.22	---	---	---	---	---	1.1	---	---	---	---
Ostracoda	0.8	0.1	---	0.1	---	---	---	---	---	---	---	---	---	---	---
Protozoa	0.5	0.3	---	---	---	---	---	---	---	---	---	---	---	---	---
Collembola	---	0.3	---	<0.1	---	---	---	---	---	---	---	2.8	0.00	---	---
Lepidoptera	---	0.1	<0.1	---	---	---	---	---	---	---	0.1	---	---	---	---
Streptelera	---	<0.1	---	---	---	---	---	---	---	---	---	0.6	---	---	---
Other Insects	0.2	2.0	7.7	0.3	141.5	0.4	---	---	---	---	---	---	---	---	---
TOTAL	58.0	243.2	159.2	11.3	626.9	6406.1	12.5	333.8	6.9	75.1	156.6	230.2	120.5	11.6	160.9

* Drifts were collected during the day only.

TABLE 4.5. Frequency of occurrence (percent) of selected items in stomachs of early life stage humpback chub, Little Colorado River, 1989-1990. L=larvae, P=pupae, A=adults, N=nymphs.

CATEGORY	1989			1990			1991		
	<25 mm (n=3)	25-50 mm (n=11)	>50 mm (n=0)	<25 mm (n=24)	25-50 mm (n=13)	>50 mm (n=2)	<25 mm (n=50)	25-50 mm (n=34)	>50 mm (n=21)
Chironomidae-L	100.0	90.9	--	70.8	38.5	0.0	80.0	55.9	57.1
Chironomidae-P	0.0	18.2	--	29.2	7.7	0.0	14.0	14.7	4.8
Chironomidae-A	66.7	18.2	--	12.5	15.4	50.0	32.0	14.7	9.5
Thysanoptera-A	66.7	27.3	--	4.2	0.0	50.0	24.0	8.8	4.8
Vegetation	0.0	0.0	--	0.0	0.0	0.0	0.0	11.8	9.5
Ostracoda	0.0	0.0	--	0.0	0.0	0.0	6.0	8.8	14.3
Inorganic	33.3	0.0	--	0.0	7.7	50.0	2.0	0.0	4.7
Ephemeroptera-N	0.0	72.7	--	0.0	23.1	0.0	0.0	2.9	0.0

TABLE 4.6. Relative volumes (percent) and frequency of occurrence (percent; in parentheses) of items in stomachs of early life stage native fishes, Little Colorado River, 1992.

Category	Humpback chub			Bluehead sucker			Finnelelmouth sucker			Speckled dace		
	Larvae (<25 mm) n=20	Post-Larvae (25-50 mm) n=1	Juveniles (51-100 mm) n=28	Larvae (<28 mm) n=13	Post-Larvae (28-50 mm) n=1	Juveniles (51-100 mm) n=1	Larvae (<28 mm) n=5	Post-Larvae (28-50 mm) n=0	Juveniles (51-100 mm) n=3	Larvae (<19 mm) n=25	Juveniles (19-50 mm) n=12	Adults (51-100 mm) n=38
Diptera	48.6 (70.0)	---	14.8 (46.4)	60.0 (61.5)	---	5.0 (5.0)	58.0 (60.0)	---	18.7 (66.7)	50.1 (76.0)	10.8 (33.3)	5.2 (36.8)
Thysanoptera	7.8 (15.0)	---	0.4 (7.1)	---	---	---	---	---	---	---	1.5 (8.3)	---
Unidentified organics	18.0 (60.0)	55.6 (100)	63.6 (92.9)	26.2 (38.5)	100.0 (100.0)	60.0 (60.0)	26.0 (40.0)	---	79.3 (100.0)	31.8 (60.0)	63.7 (91.7)	71.7 (100.0)
Inorganic materials	3.7 (20.0)	---	1.4 (3.6)	13.8 (30.8)	---	35.0 (35.0)	8.0 (40.0)	---	---	8.6 (36.0)	6.9 (41.7)	5.0 (23.7)
Seeds	21.9 (40.0)	---	1.8 (3.6)	---	---	---	8.0 (40.0)	---	---	4.0 (8.0)	1.0 (16.7)	2.4 (5.3)
Hymenoptera	---	33.3 (100.0)	3.6 (14.3)	---	---	---	---	---	---	0.8 (4.0)	1.7 (8.3)	1.8 (2.6)
Collembola	---	11.1 (100)	1.2 (3.6)	---	---	---	---	---	---	---	---	---
Hemiptera	---	---	0.5 (3.6)	---	---	---	---	---	---	3.1 (16.0)	8.5 (16.7)	---
Nematoda	---	---	2.9 (14.3)	---	---	---	---	---	---	0.4 (8.0)	---	1.3 (2.6)
Homoptera	---	---	0.6 (3.6)	---	---	---	---	---	---	---	---	---
Trichoptera	---	---	0.5 (3.6)	---	---	---	---	---	---	---	---	6.5 (15.8)
Coleoptera	---	---	2.2 (3.6)	---	---	---	---	---	---	---	---	---
Ephemeroptera	---	---	3.6 (3.6)	---	---	---	---	---	---	---	---	1.8 (7.9)
Mollusca	---	---	0.2 (3.6)	---	---	---	---	---	2.0 (33.3)	---	---	---
Aquatic vegetation	---	---	1.3 (14.3)	---	---	---	---	---	---	0.2 (4.0)	---	3.0 (13.2)
Detritus	---	---	---	---	---	---	---	---	---	---	4.2 (8.3)	---
Other organisms	---	---	1.3 (10.7)	---	---	---	---	---	---	---	0.2 (8.3)	0.6 (5.3)

TABLE 4.7. Frequency of occurrence (percent; sample size in parentheses) of Asian tapeworm, *Bothriocephalus acheilognathi*, infestati on in stomachs of humpback chub and speckled from the Little Colorado River, 1989-1992.

	1989	1990	1991	1992
Humpback chub				
Larvae (<25 mm)	0 (3)	92 (24)	0 (50)	0 (20)
Post-larvae (25-50 mm)	0 (11)	100 (13)	0 (34)	100 (1)
Early juvenile (50-100 mm)	---	100 (2)	62 (21)	64 (33)
Adult/sub-adult (> 100 mm) ^a	0 (47)	44 (18)	---	---
Speckled dace				
Larvae (<19 mm)	---	---	0 (130)	---
Juvenile (19-50 mm)	---	---	2 (45)	23 (13)
Adult (> 50 mm)	---	---	0 (53)	15 (40)

^a includes specimens from the mainstem Colorado River

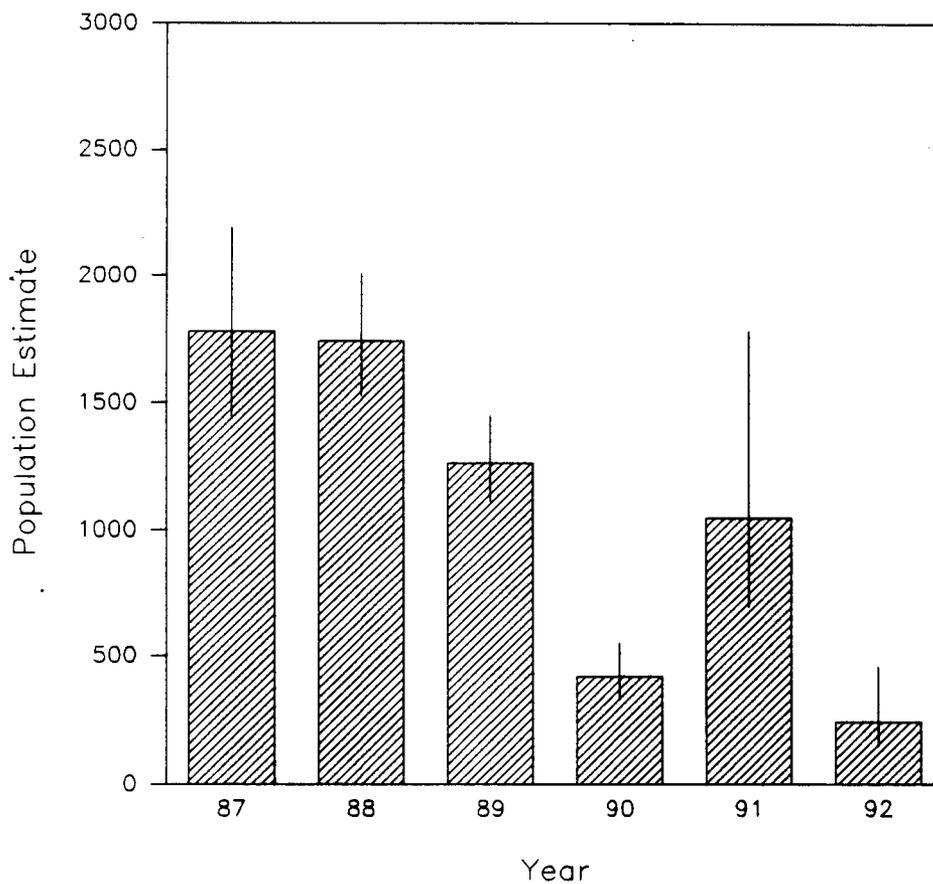


FIGURE 4.1. Modified Schnaebel population estimates for humpback chub > 150 mm total length from the Little Colorado River, 1987-1992. Estimates were based on 30 day spring monitoring periods in the lower 1200 m of the river. Vertical lines indicate 95% confidence intervals.

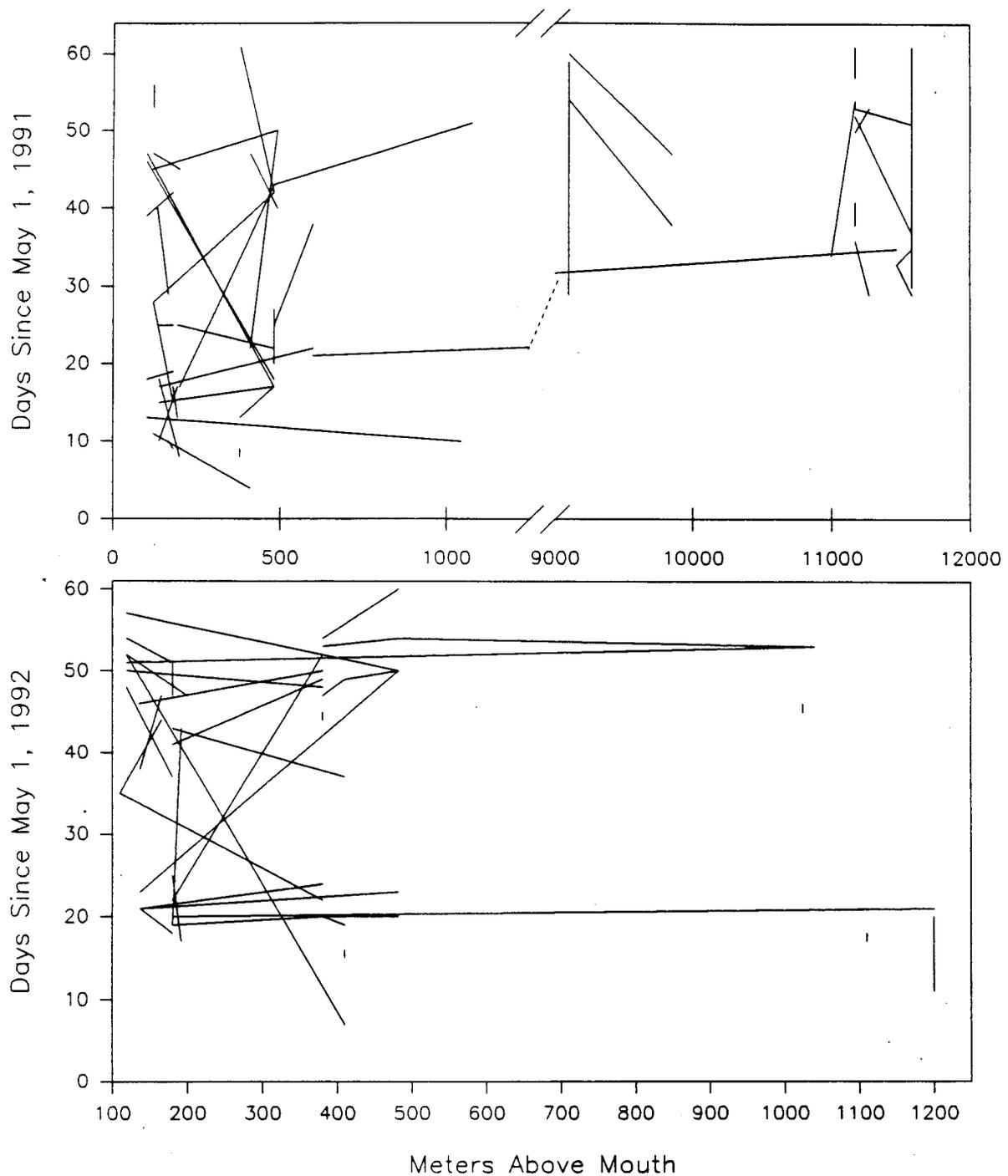


FIGURE 4.2. Movements of humpback chub >150 mm total length based on hoop net recaptures in the Little Colorado River. Movements from 1991 are based on net sets in the lower 12 km (top), and movements from 1992 are based on net sets from the lower 1.2 km (bottom).

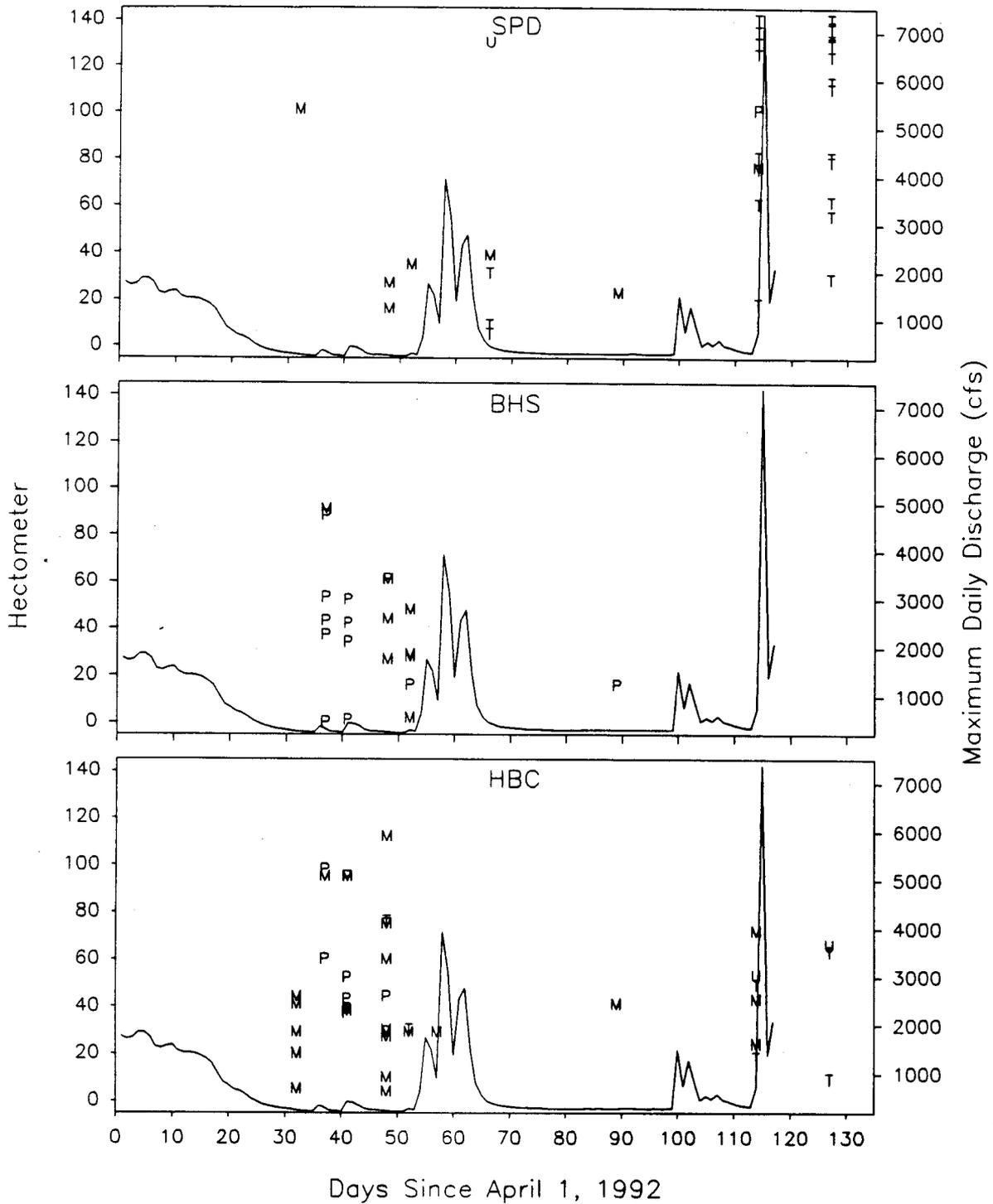


FIGURE 4.3. Longitudinal and temporal distributions of larvae and mean daily discharge (cfs), Little Colorado River, 1992. Larval occurrence data from the longitudinal surveys are shown for the final day of each survey (32, 37, 41, 48, 52, 57, 66, 74, 89, 114, 127, and 156 days past April 1). Symbols indicate the following larval stages: P=protolarvae, M=mesolarvae, T=metalarvae, U=unknown.

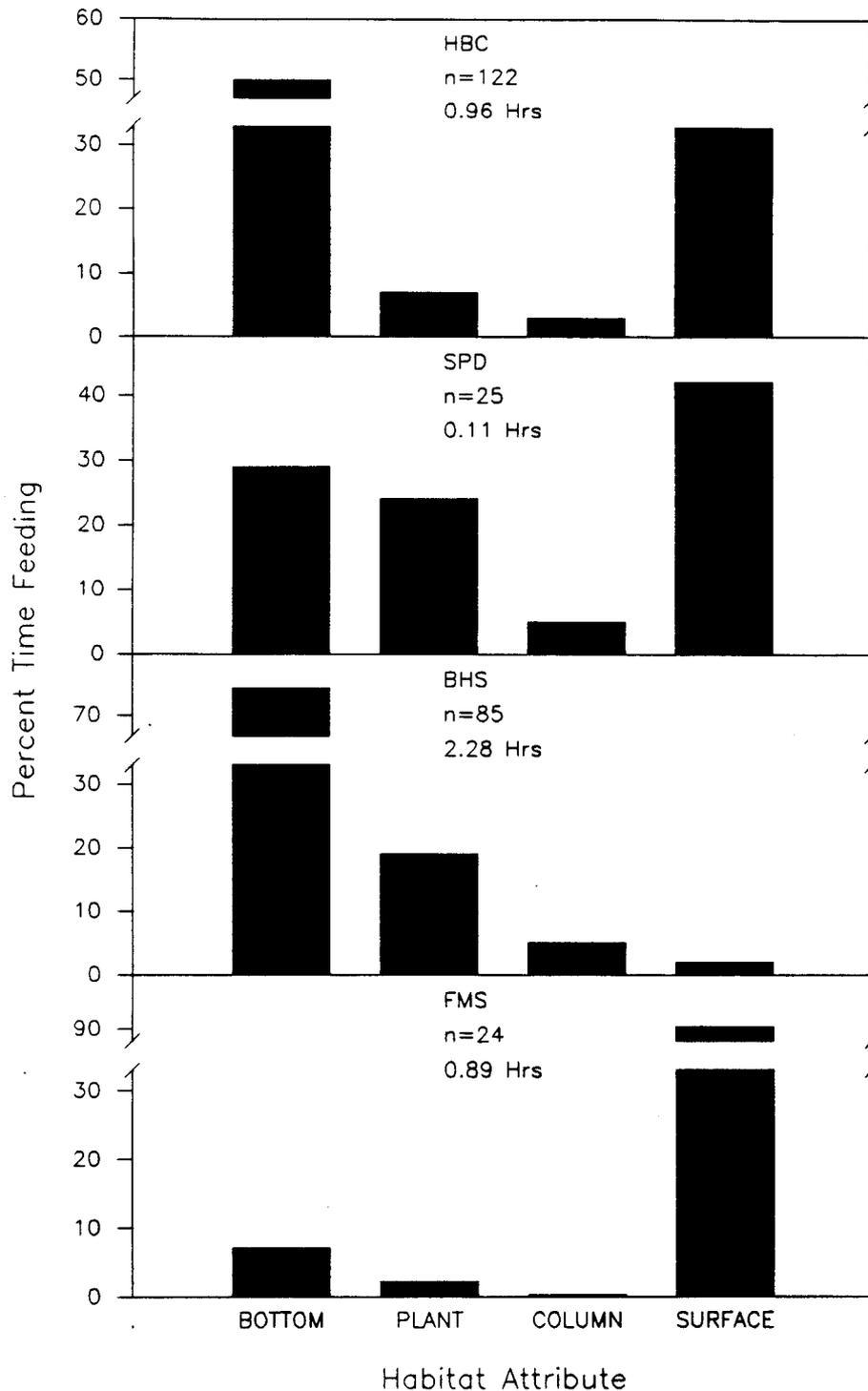


FIGURE 4.4. Foraging time budgets (percent) of early life stage native fishes in the Little Colorado River, 1991. The number of fish (n) and total time of observation (hrs) spent foraging are presented. Total hours observed (including non-feeding activity) for each species was: humpback chub (HBC)=9.25, speckled dace (SPD)=1.80, bluehead sucker (BHS)=6.42, flannelmouth sucker (FMS)=1.80.

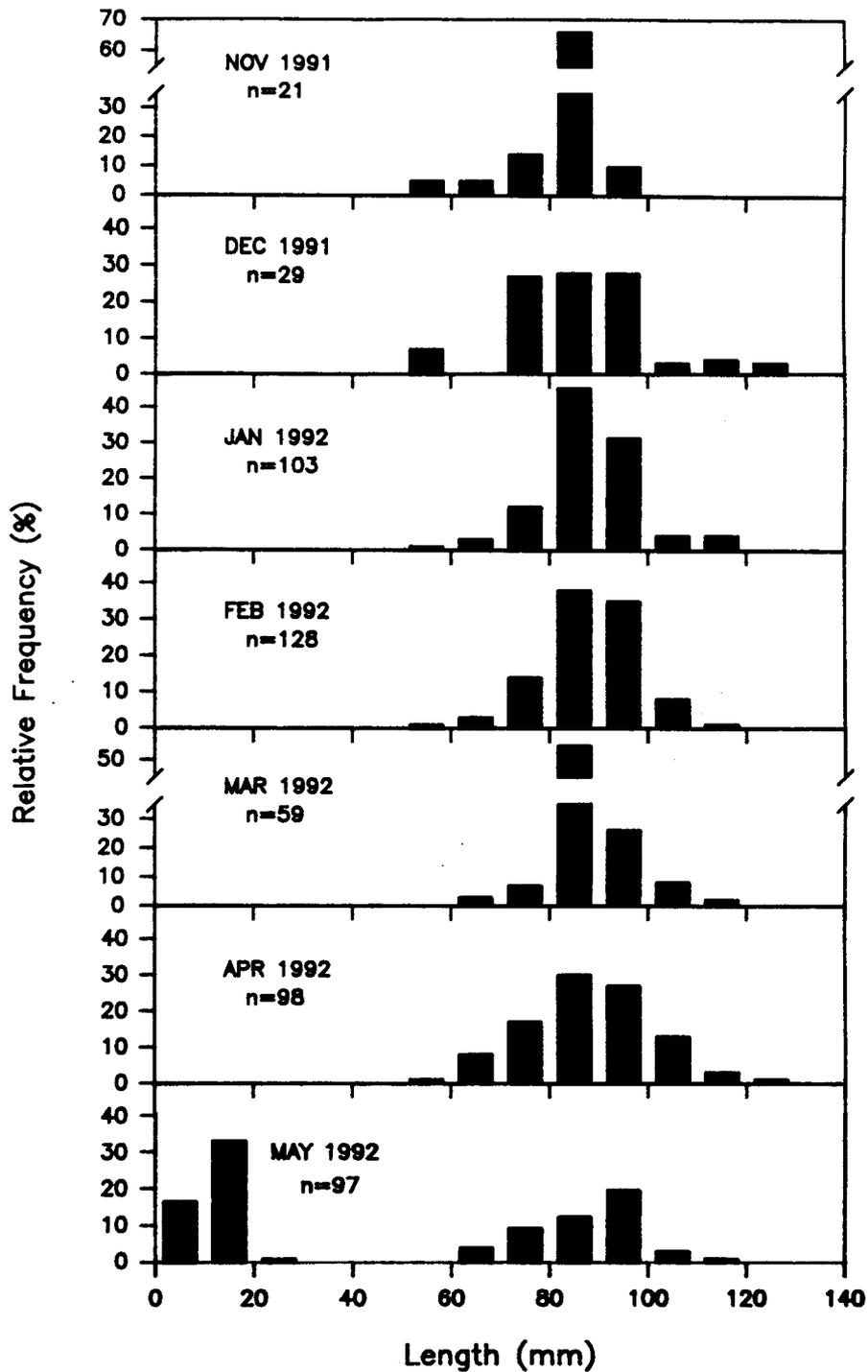


FIGURE 4.5. Length-frequency distributions for putative age-0 (except May) humpback chub collected by seine and dip net in the Little Colorado River, November 1991-May 1992.

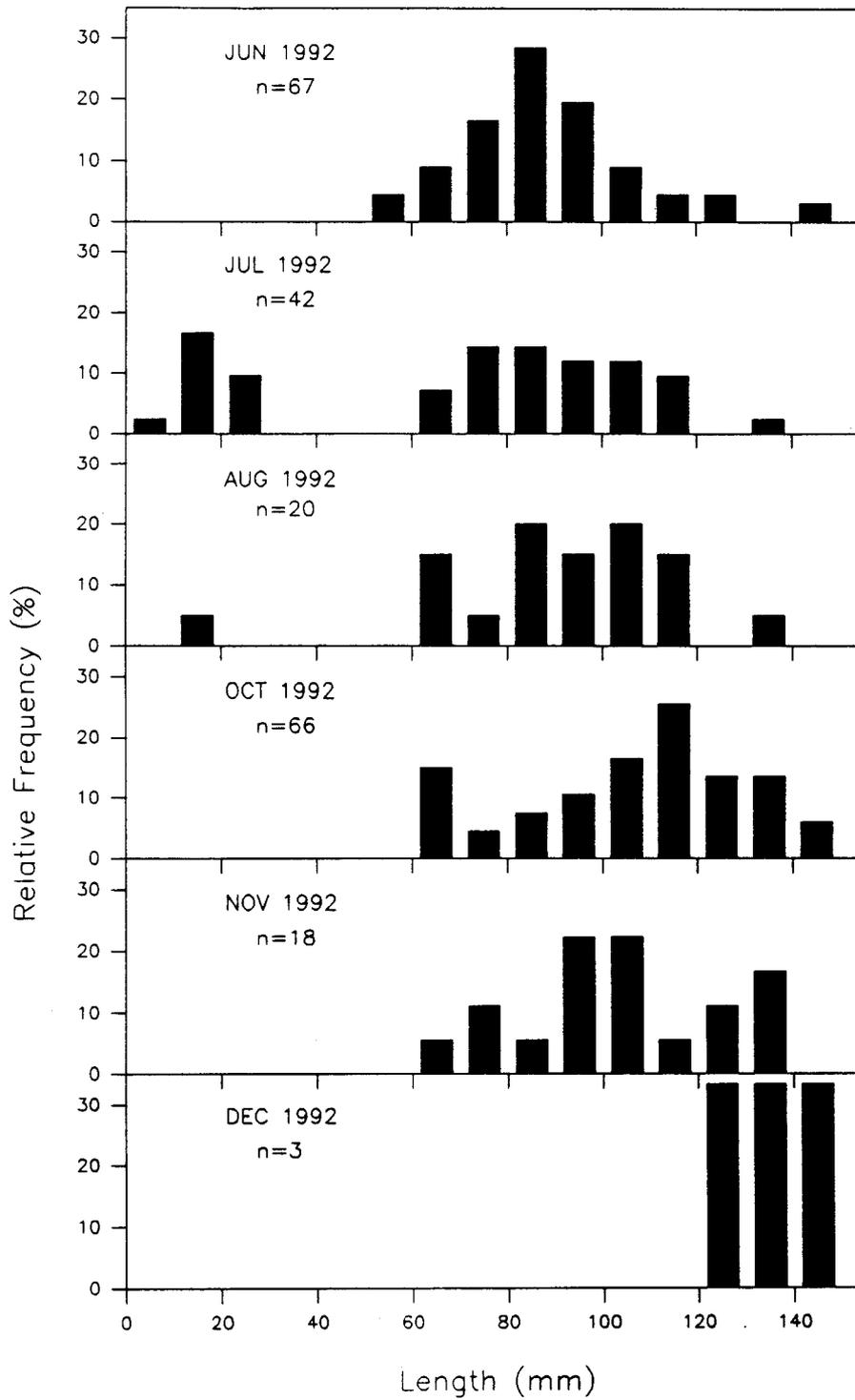


FIGURE 4.6. Length-frequency distributions for putative age-0 and age-1 humpback chub collected by seine and dip net in the Little Colorado River, June 1992-December 1992.

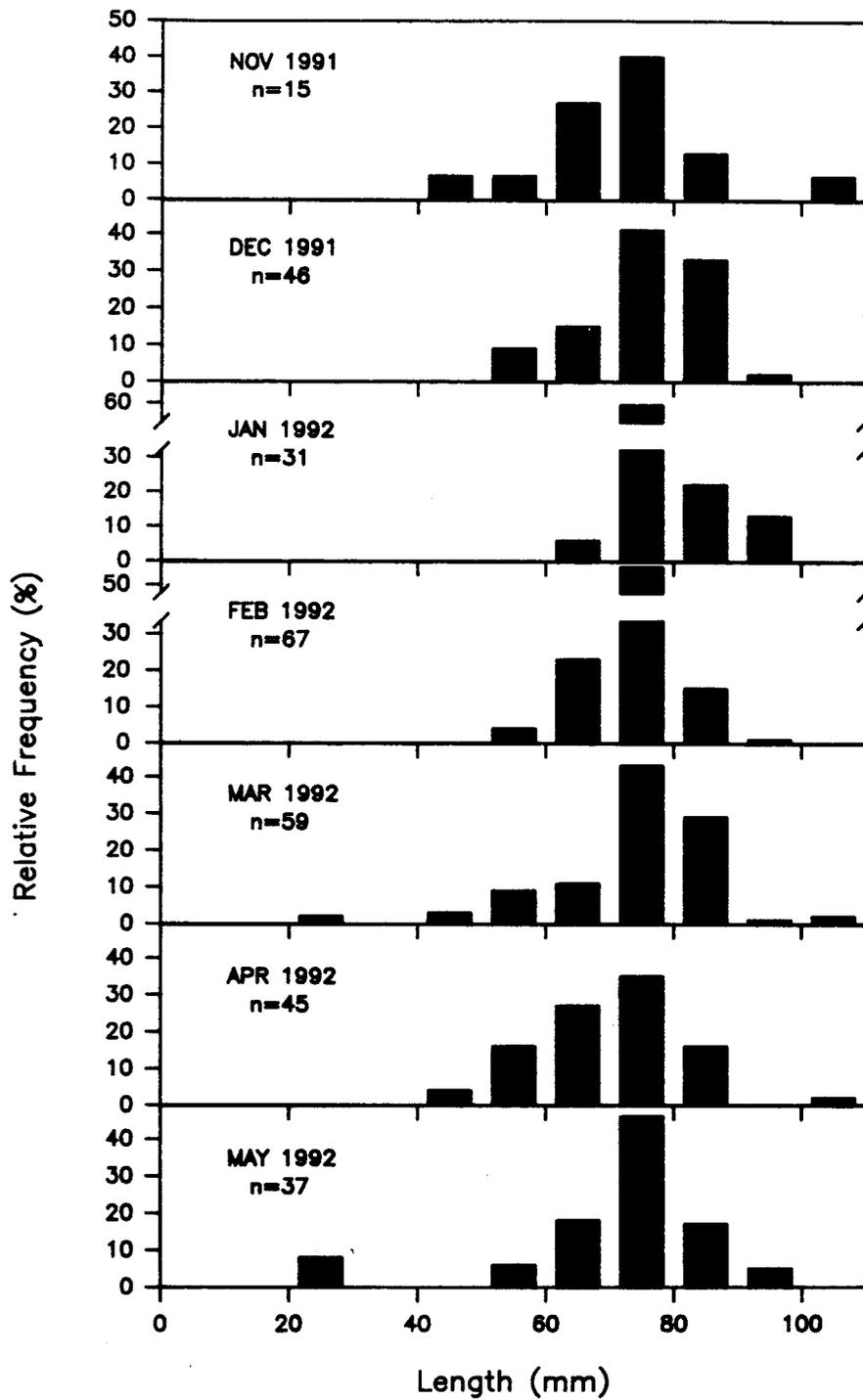


FIGURE 4.7. Length-frequency distributions for speckled dace of mixed age collected by seine and dip net in the Little Colorado River, November 1991-May 1992.

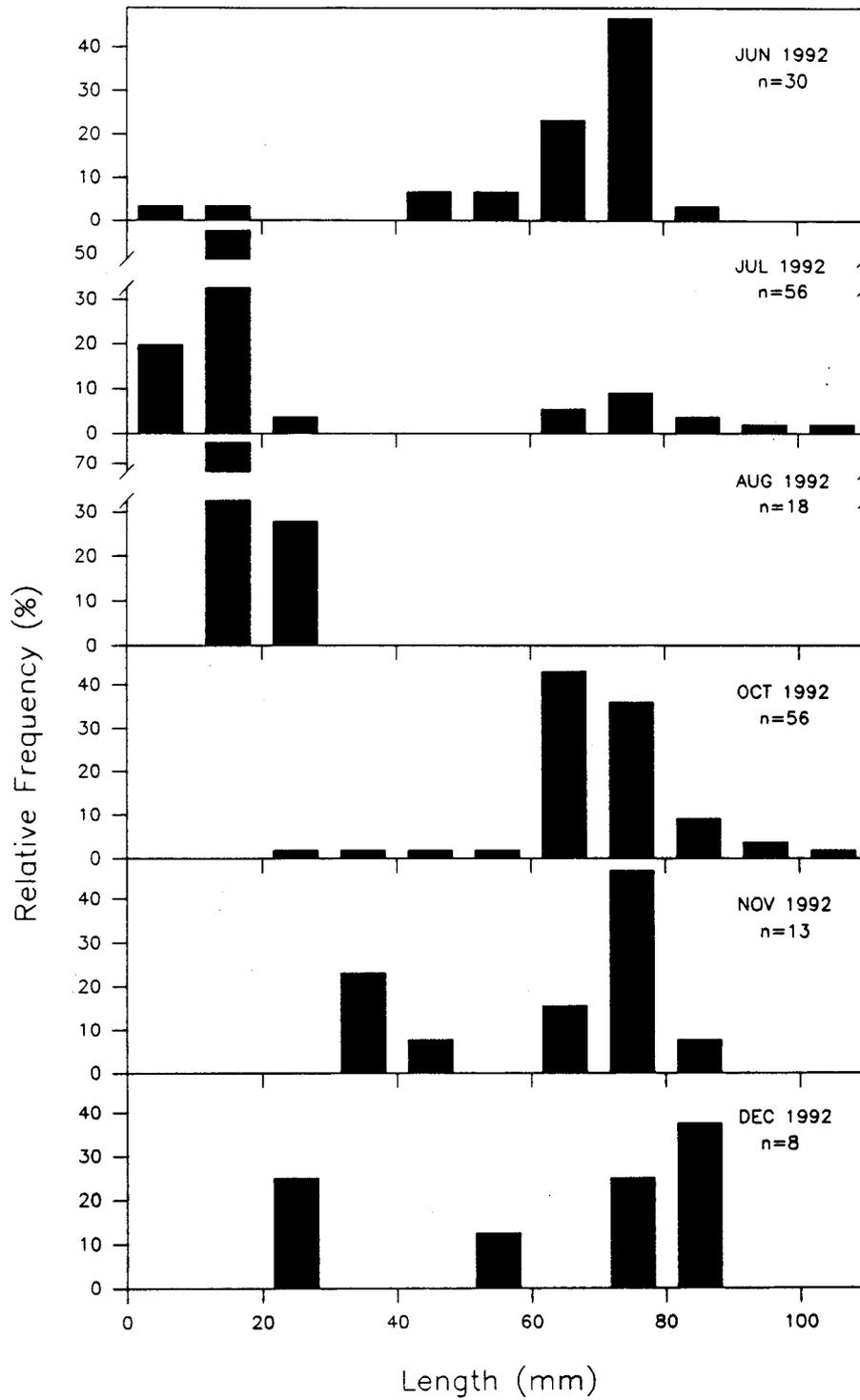


FIGURE 4.8. Length-frequency distributions for speckled dace of mixed age collected by seine and dip net in the Little Colorado River, June 1992-December 1992.

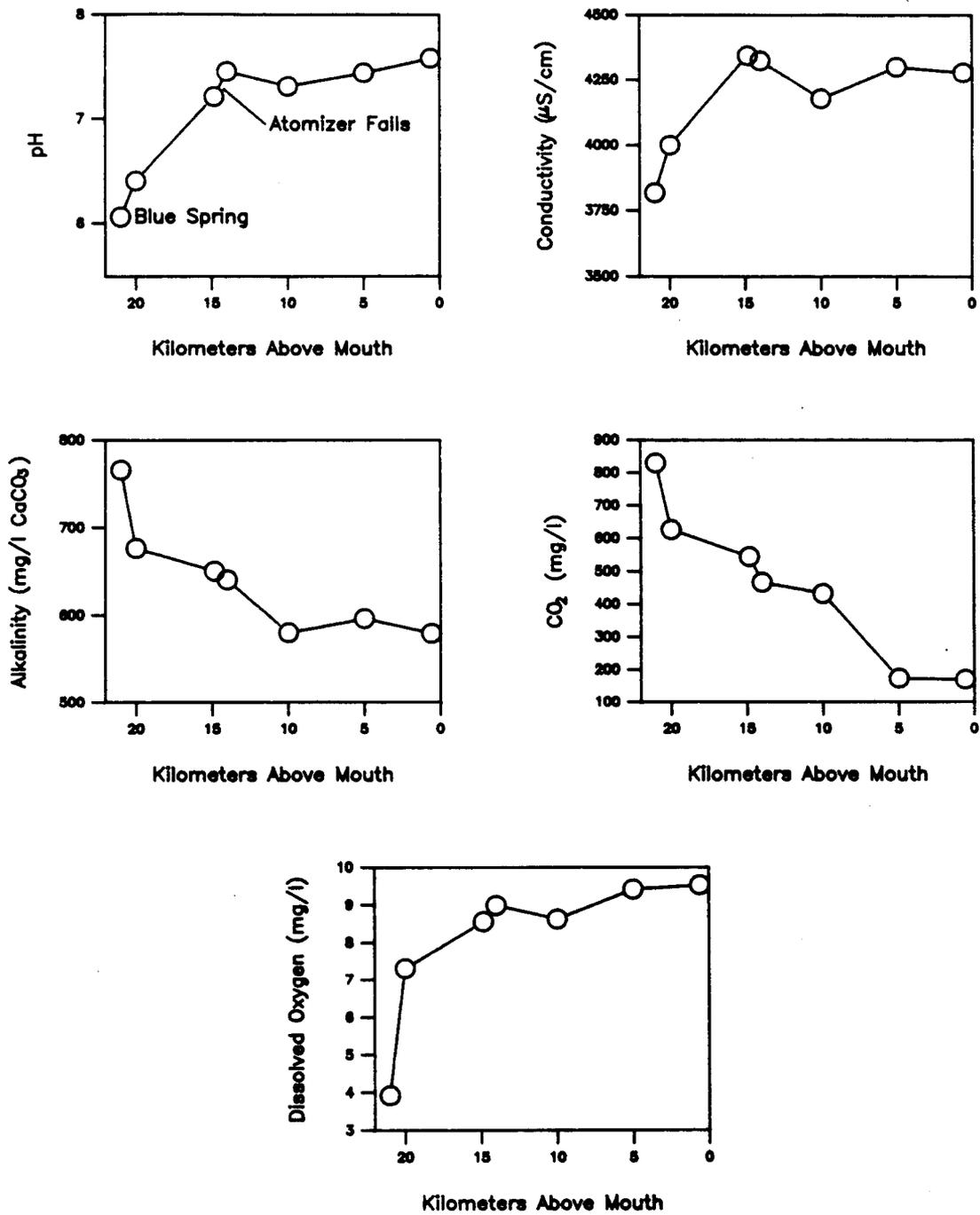


FIGURE 4.9. Longitudinal patterns of selected water quality parameters from the Little Colorado River, January 1992.

APPENDIX 4.1

**PROGRESS REPORT ON A STUDY OF THE UTILITY OF
DATA OBTAINABLE FROM OTOLITHS TO
MANAGEMENT OF HUMPBACK CHUB (*GILA CYPHA*) IN
THE GRAND CANYON**

submitted to:

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February 5, 1993

INTRODUCTION

Daily growth increments of otoliths of fishes have been useful in many fishery applications since they have been demonstrated to provide a precise method of ageing individuals and reconstructing individual growth and, possibly, movement or habitat histories. These techniques have not been previously applied to humpback chub, but are believed to have considerable potential for providing knowledge of this difficult to sample and little-understood species. Large temperature and water quality gradients apparently traversed by individuals of this species in the Grand Canyon are of a magnitude likely to produce structural and/or chemical signals in the crystalline calcareous otoliths. If so, since otoliths grow by accretion of daily increments (much like trees develop yearly growth rings), and are stable structures, which unlike scales, are not susceptible to reabsorption except in the most extreme conditions, they retain a structural and chemical chronology of habitats occupied. If the relationships of ambient physical and chemical conditions to otolith structure and composition can be described, a chronology of habitat occupancy and growth for individuals could theoretically be reconstructed with daily precision. Such reconstructions of growth rates, birth dates, movement histories, and possibly, birth place (based on chemistry at otolith formation or during early life), could provide extremely valuable life-history information regarding timing of spawning, cohort recruitment, mortality rates, and data on other population parameters critical for management of this endangered species.

The feasibility of using otoliths and opercles of humpback chub for age estimation of individuals has been preliminarily investigated by examining otoliths and opercles from a total of 47 juvenile (ages 0 through 1+) and 43 adult (estimated ages 2 - 23) specimens collected in the Little Colorado River (71 specimens) and mainstream Colorado River (19 specimens) at various places in the Grand Canyon between 1988 and 1992. Studies are continuing, and at this point, due to both sample size and numerous other limitations, and ongoing refinements of techniques, conclusions made here are preliminary.

Structures prepared and examined included opercles of 35 specimens, one asteriscus from each of 47 specimens and a lapillus from each of 56 specimens. Seventeen specimens were evaluated using all three calcareous structures (lapillus, asteriscus and opercle). The sagitta was also examined, but found to be unsuitable for ageing purposes due to its long, delicate form and irregular increments after the larval/juvenile stage. Additional lapilli have been removed from other available specimens, and a complete inventory of specimens available for further study of calcified structures is provided.

Studies of micro-spatial variation in chemical composition of selected lapilli is in progress, using the highly accurate proton probe at the Institute of Geological and Nuclear Sciences in Lower Hutt, New Zealand. This method of analysis shows great promise of overcoming what has been indicated in recent literature to be significant inaccuracies of other techniques (Energy Dispersive X-ray diffraction and Wave Length dispersive X-ray diffraction) used in many of the published studies of microspatial elemental analysis of otoliths.

METHODS

FIELD COLLECTIONS

Adult and sub-adult humpback chub were collected during late-spring and early summer field seasons in 1989 and 1990. These were euthanized, weighed, measured, and (usually) sexes recorded prior to removal of the majority of muscle tissue and internal organs from the skeleton. Skeletons were then tagged and hung to desiccate in the generally high-temperature, dry air of the field sites. Otoliths and opercles were removed after final preparation as skeletons using dermestid beetles. If otoliths were not found outside the skull after passage through the dermestid colony, they were extracted using forceps with as little damage to the skeleton as possible.

Young-of-the-year collected from 1990 through 1992 were preserved in the field in 95% ethanol. Otoliths were extracted by removal of the dorsal surface of the cranium.

SPECIMEN PREPARATION AND EXAMINATION

Opercles were cleaned of residual soft tissues and examined under reflected and transmitted light under a binocular stereo microscope. Age estimations reported here were provided by Mr. Gary Scoppetone (United States Fish and Wildlife Service, Reno, Nevada), who has had considerable experience ageing other long-lived regional cypriniform fishes (Scoppetone, 1988; Scoppetone et al. 1986; Scoppetone and Vinyard, 1991). Subsequent estimates independently done by myself generally agreed well with those of Scoppetone. In the case of disagreement between estimates made by the author and those by Scoppetone (almost always on older individuals), the author carried out a second revision of the specimens, and in all cases, was able to understand how Scoppetone arrived at his estimate. All estimates reported here as derived from opercles are those provided by Scoppetone. When uncertainty existed, both minimum and maximum ages were reported.

Asterisci were removed from skeletonized adults, and then were mounted, sectioned and examined by Mr. Michael McCarthy, who has had experience utilizing otoliths to estimate ages of razorback sucker (McCarthy and Minckley, 1987), another long-lived, Colorado River endemic cypriniform. The author then examined the same specimens and was unable to estimate ages from them since asterisci in this species appear to grow along temporally variable growth axes. While marks which appear as though they might be annual features are visible, they are discontinuous and it is often impossible to reconstruct chronologies of growth axis shifts. Estimated ages reported here as derived from examination of asterisci are those of by McCarthy, who provided a single age estimate for each specimen.

Dr. Ed Brothers, who has extensive experience in otolith ageing studies involving a wide variety of species, concurred with this conclusion and recommended using the lapillus for ageing in this species. The sagitta was also examined but found to be extremely delicate and increments were clear only during early life. Lapilli were removed from skeletonized specimens or from young-of-the-year as described above and were then mounted, ground and examined by Dr. Ed Brothers. All age estimates based on lapilli are those of Brothers, who provided minimum and maximum estimates whenever uncertainty existed.

All counts of presumed daily increments and annuli were done on specimens by persons unaware of the size or capture dates and locations so as to assure that knowledge of collection conditions did not bias estimates. Whenever uncertainty existed regarding interpretation of one or more marks, estimated minimum and maximum ages were reported. Daily growth increment counts are the average of two counts. Counts were made on a variety of otolith fields (wherever clear increments could be found) and not on a single axis. This was done simply for convenience at this point in the study, but counts and increment measurements could be done along a fixed axis for growth reconstructions.

Length data plotted in all Figures below are actual Standard Lengths, where available, or estimated Standard Lengths derived from actual Total Lengths using regression statistics. This is due to the fact that TL only is the standard measurement taken by field collectors. SL was found to be a much more precise indicator of size with significantly lower variance than TL. The linear correlation coefficient of the SL to TL relationship for all specimens for which both measurements were available ($n=126$, 13 to 100 mm SL*) was found to be $r^2=.997$. This relationship is described by the following equation (used to compute estimated SL from measured TL):

$$TL = 1.2779979 (SL) + .0749086$$

* (note that this relationship was applied, admittedly inappropriately, to compute SL for specimens far larger than the largest specimen used in developing the relationship. This was done only because only TL was available for all larger specimens.)

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RESULTS

Progress on each of the items outlined in the proposal for this study is reported as follows:

(C indicates those items mentioned in proposal as contingent on availability of experimentally spawned ova and cultured larvae/fry and provision of adequate hatchery support facilities and staff.)

1. "A comprehensive bibliography of literature relevant to methods and problems of estimating age and growth of *Gila cypha* and chemical composition of otoliths as related to application of otolith chemistry to reconstruction of the environmental history of individuals." **The attached bibliography is provided in fulfillment of this product.** New literature relevant to this project is appearing at a very high rate. As evidence of the great interest in this highly specialized field, an international conference on "Fish Otolith Research and Application" held just before this report was finished was attended by 350 persons from 27 countries. The bibliography provided in this report will be updated in the final report. (Note that literature citations in text in this report, reflecting its interim status, are very scarce. The final report will incorporate extensive discussion of the literature).
2. "An inventory of all currently available specimens of *Gila cypha* from the Grand Canyon which are potentially useful for age and growth studies." **A complete inventory of all specimens currently housed at the Texas Natural History Collection (TNHC) of the Texas Memorial Museum at The University of Texas at Austin is provided in Appendix 1, as fulfillment of this product.** Extensive additional data on each specimen listed in Appendix 1, but not printed there, is available directly from the author. This includes additional collection location and time information, additional tag/recapture data, current locations and shipping dates of various parts (head, body, skeleton, lapilli, asterisci, opercles, gut, etc.) of each specimen, museum (Arizona State University) catalog numbers for some specimens, and notes from field collections and laboratory observations of otolith micro-structure.
- 3*. "Experimental validation of the periodicity of growth increments in *Gila cypha*." **Two approaches have been taken to validate daily increments, but difficulties have been encountered in successful completion of each.** In the first experiment, young-of-the-year specimens captured in the Little Colorado River (LCR) during May were caged and subjected to three treatments. One group was moved alternately every three days between the LCR and mainstream, while the other groups were left for the same total period in either the mainstream or LCR. Abrupt temperature changes associated with movements from one river to the other should have produced marks on otoliths which would allow both validation of their periodicity and demonstration of the nature of the mark produced by this movement if it occurred naturally. Unfortunately, the majority of the specimens in all groups did not survive the treatments. Mortality appeared to be related more to effects of being caged than to effects of temperature. Survival was lowest in cages maintained continually in the warm LCR, and highest in those held continually in the cold mainstream. Sample sizes were not intended to be adequate to demonstrate effects of temperature treatments on mortality. Otoliths of these experimental specimens have not yet been examined since such intense stress was felt likely to have invalidated the experiment.

In the second attempt to validate growth increments (and investigate temperature effects on otolith structure and chemistry - see below), experiments were conducted at Dexter National Fish Hatchery. Since humpback chub were not being cultured, a surrogate species, *Gila elegans*, was used. Eggs were fertilized and incubated until hatching following standard protocol at the hatchery. At hatching, larvae were separated into three groups held at relatively constant temperatures of 15, 21 and 27°C. Specimens were preserved from each treatment at frequent intervals for subsequent analysis of otoliths. Densities and food availability were constant among treatments, but growth rate at all temperatures was very low. Individuals of the same cohort stocked in earthen ponds on the hatchery grew at a much higher rate, but were released to wild habitats (Lake Mohave) without sampling for

otoliths. Otoliths of specimens from the temperature treatments have yet to be examined, but recently reported results from several similar studies indicate that resolution of daily increments may be difficult under such low-growth conditions. Specimens from the Dexter temperature treatment studies are at TNHC, but are not included in Appendix 1.

4. "Age estimates (years of age) for 50 selected skeletonized adult specimens of *Gila cypha* collected from the Grand Canyon by Arizona Game and Fish Department in 1989 and 1990." All age estimates obtained to date from examination of lapilli are presented in Table 1. Considering only ages estimated from lapilli, totals to date are 18 specimens more than 1 year old and 22 one year olds. Data are summarized graphically in various ways in Figures 12 - 17. Additional estimates utilizing material listed in Appendix 1 (and selected newly provided material), and re-examinations of selected specimens in Table 1, will be completed prior to filing of the final report.
5. "Age estimates (days of age) for 100 selected young-of-the-year *Gila cypha* collected by Arizona Game and Fish Department in 1989 and 1990. Contingent on outcome of 3 (above)." A total of 18 young-of-the-year (age 0+) have been aged to date (Table 1). Specimens captured subsequent to 1990 and recently provided to the author were also included in this total. Additional material from among that listed in Appendix 1, selected newly provided material, and selected re-examinations of material from Table 1, will be analyzed prior to completion of the final report.

Presumptive daily growth increments are clearly visible under light microscopy in lapilli of the smallest specimens examined. During earliest portions of otolith growth, these can generally be easily counted, but increment interval becomes increasingly small with increasing age, sometimes resulting in great difficulty resolving increments and counting them without extensive specimen preparation. Some specimens displayed interesting rapid transitions of otolith growth rates (see Plates in Appendix 2).

6. "Analysis of the feasibility of determining annual growth period duration from otoliths of post young-of-the-year individuals of *Gila cypha* for all growth periods throughout age of specimen." Daily increment counts in year 2 of life for relatively young specimens has proven possible in some specimens without extensive otolith preparation. Data on numbers of increments in years 2 and 3 for specimens where they could be counted are provided in Table 1. Increasing otolith thickness and narrowing increments as growth slows in later years, make resolution of daily increments in later years of life very difficult. The value of such data at this point, at least for the relatively small sample sizes, was not apparent, and therefore additional effort has not been devoted toward this objective. Though countable increments can be seen under light microscopy in years two and three in some specimens less than 4 years old, counting them becomes very subjective without extensive specimen preparation and (likely) use of SEM.
- 7*. "Experimental analysis of the effects of temperature changes on otolith structure in *Gila cypha*." The experiment described under item 3 above (movement of caged individuals between LCR and mainstream Colorado River) was intended also to address this objective. Apparent failure of that experiment was described above, and otoliths have not yet been examined. Examination of otoliths of selected individuals from this experiment will be completed prior to completion of the final report. Field repetition of this experiment (as has already been done once by AGFD personnel with similar results) would likely again produce the same results. Repetition of this experiment in a hatchery environment with large sample sizes is recommended (see also item 11 below), but selected otoliths from earlier attempts will be analyzed despite perceived "failure" to carry the experiment to completion as designed.
8. "Analysis of micro-spatial (=chronological) variation in elemental composition in otoliths of 20 selected individual *Gila cypha* specimens from the Grand Canyon with evaluation of the utility of such techniques for reconstruction of movement history of individuals." X-ray diffraction analysis

for elemental composition, as employed in early studies of microdistribution of elements in otoliths, and as proposed initially for this study, is now indicated to be of limited utility in this application due to low precision and relatively high detection levels. Newer techniques capable not only of detecting much lower concentrations, but which are also much more precise, are now beginning to be used in this application. Consequently, it was decided to further investigate alternative analytical techniques. A few samples were sent in December 1992 to Dr. Graeme Coote for analyses on the proton probe at the Institute of Geological and Nuclear Sciences in Lower Hutt, New Zealand. Preliminary results from that work are anticipated within a month or two of the date of this report.

- 9*. "Comparisons of total elemental composition among otoliths of 5 selected individual specimens of young-of-the-year *Gila cypha* captured in the Little Colorado River, otoliths of 5 hatchery-reared young-of-the-year *Gila cypha*, and otoliths of 5 selected *Gila cypha* suspected or known to have moved between the Little Colorado River and mainstem Colorado River in the Grand Canyon. Among sample comparisons would be used to investigate the hypothesis that elemental composition of otoliths reflects ambient water composition. Emphasis would be placed on a search for elemental markers which might be applied to determine origin (birthplace) of specimens." This set of analyses has also been delayed temporarily awaiting additional exploration of alternative analytical techniques. It is also proposed to incorporate in this analysis some other specimens from individuals of known histories in other waters. These would include bonytail reared as part of the temperature effects experiment described above.
- 10*. "Analysis of the isotopic composition of a subsample of the same (or comparable) specimens described in 9 (above). Among sample comparisons will be used to investigate the hypothesis that isotopic composition of otoliths reflects ambient water composition and or temperature. Emphasis would be placed on a search for isotopic markers which might be applied to determine origin (birthplace) of specimens." Currently, radioisotope analyses generally require sample sizes that approach or exceed whole lapilli of adult chubs. Since age and otolith structural data will be required for interpretation of results from these analyses, radioisotope studies will be performed on selected samples after completion of ageing. Alternate techniques which might be capable of revealing micro-spatial distribution of radioisotopes in sectioned otoliths is being investigated as a preliminary step toward attainment of this objective.
- 11*. "Experimental analysis of the effects of ambient temperature on otolith elemental and isotopic composition of individuals reared in constant water quality conditions." See item 9 above.
12. "Assessment of the utility of age, growth and correlative environmental history data obtainable from otoliths for humpback chub population monitoring and management in the Grand Canyon, and recommendations for future studies." See Conclusions and Discussion.

CONCLUSIONS AND DISCUSSION

Presumptive daily increments are clearly visible in humpback chub otoliths (Figure 1). Counts of all such increments have been relatively easily and reliably done on any specimens captured in the LCR prior to their first winter or prior to movement to the mainstream Colorado. Increments are generally clearly visible to the margin (Figure 2), thus providing reliable ageing of these specimens with daily precision. Relatively little preparation is generally required with such very small specimens. Though daily periodicity of increment formation under a diversity of conditions has not been validated, the limited and highly preliminary data available so far, and a voluminous literature on other species, indicate that increments formed in the LCR are almost certainly daily. Back-calculated hatch dates for young-of-the-year captured in the LCR (Table 1) agree well chronologically with anecdotal field observations of likely reproductive activity. Periodicity of increment formation should be validated, as should time of first

increment formation. The literature indicates that the first increments form almost always within a few days before or after, or exactly upon, hatching. Preserved specimens of bonytail chub from experiments carried out at Dexter should be useful for determination of time of first increment formation in that closely related species, but the same should be done with humpback chub if hatchery stocks are obtained and artificially spawned.

Most specimens taken from the mainstream Colorado River have proven much more difficult to read than are specimens of similar sizes from the LCR. Daily age estimates are impeded by narrow, poorly defined increments and odd patterns. Poorly defined increments have been reported in the literature from other species when held in cold, constant temperatures, so it is not surprising to find such structures in this river. Though age estimates were not obtainable for all specimens of young-of-the-year from the mainstream Colorado, most could be aged. Figure 3 illustrates poorly defined increments in a specimen from the mainstream Colorado which could be counted, but only with some difficulty. Some specimens taken from the mainstream Colorado display unusual patterns of very abrupt transitions between periods of presumptive rapid growth, probably in habitats with thermal fluctuations on a diel cycle (as indicated by well-defined increments), to periods of very narrow increments such as might be typical of much lower temperatures (Figure 4). Some specimens displayed interesting repeated rapid transitions among brief (several days) periods of each rapid and slow growth (Figure 5). These marks are very similar to otolith structural patterns purposefully produced in hatcheries to mark batches of fish for stocking (Brothers, 1990) so that hatchery and batch origin can be determined upon recapture. Such marks are produced in hatcheries through temperature manipulations.

It appears to be possible to age adult specimens on the basis of presumptive annular marks (Figure 6 and Figure 7), but, once again, periodicity of such marks has not been validated. Due to the larger size of otoliths from adults, this process requires additional specimen preparation (grinding). Distances between annual marks could be easily measured for reconstruction of individual growth histories. Rigorous validation of annual periodicity of such marks will likely require study of otoliths from mark-recapture studies. Use of chemical marking (Tetracycline or Alizarin), in conjunction with PIT tags, would be preferable, but much progress could be made utilizing non-chemically-marked specimens with histories well-known from the standard, ongoing mark-recapture program.

Presumptive daily increments can also be resolved in otoliths of adults, and in some cases, are clear enough so that those between annular growth interruptions (Figure 8) may be counted. Such counts likely reflect the length of the growing season experienced in each year by individuals. Increments, however, generally become less clear with increasing age (Figure 9 as compared to Figure 1), but may still be countable in later years (e.g. year 6, Figure 8). It does not appear practical to expect to determine birth dates of specimens that have entered or passed through their first winter.

Remarkably abrupt transitions in growth rates are also apparent in adults (Figure 10). Such abrupt marks are likely related to abrupt temperature changes, such as might be encountered by specimens moving between the LCR and mainstream during summer months. Evidence of frequent movements back and forth over short periods between cold and warm waters might be reflected in otolith structural patterns such as illustrated in Figure 11.

Table 1

Tag number, capture locality, lengths, weights, and estimated ages of humpback chub from the Grand Canyon. Specimens are separated by river of collection, and within rivers sorted by estimated ages based on lapilli. Minimum and maximum ages are provided whenever uncertainty existed, and independent estimates are listed for each different calcareous structure examined. Unless otherwise stated, all ages or estimated dates are based on age estimates from lapilli. Date of first increment formation is an approximation of hatching date. Numbers of daily increments in the first and second years of life approximate lengths of growing seasons in those years of life.

TABLE 1 - OTOLITHS EXAMINED

TAG NO.	TAG TYPE	TAG COL.	RIVER	CAPTURE LOCALITY	DATE CAPTURED	N	SL (mm)	TL (mm)	WT (gm)	SEX	MIN. AGE (DAYS)	MAX. AGE (DAYS)	DATE 1st FORMED (LAP)	MIN. AGE (YRS)	MAX. AGE (YRS)	INCR. MENTS YR. 1	INCR. MENTS YR. 2	EARLY YEAR CLASS	LATE YEAR CLASS	MIN. AGE (YRS) (ASTER)	MAX. AGE (YRS) (ASTER)	MIN. AGE (YRS) (OPERC)	MAX. AGE (YRS) (OPERC)	
LITTLE COLORADO RIVER																								
588	CAR	YE	LCR	LCR: ABOUT 250 M ABOVE MOUTH	5/28/88	1	481.00																	
481	CAR	YE	LCR	LCR: ABOUT 250 M ABOVE MOUTH	5/15/89	1	382.00			F	16	16		16	16			1988	1987	18	18	21	21	
340	FL	BL	LCR	LCR: SALT CANYON	5/2/89	1	350.00	318		M	13	15		13	15			1973	1973	14	14	15	16	
548	CAR	YE	LCR	LCR: AT MOUTH	5/23/88	1	438.00	855		M	13	13		13	13			1974	1976	14	14	16	16	
550	CAR	YE	LCR	LCR: ABOUT 250 M ABOVE MOUTH	5/26/88	1	481.00			F	13	14		13	14			1975	1976	13	13	15	15	
591	CAR	YE	LCR	LCR: AT MOUTH	5/25/88	1	425.00	770		F	12	12		12	12			1978	1977	22	22	14	14	
350	FL	BL	LCR	LCR: SALT CANYON	5/6/88	1	340.00	303		M	10	18		10	18			1979	1979	13	13	11	11	
981	CAR	OR	LCR	LCR: 180 NS D HOOP	5/7/80	1	195.00	67		F	10	10		10	10			1979	1980	15	15	5	5	
498	CAR	YE	LCR	LCR: FOUR MILES ABOVE MOUTH	5/17/89	1	284.00	107		M	8	10		8	10			1979	1980	14	14	12	12	
439	CAR	YE	LCR	LCR: ABOUT 250 M ABOVE MOUTH	5/6/89	1	370.00	383		F	8	8		8	8			1981	1981	14	14	12	12	
647	CAR	OR	LCR	LCR: 192 SS D HOOP	5/7/80	1	342.00	343		M	8	8		8	8			1981	1982	12	12	6	6	
338	FL	BL	LCR	LCR: SALT CANYON	5/2/89	1	357.00	318		F	6	7		6	7			1981	1982	12	12	6	6	
474	CAR	YE	LCR	LCR: 14 MI ABOVE COLORADO MAIN	10/19/80	1	168.00				6	6		6	6			1983	1984	12	12	5	5	
487	CAR	YE	LCR	LCR: 4 MILES ABOVE MOUTH	5/17/89	1	295.00	318		F	6	6		6	6			1983	1983	12	12	5	5	
498	CAR	YE	LCR	LCR: 4 MILES ABOVE MOUTH	5/17/89	1	230.00	61		F	5	5		5	5			1984	1984	13	13	3	3	
343	FL	BL	LCR	LCR: ATOMIZER FALLS	5/6/89	1	108.00				2	2		2	2			1987	1987	2	2	1	1	
495	CAR	YE	LCR	LCR: 1225 M ABOVE MOUTH	5/17/89	1	223.00	87		M	2	2		2	2			1987	1987	5	5	3	3	
341	FL	BL	LCR	LCR: ATOMIZER FALLS	5/6/89	1	128.00				1	1		1	1			1988	1988	2	2	1	1	
480	CAR	YE	LCR	LCR: NEAR SALT CANYON	5/15/80	1	121.00	14			1	1		1	1			1988	1988	2	2	1	1	
480	CAR	YE	LCR	LCR: NEAR SALT CANYON	5/15/80	1	100.36				1	1		1	1			1988	1988	2	2	1	1	
470	CAR	YE	LCR	LCR: 5432/SIPAPU	5/6/80	1	71.67	98.35			1	1		1	1			1989	1989	2	2	1	1	
481	CAR	YE	LCR	LCR: 9850/SALT TRAIL CAMP	5/15/80	1	88.23	111.12			1	1		1	1			1989	1989	2	2	1	1	
502	CAR	YE	LCR	LCR: 1225 M ABOVE MOUTH	5/15/80	1	59.20	79.47			1	1		1	1			1989	1989	2	2	1	1	
510	CAR	YE	LCR	LCR: 1225 M ABOVE MOUTH	5/24/88	1	74.85	94.81			1	1		1	1			1989	1989	2	2	1	1	
557	CAR	YE	LCR	LCR: O/E XPERIMENTAL	4/26/80	1	67.89	86.87			1	1		1	1			1989	1989	2	2	1	1	
570	CAR	YE	LCR	LCR: 5432/SIPAPU	5/6/80	1	93.29	104.52			1	1		1	1			1989	1989	2	2	1	1	
588	CAR	YE	LCR	LCR: 5432/SIPAPU	5/6/80	1	98.16	127.88			1	1		1	1			1989	1989	2	2	1	1	
484	CAR	YE	LCR	LCR: 9850/SALT TRAIL CAMP	5/15/80	1	28.38	37.33			63	63		63	63			1989	1989	14	14	3	3	
512	CAR	YE	LCR	LCR: 114 MILE UP	10/16/80	1	85.00				200	200		200	200			1990	1990	18	18	4	4	
514	CAR	YE	LCR	LCR: 9850/SALT TRAIL CAMP	5/15/80	1	28.82	35.58			64	64		64	64			1990	1990	18	18	4	4	
529	CAR	YE	LCR	LCR: 9850/SALT TRAIL CAMP	5/15/80	1	14.24	18.44			34	34		34	34			1990	1990	18	18	4	4	
543	CAR	YE	LCR	LCR: 9850/SALT TRAIL CAMP	5/15/80	1	26.78	35.85			63	63		63	63			1990	1990	18	18	4	4	
587	CAR	YE	LCR	LCR: 9850/SALT TRAIL CAMP	5/15/80	1	18.82	22.08			50	50		50	50			1990	1990	18	18	4	4	
580	CAR	YE	LCR	LCR: 9850/SALT TRAIL CAMP	5/15/80	1	12.88	15.87			36	36		36	36			1990	1990	18	18	4	4	
581	CAR	YE	LCR	LCR: 9850/SALT TRAIL CAMP	5/15/80	1	23.85	31.05			58	58		58	58			1990	1990	18	18	4	4	
1	0	0	LCR	LCR: 975 M ABOVE CONFLUENCE	5/23/88	1	20.12	25.12			53	53		53	53			1990	1990	14	14	3	3	
3	0	0	LCR	LCR: 975 M ABOVE CONFLUENCE	5/6/89	1	35.00	49.0			14	14		14	14			1990	1990	16	16	3	3	
339	FL	BL	LCR	LCR: ATOMIZER FALLS	5/6/89	1	351.00	353		M	9	9		9	9			1990	1990	10	10	8	8	
344	FL	BL	LCR	LCR: 100 M ABOVE BIG CANYON	5/4/89	1	278.00				10	10		10	10			1990	1990	10	10	8	8	
348	FL	BL	LCR	LCR: ATOMIZER FALLS	5/6/89	1	236.00	122			2	2		2	2			1990	1990	10	10	8	8	
349	FL	BL	LCR	LCR: ATOMIZER FALLS	5/6/89	1	118.00				2	2		2	2			1990	1990	10	10	8	8	
4	0	0	LCR	LCR: 975 M ABOVE CONFLUENCE	5/23/88	1	342.00	322		M	14	14		14	14			1990	1990	13	13	16	16	
440	CAR	YE	LCR	LCR: 200 M ABOVE MOUTH	5/6/89	1	390.00	465		F	13	13		13	13			1990	1990	11	11	15	15	
441	CAR	YE	LCR	LCR: AT MOUTH	5/6/89	1	330.00	283		M	11	11		11	11			1990	1990	11	11	15	15	
442	CAR	YE	LCR	LCR: AT MOUTH	5/6/89	1	389.00	404		F	16	16		16	16			1990	1990	16	16	7	7	
444	CAR	YE	LCR	LCR: 1225 M ABOVE MOUTH	5/6/89	1	274.00	137		F	14	14		14	14			1990	1990	16	16	7	7	

TABLE 1 - OTOLITHS EXAMINED

TAG NO.	TAG TYPE	TAG COL.	RIVER	CAPTURE LOCALITY	DATE CAPTURED	N	SL (mm)	TL (mm)	WT (gm)	SEX	MIN. AGE (DAYS) (LAP)	MAX. AGE (DAYS) (LAP)	DATE 1st INCREMENT FORMED (LAP)	MIN. AGE (YRS) (LAP)	MAX. AGE (YRS) (LAP)	INCR. MENTS YR. 1	INCR. MENTS YR. 2	EARLY YEAR CLASS	LATE YEAR CLASS	MIN. AGE (YRS) (LASTER)	MAX. AGE (YRS) (LASTER)	MIN. AGE (YRS) (OPENC)	MAX. AGE (YRS) (OPENC)	
5	0	0	LGR	0.75 M ABOVE CONFLUENCE	5/23/88	1	348.00	351													15	15	3	4
500	CAR	VE	LGR	1225 M ABOVE MOUTH	5/24/89	1	182.00	52		F											4	4	2	2
501	CAR	VE	LGR	1225 M ABOVE MOUTH	5/24/89	1															3	3	1	1
503	CAR	VE	LGR	1225 M ABOVE MOUTH	5/24/89	1															1	1	1	1
504	CAR	VE	LGR	1225 M ABOVE MOUTH	5/24/89	1															1	1	1	1
519	CAR	VE	LGR		5/15/89	1															1	1	1	1
522	CAR	VE	LGR		5/15/89	1															1	1	1	1
533	CAR	VE	LGR		5/15/89	1															1	1	1	1
534	CAR	VE	LGR		5/15/89	1															1	1	1	1
535	CAR	VE	LGR		5/15/89	1															1	1	1	1
546	CAR	VE	LGR	AT MOUTH	5/28/89	1	372.00														18	16	15	15
549	CAR	VE	LGR	AT MOUTH	5/15/89	1															6	6	4	4
552	CAR	VE	LGR		5/15/89	1															1	1	1	1
553	CAR	VE	LGR		5/15/89	1															1	1	1	1
580	CAR	VE	LGR	AT MOUTH	5/15/89	1	373.00														2	2	12	12
585	CAR	VE	LGR	200 M ABOVE CONFLUENCE	5/7/89	1	388.00	456		F											13	13	14	14
596	CAR	VE	LGR	AT MOUTH	5/7/89	1	104.00	8		M											2	2	1	1
600	FL	RE	LGR	ATOMIZER FALLS	5/6/89	1	309.00														13	13	1	1
605	FL	RE	LGR	ATOMIZER FALLS	5/6/89	1	121.00														3	3	1	1
612	FL	RE	LGR	ATOMIZER FALLS	5/6/89	1	106.00														2	2	1	1
902	CAR	VE	LGR	AT SALT CANYON	5/13/89	1	350.00	331		F											13	13	2	13
COLORADO RIVER MAINSTREAM																								
489	CAR	VE	COL	COLORADO RIVER MAINSTEM RM 83.9L	10/22/90	1	202.00																	
266	CAR	OR	COL	COLORADO RIVER AT RM 64.5	6/24/92	1	25.35	33.25																
274	CAR	OR	COL	COLORADO RIVER AT RM 122.5	4/6/91	1	28.10	35.34																
322	CAR	OR	COL	COLORADO RIVER AT RM 122.5	4/6/91	1	29.00	37.49																
331	CAR	OR	COL	COLORADO RIVER AT RM 122.5	4/6/91	1	28.92																	
365	CAR	OR	COL	COLORADO RIVER AT RM 64.5	4/15/92	1	30.40	37.82																
287	CAR	OR	COL	COLORADO RIVER AT RM 70.3	5/12/91	1	33.50	42.10																
371	CAR	OR	COL	COLORADO RIVER AT RM 193.9	5/23/91	1	46.70	66.00																
381	CAR	OR	COL	COLORADO RIVER AT RM 64.5	6/24/92	1	28.97	35.45																
396	CAR	OR	COL	COLORADO RIVER AT RM 122.0	4/18/92	1	39.05	46.73																
455	CAR	VE	COL	OCOLO. COLD CONTROL	4/28/90	1	75.84	94.64	44															
511	CAR	VE	COL	COLORADO. 0.2 MI ABOVE CARDENAS	10/22/90	1	89.00																	
481	CAR	VE	COL	COLORADO MAINSTEM. RM 85.3 L	10/20/90	1	58.00																	
539	CAR	VE	COL	COLORADO RIVER MAINSTEM. RM 70.9	10/22/90	1	29.40	37.40																
275	CAR	OR	COL	COLORADO RIVER AT RM 88.1	6/13/91	1	25.10	31.85																
320	CAR	OR	COL	COLORADO RIVER AT RM 88.1	6/24/92	1	19.53																	
328	CAR	OR	COL	COLORADO RIVER AT RM 192.3	6/24/92	1	19.55	25.10																
295	CAR	OR	COL	COLORADO RIVER AT RM 122.1	6/28/92	1	14.17	17.50																
376	CAR	OR	COL	COLORADO RIVER AT RM 88.1	6/24/92	1	14.30																	
387	CAR	OR	COL	COLORADO RIVER AT RM 88.1	6/24/92	1	13.70																	
488	CAR	VE	COL	MAINSTEM COLORADO. RM 85.3 L	10/20/90	1	33.00														143	143	0	0

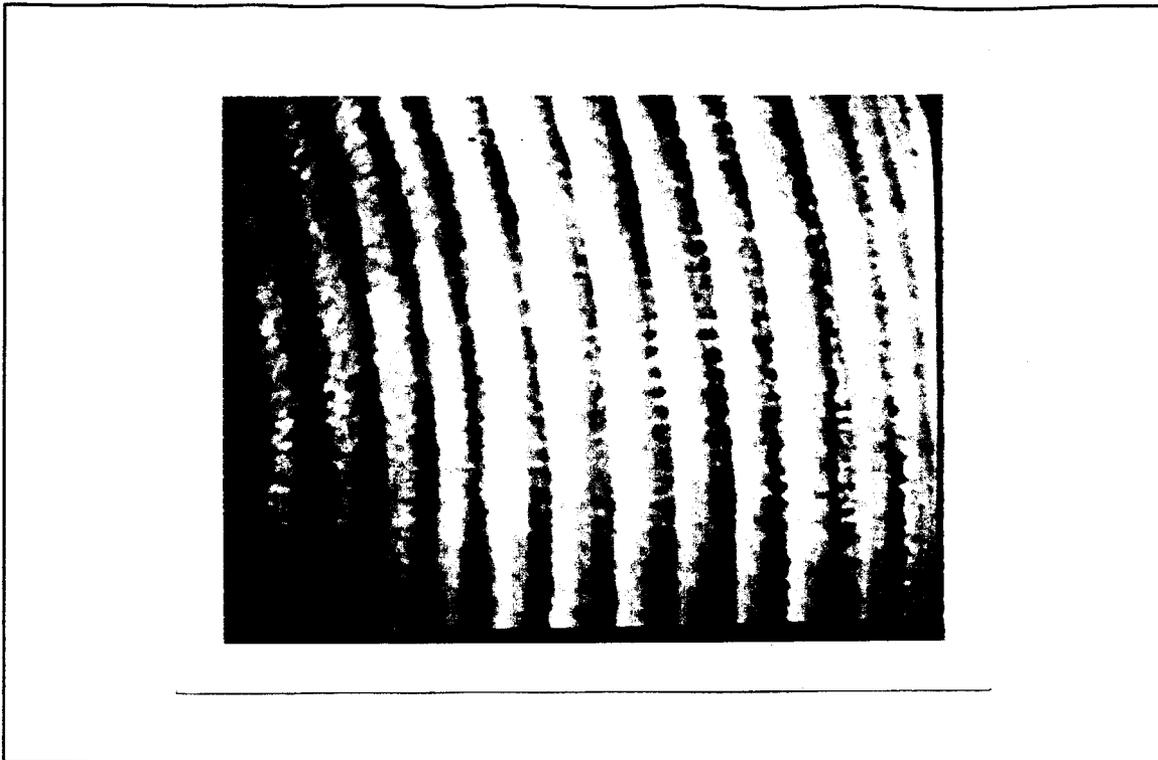


Figure 1. Clear presumptive daily increments in the first year of growth of a 1⁺ year-old fish (tagno 502 YC) captured in the LCR about 1 km above its mouth.

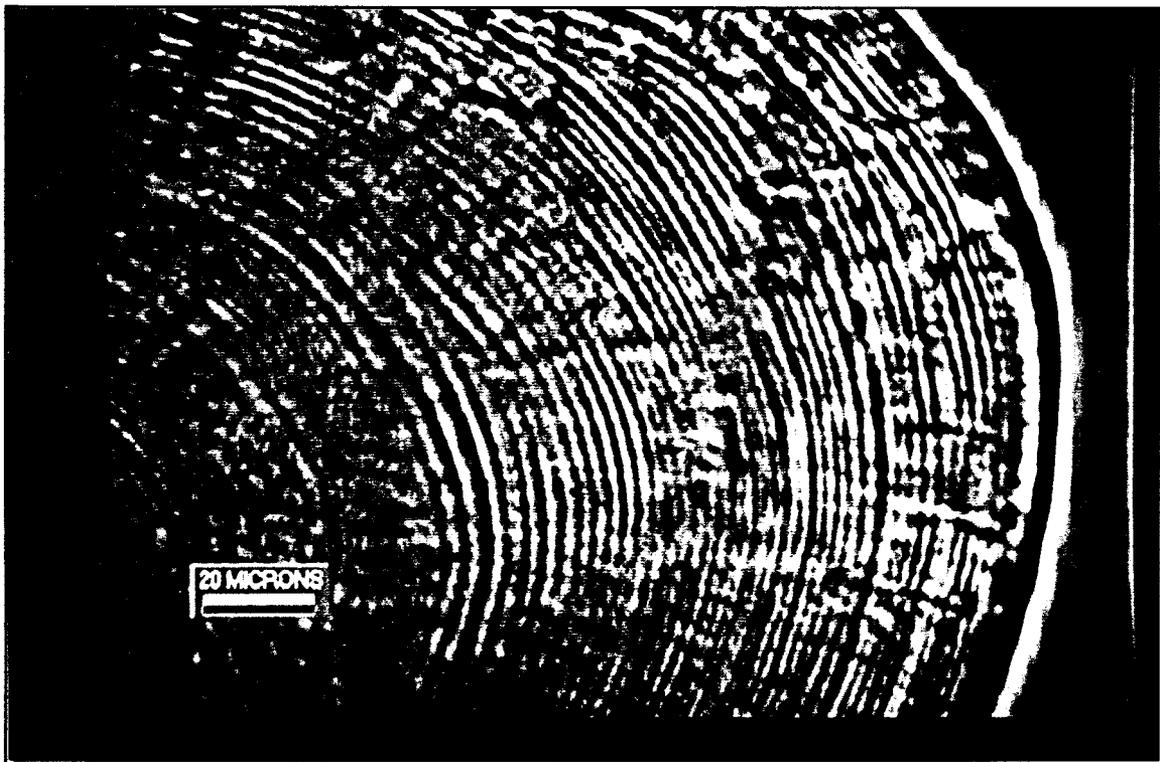


Figure 2. Daily increments to edge in lapillus of an age 0⁺ specimen from River Mile 68.1 collected September 13, 1991. Note clear increments extending to edge. Specimen estimated to be 110 days old (thus, estimated hatch date = 5/26/91).

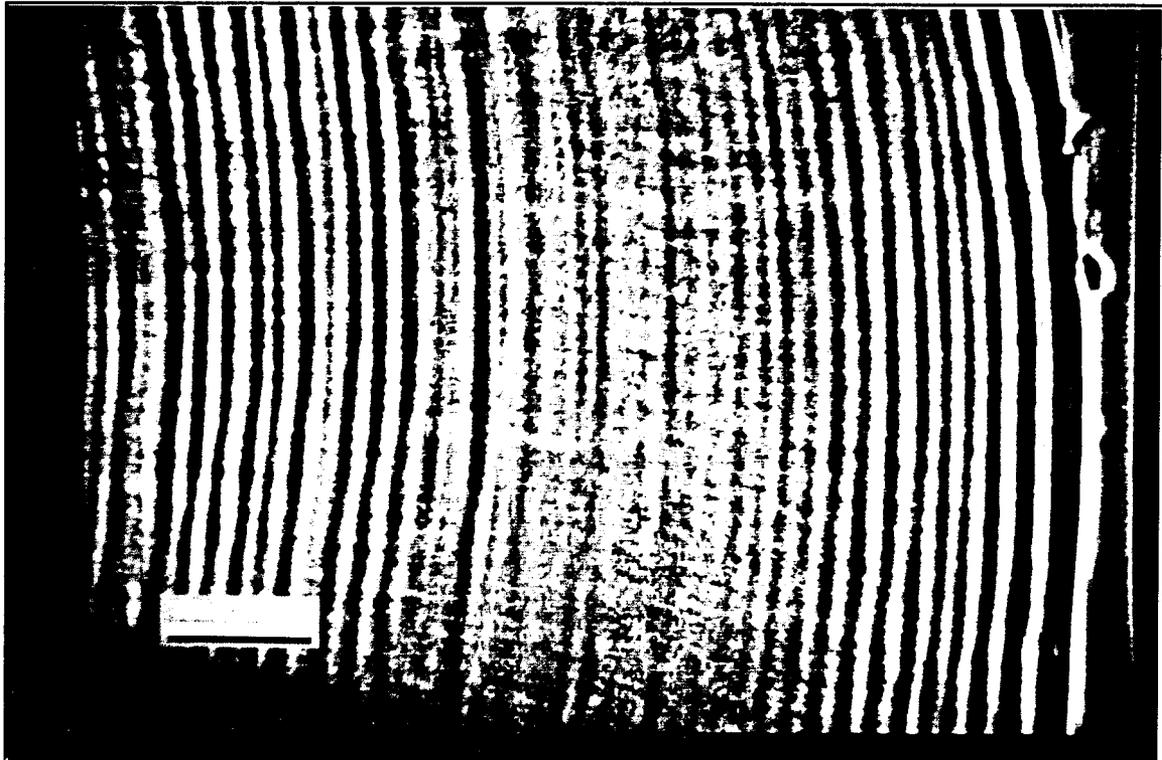


Figure 3. Well defined and poorly defined increments in lapillus from a young-of-the-year specimen (tag number 328) from the mainstream Colorado at River Mile 192.3.

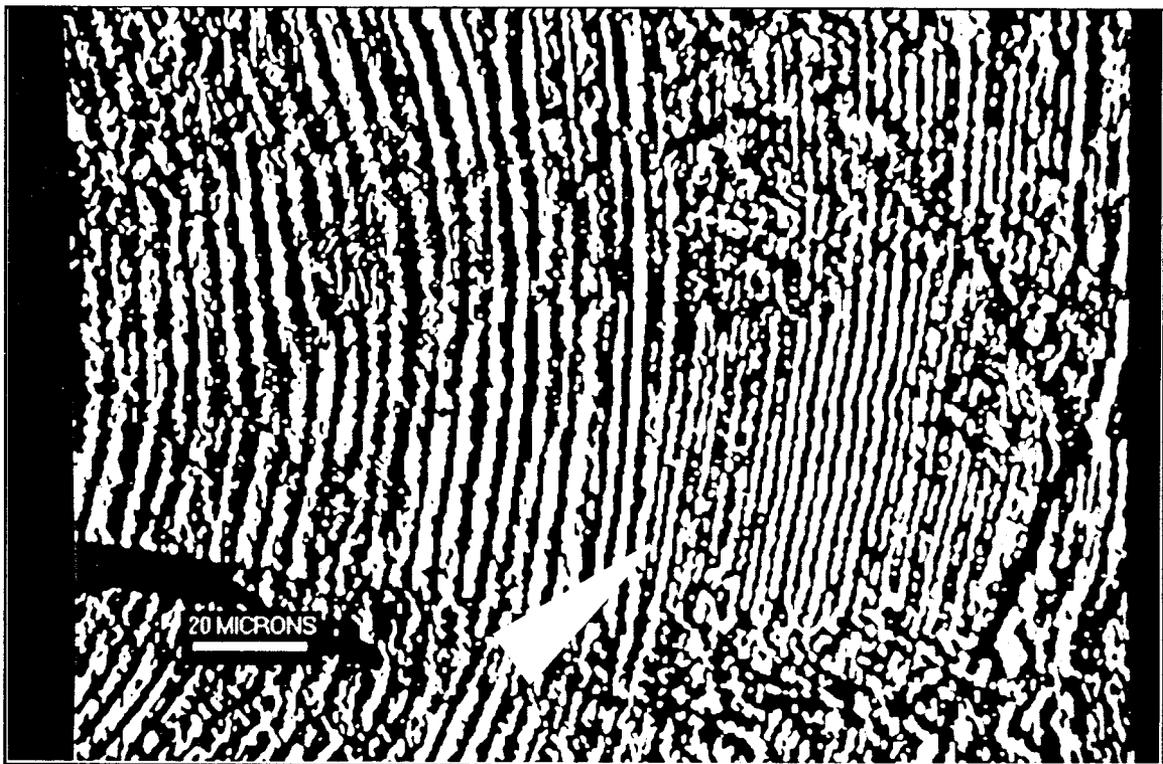


Figure 4. Rapid transition from wide to narrow growth increments in a specimen taken in the mainstream Colorado at River Mile 65.3 on October 20, 1990. Specimen estimated to be 143 days old.

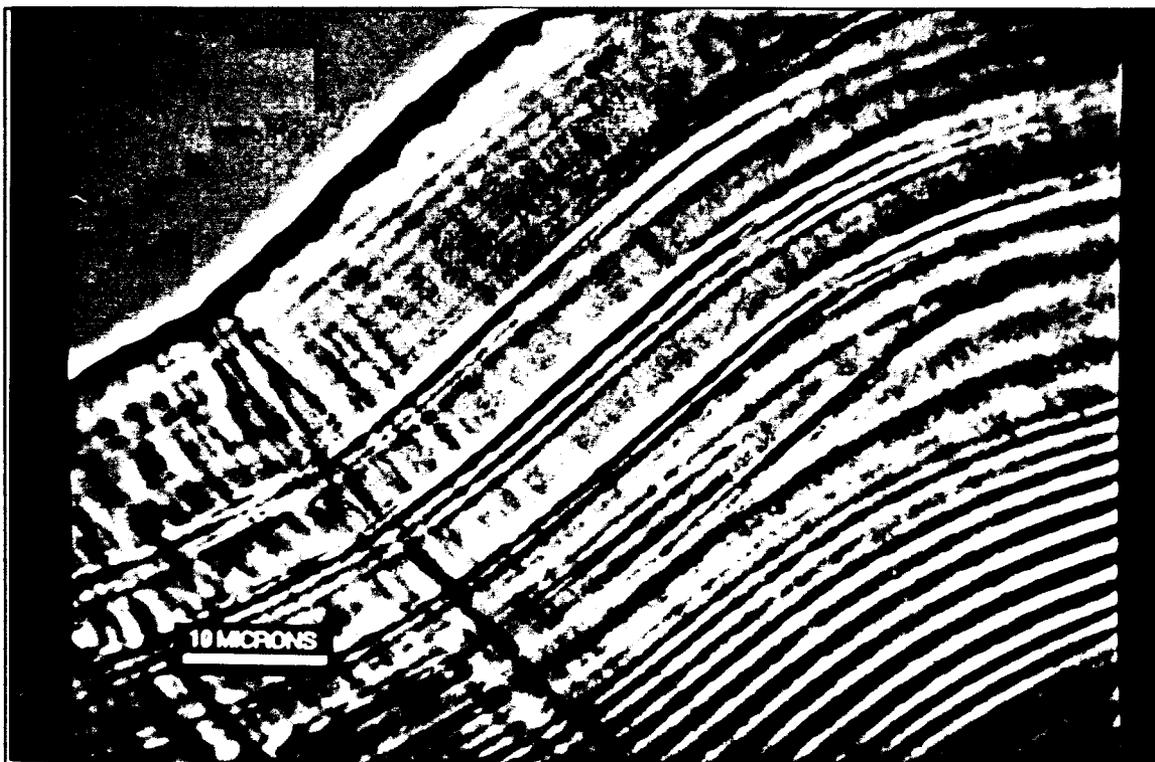


Figure 5. Fluctuations between brief periods of wide and narrow increments near edge of lapillus from specimen (tagno 539) taken in mainstream Colorado River at River mile 70.9 on October 22, 1990.

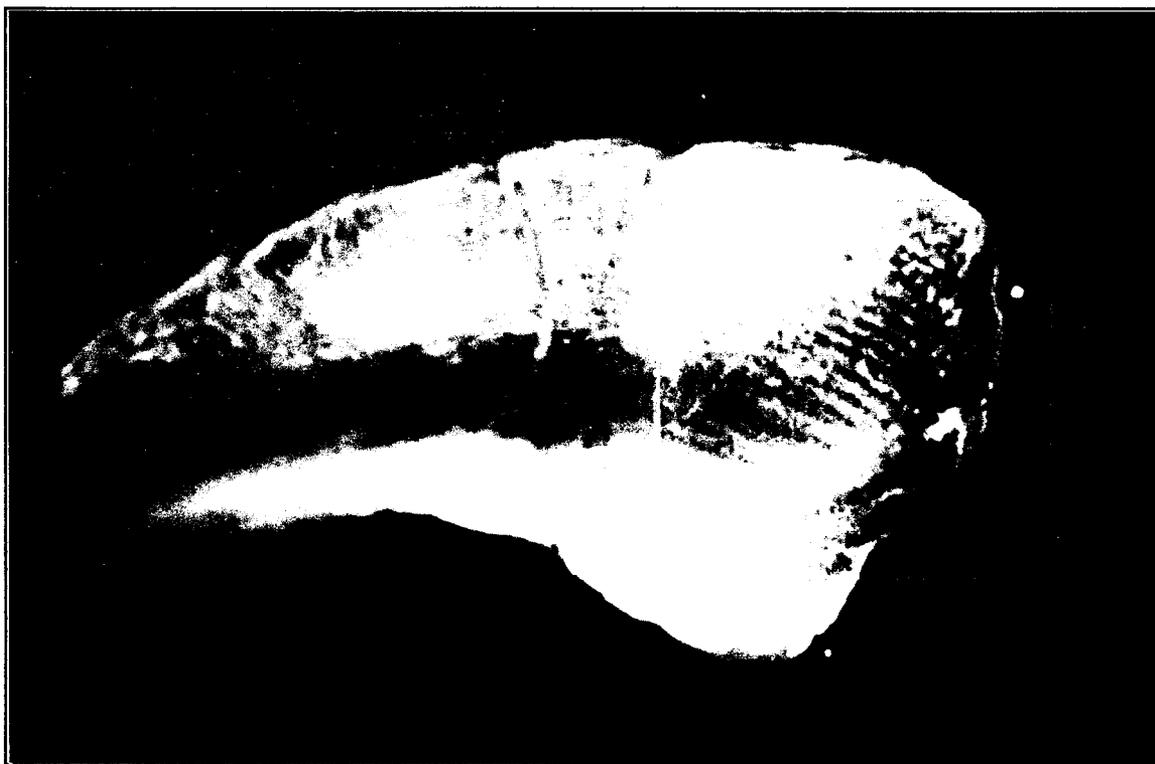


Figure 6. Annuli in the lapillus of the oldest specimen examined (tagno 586), estimated to be 22 or 23 years old.

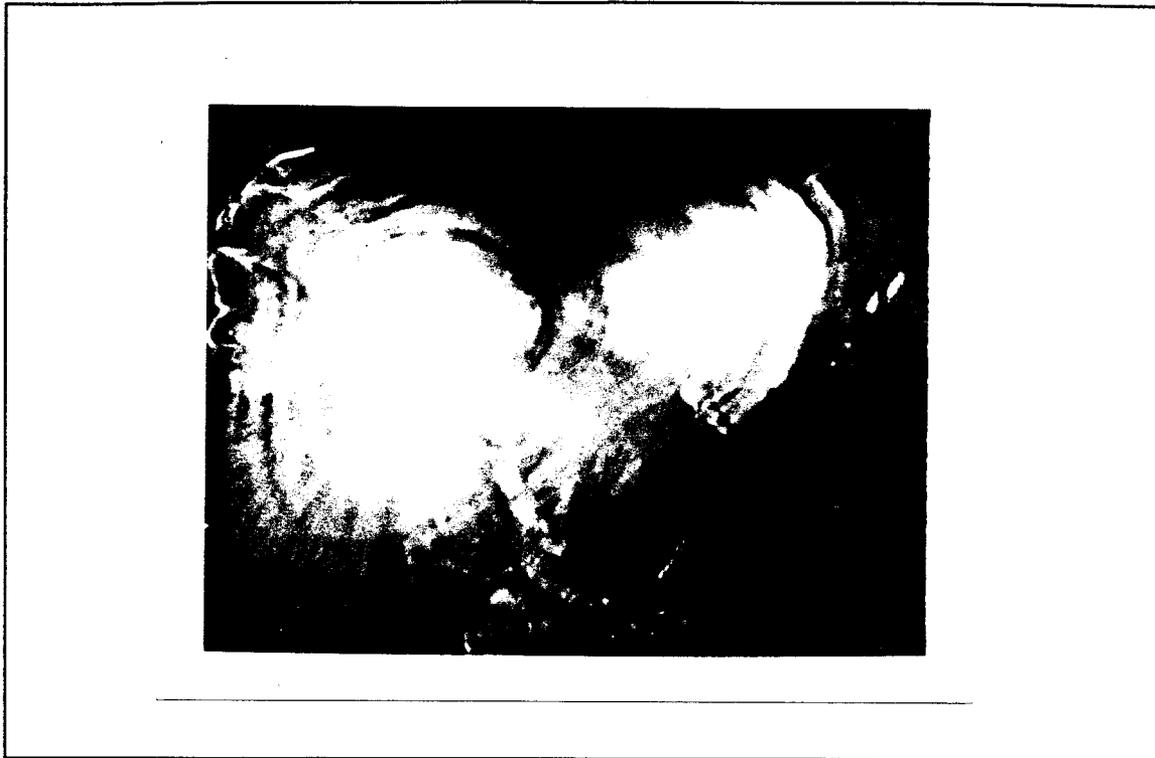


Figure 7. Thirteen to 15 annuli visible in lapillus of specimen 548, as seen in reflected light.

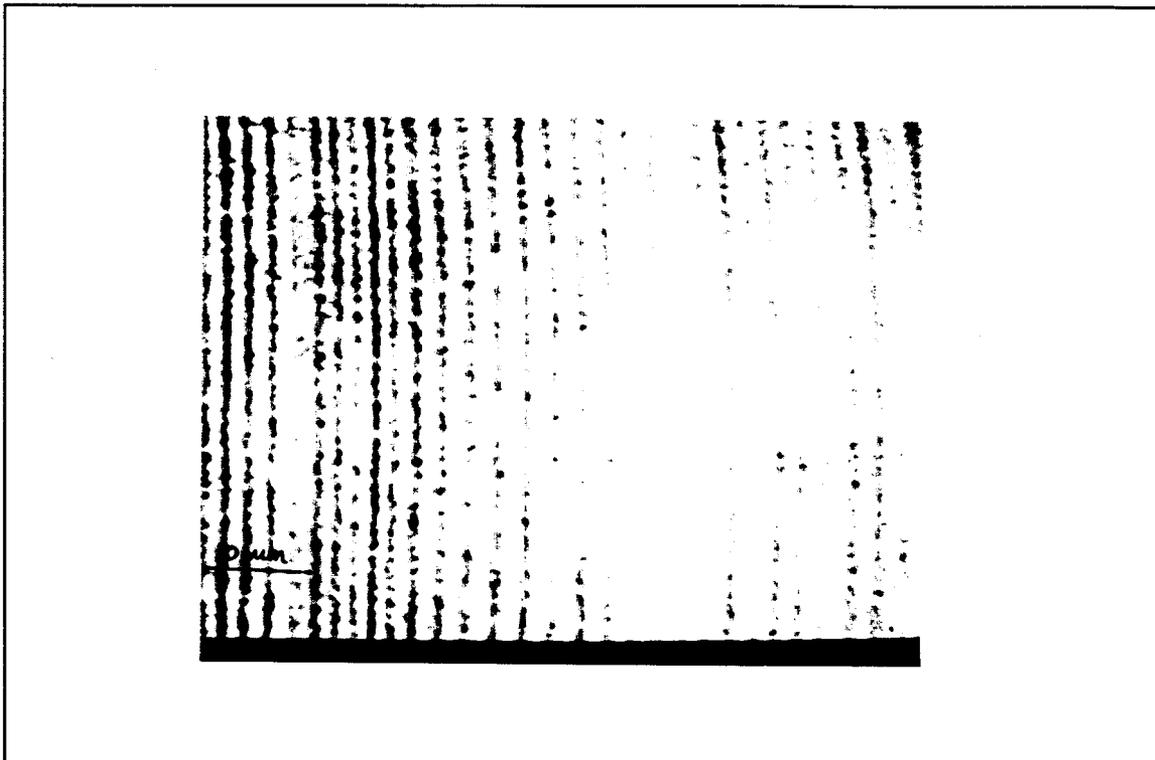


Figure 8. Daily increments visible in that portion of the lapillus corresponding to year 6 of life of a 13 to 15-year old specimen (tag number 548).

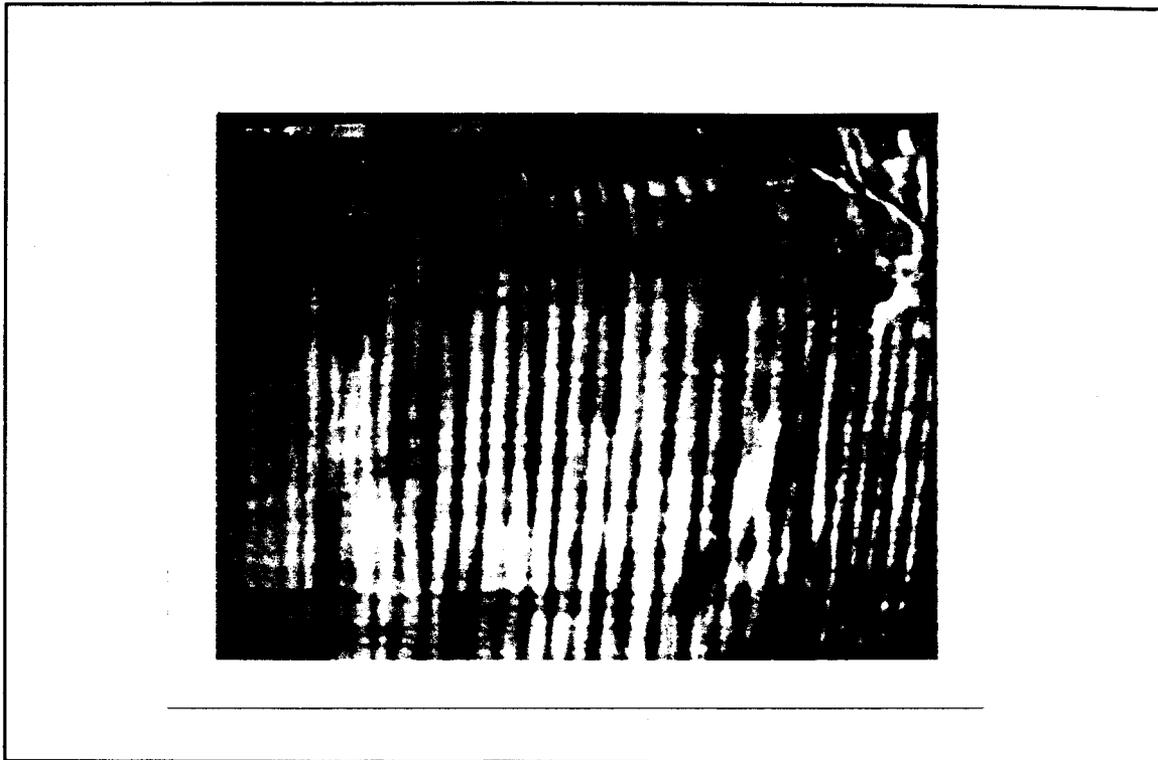


Figure 9. Increments in second year of growth of a 1⁺ age specimen (tag number 502) captured in the Little Colorado River.

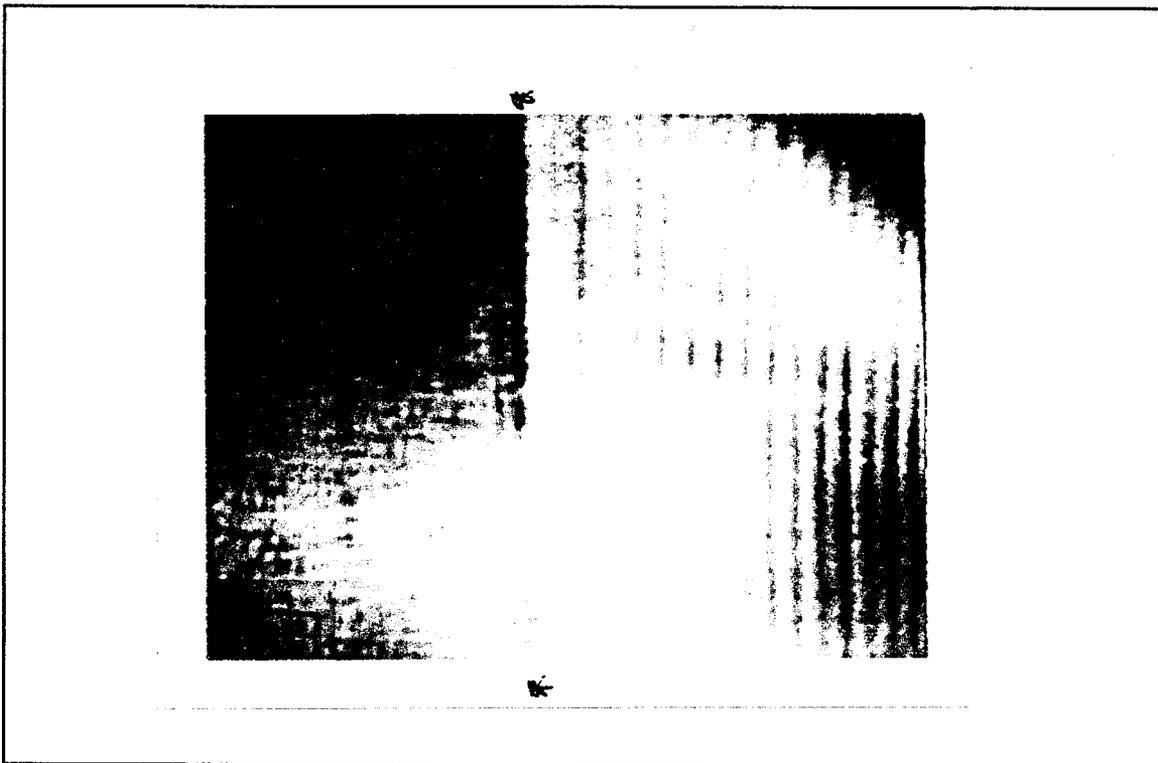


Figure 10. Abrupt transition from wide to narrow increments near start of 3rd growing season in specimen 495.

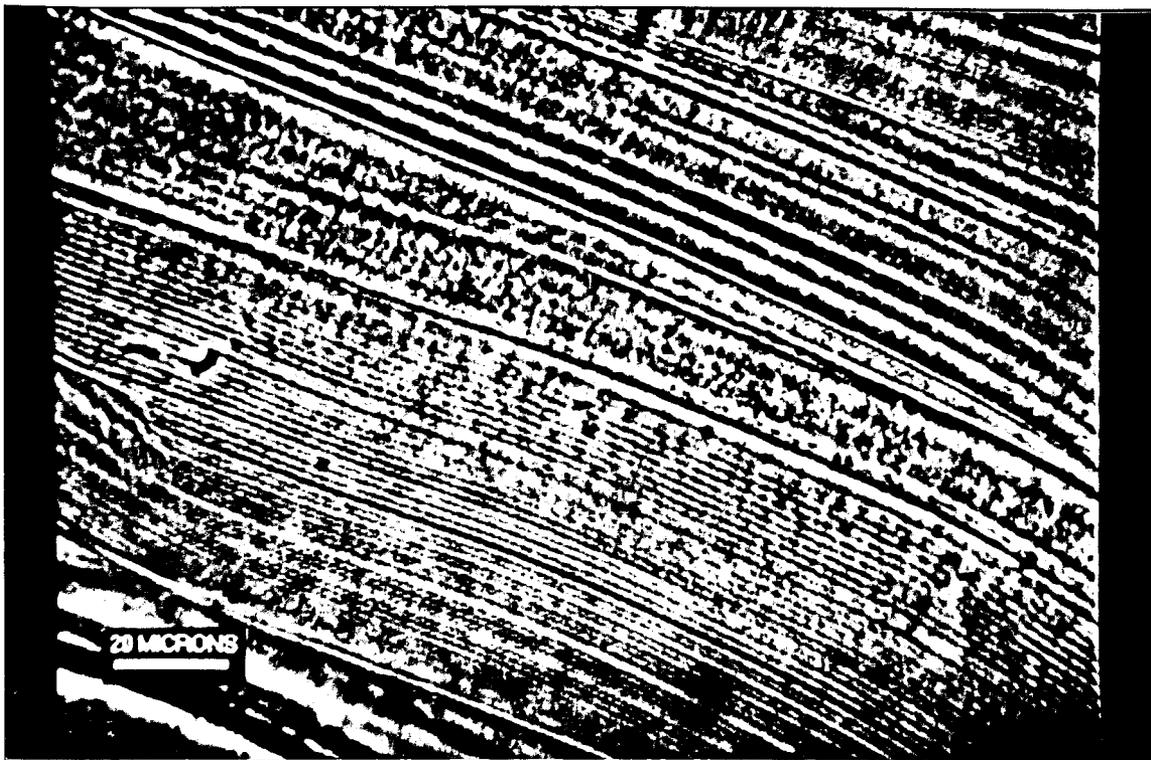


Figure 11. Odd patterns in adult specimen (tag number 495) possibly produced by repeated movements across temperature differentials.

Ages of adults as estimated from opercles are in fairly good agreement with those estimated independently from lapilli, however, the single independent estimates from asterisci are generally higher (Figure 12). Lapilli are clearly the preferred structure for ageing. Both daily increments and annuli in asterisci are comparatively much more difficult to interpret. Opercles appear to provide a reasonable means of obtaining yearly ages of adults and have the advantage of requiring less preparation than do otoliths. Opercles, however, have the disadvantage, like all bone, of being susceptible to periodic mobilization of calcium and other elements which could also alter structure. Otoliths are well known to be much more stable than bone. Additionally, opercles do not provide the same detailed daily history within years that can be obtained from otoliths. This

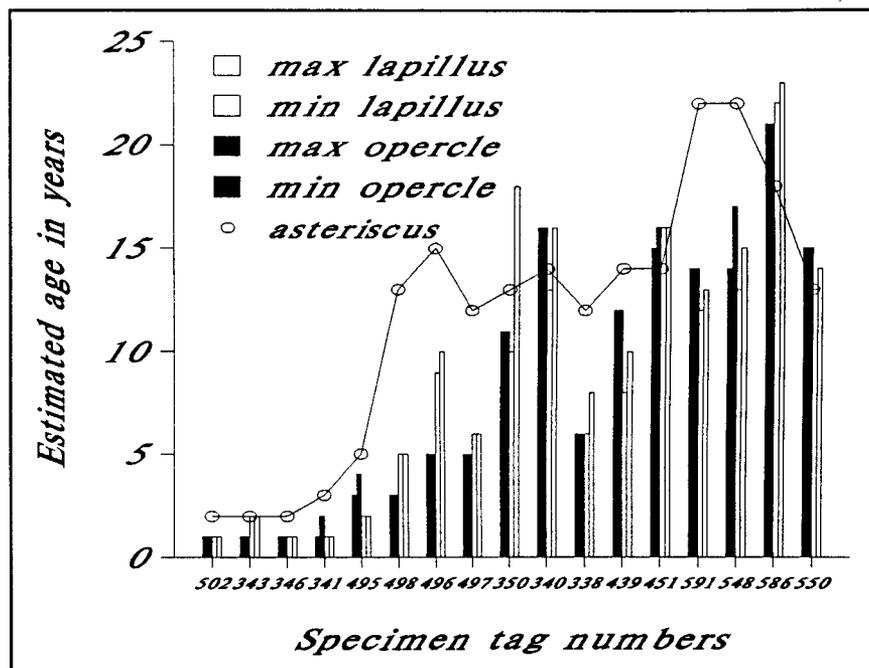


Figure 12. Minimum and maximum age estimates using lapilli and opercles (bars) and asterisci (circles) for fish > 1 yr. old.

might be significant once larger sample sizes have been analyzed. Year-specific natural marks in daily increments have been utilized as useful cohort markers in other species, and could be useful in validating ages. It is probable that events such as unusual summer floods in the LCR might produce characteristic patterns that would unambiguously allow assignment of those zones to that event in specimens captured many years subsequently. Utilization of either lapilli or opercles for yearly ageing or for annual growth estimation will require validation of the periodicity of presumptive annuli. It seems probable that stress associated with such marked and rapid transitions as that experienced when moving between the LCR and mainstream would form marks on either otoliths or opercles which could be mistaken as an annual mark.

On the basis of data compiled to date from lapilli and opercles it appears that growth rates of humpback chub in the Grand Canyon are highly heterogeneous. Size is not a good predictor of age (Figure 13 and Figure 14).

Variations in growth rate may be a function of inherent individual variation and/or temporally and spatially expressed habitat effects. On the basis of the small sample examined to date, variation in growth rate appears to be expressed early in life, and to be markedly affected by habitat. Nearly all young-of-the-year from the LCR were larger than others of similar age taken from the cold mainstream Colorado River (Figure 15). Similarly, one-year old fish taken from the LCR in April and May of 1990 averaged more than double the size of one-year olds taken from the mainstream almost exactly one year later. This is despite the indication from estimated ages that the 1991 yearlings

from the mainstream had been growing for 30 to 50 days more in the year of capture than had the 1990 yearlings from the LCR (Table 1). Though comparisons of first year growth between these 1989 and 1990 year classes have not been done (but would be possible with back-calculation techniques using increment widths), the effect of lower mainstream temperatures on growth appears large, and is probably significant in terms of consequences for mortality rates. In most well-studied fisheries, lower growth rates are associated with higher mortality. Measurements of daily growth increments could easily be used to quantify the effect of life in the mainstream on growth rates.

Part of the extensive variation in the relationship of estimated age and Standard Length may be due to sexual dimorphism, but not nearly enough data are available in the small data set developed to date to allow attempts to factor out this source of variation (Figure 16 and Figure 17).

Marked structural changes in daily increments found thus far are promising in that it is likely that environmental changes of the magnitude required to produce such dramatic structural changes in the otoliths are likely to have produced by changes in otolith chemical composition which might be found to correlate with ambient water quality or temperature. The unique physical and chemical properties of water

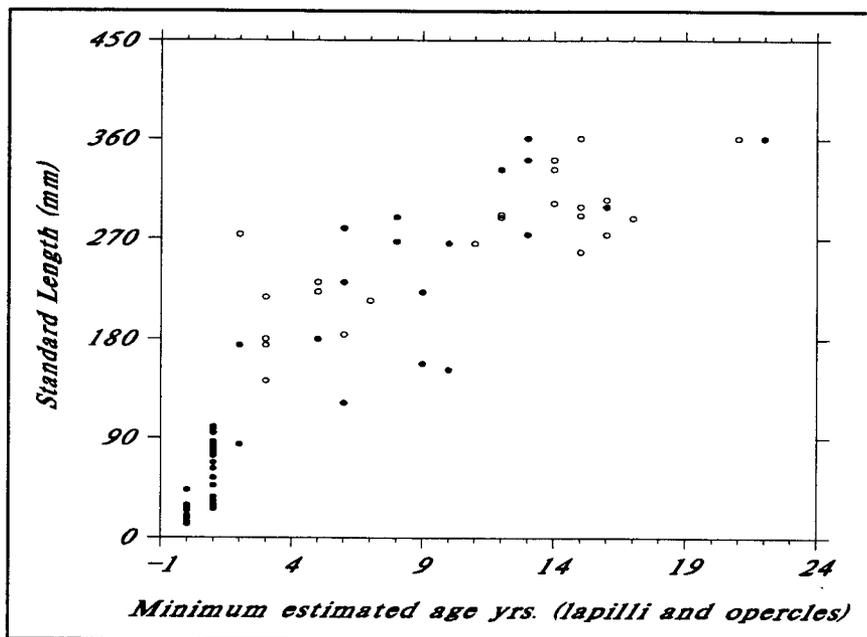


Figure 13. Scatter of relationship of minimum ages as determined from lapilli (solid circles) and opercles (open circles) and Standard Length of humpback chub.

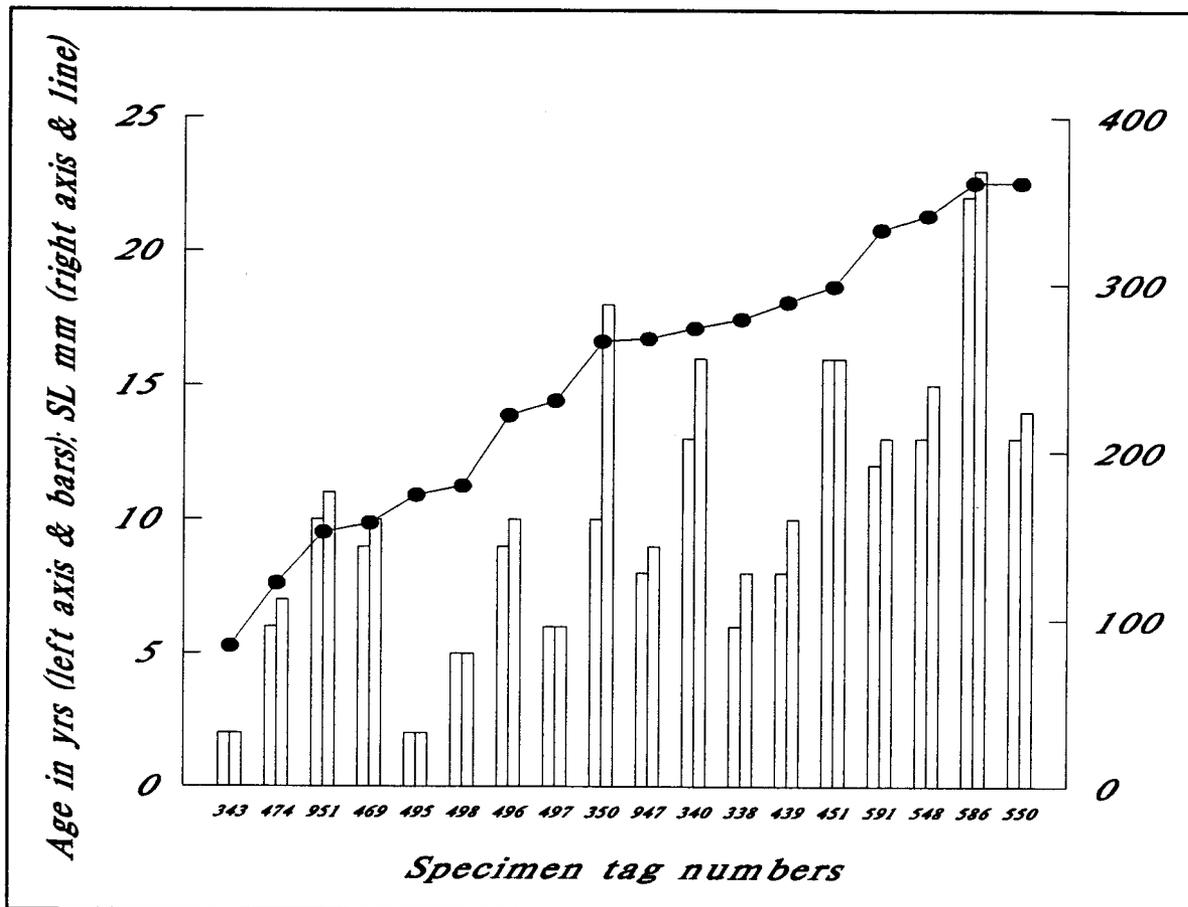


Figure 14. Minimum and maximum age in years estimated from lapilli and Standard Length for all specimens estimated to be more than one year old.

quality in the LCR that clearly distinguish it from the mainstream Colorado River seem to provide a very appropriate system in which to test rapidly developing hypotheses of the relationship of otolith chemistry to environmental factors.

REQUESTS FOR ADDITIONAL SPECIMENS, DATA AND SUGGESTIONS

ACCURACY OF THE OTOLITH DATA BASE

The entire inventory of specimens currently available to the author for otolith studies is provided in Appendix 1 and (with much more detail) in a file on disk (hbinvtry.xls). Some questions remain regarding exact collection localities for some specimens, as well as habitat conditions. It is hoped that these data can be provided by the field crews who collected them and that they will generally prove once again the entire data base. Additionally, sex is unknown for many specimens from which it might still be obtainable from preserved materials not currently available to the author. Sex determinations are needed since current scatter in the distribution of length at age (Figure 13) greatly compromises precision of attempts at back-calculation of lengths at various ages as will be required to reconstruct growth histories of individuals. Removal of the effect of sexual dimorphism in size from the length-age relationship would almost certainly allow more precise reconstructions of growth histories.

ADDITIONAL SPECIMENS

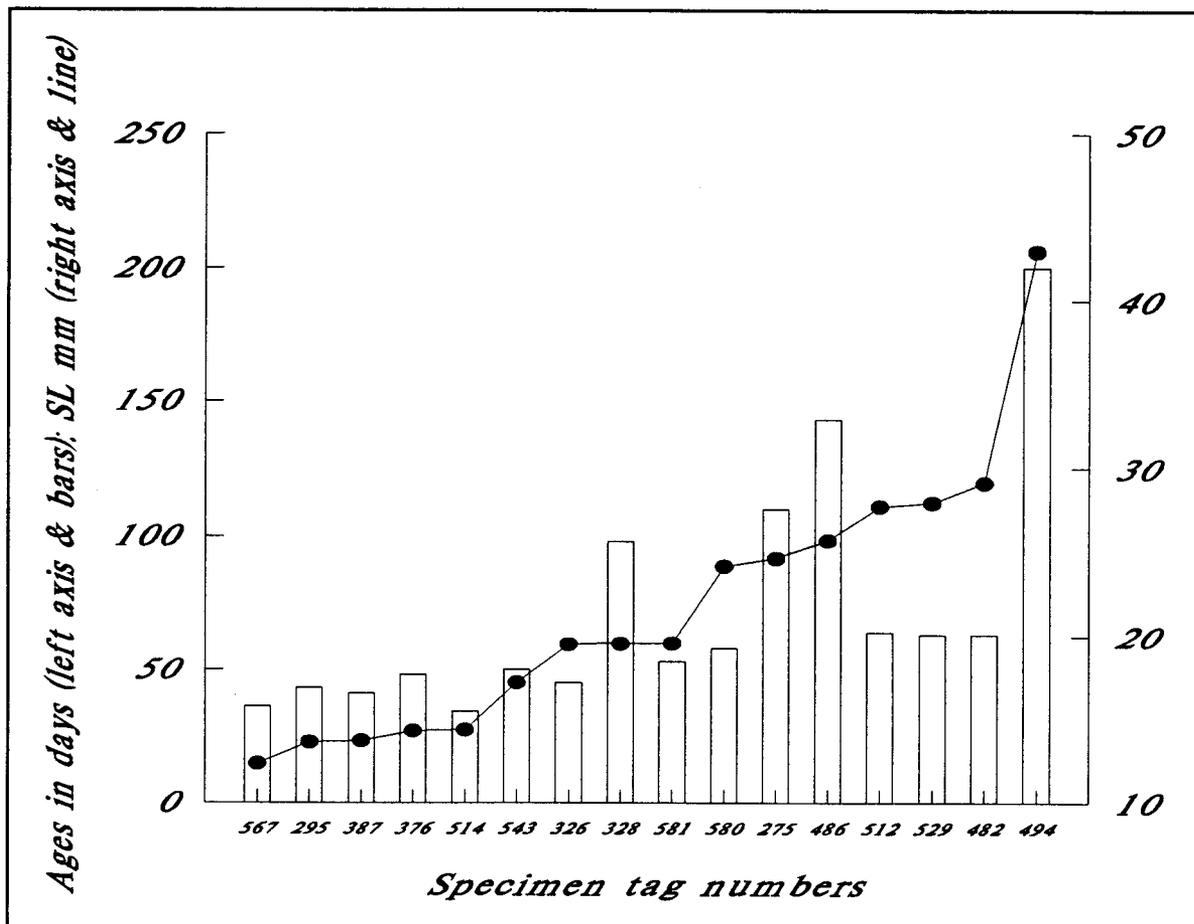


Figure 15. Age in days and Standard Length for age 0+ specimens. Individuals from Colorado River mainstream (295, 387, 376, 326, 328, 275, 486) are generally smaller than specimens from LCR of comparable ages.

Additional select specimens could be effectively used to fill gaps in coverage and to answer specific questions. These include:

1. Wild-caught larval to juvenile humpback chubs, especially any which lived during periods for which daily water quality and discharge, or other water quality data, are available. Currently the smallest specimens of humpback chub available from the LCR or mainstream Colorado River are 14 mm SL, which appears to be reached at about 30 - 40 days of age. Though daily increments can be counted in these to allow estimation of hatching date, the otolith size:fish size relationship remains unknown in the smaller size ranges and is still inadequately defined in intermediate size ranges. Empirical development of this relationship will be necessary to allow attempts at back-calculations of size at age, and thus reconstruction of instantaneous growth rates, which might be useful for among cohort and among year comparisons of growth histories, as well as for analysis of effects of environmental variables on fish growth. Effects of environmental variables can not be assessed without appropriate data on the quality of the environment. Temperature and discharge are two very appropriate parameters likely to be available.

2. Wild-caught adults with well-known location and growth histories. Ongoing extensive tag-recapture studies and radiotelemetry studies are providing highly detailed data on movement history of individuals. Otoliths from specimens with well-known location histories from tagging studies could prove to be especially valuable for comparison of otolith-derived hypotheses of growth and movement histories with known histories. Provision of such specimens to the author without data on movement or growth

information would allow blind comparisons of otolith and tag-derived histories. Particularly valuable would be multiply-recaptured young adult fish with clearly demonstrable growth between original capture and recaptures. Also useful might be radiotelemetered individuals known to have passed through major environmental gradients such as the LCR-Mainstream interface during the growing season in which sacrificed. Especially informative for future work would be intentional chemical marking of otoliths of selected individuals in the field (utilizing Tetracycline or Alizarin). If accompanied by PIT-tagging, otolith-marked individuals recaptured in the future could be used to validate periodicity of both daily and annual marks.

3. Specimens captured far from the Little Colorado River.

Humpback chub encountered in the lower Grand Canyon may or may not be part of the LCR gene pool. In particular, it seems unlikely that small specimens taken in lower canyon reaches originated in the LCR. To date relatively few specimens from locations far below the LCR have been made available for otolith research and it is recommended that otoliths of specimens taken in the future from lower canyon areas be taken for ageing, examination of daily increment patterns in

the first year of life, and analyses of chemical composition. Some specimens already examined from the lower Canyon which are of ages that would seem to make it quite unlikely that they were born in the LCR. For example, specimen 328, a 98-day old fish, was taken at River Mile 192.3, or about 130 miles below the LCR. Unfortunately, no 1991 year class young-of-the-year from the LCR have yet been

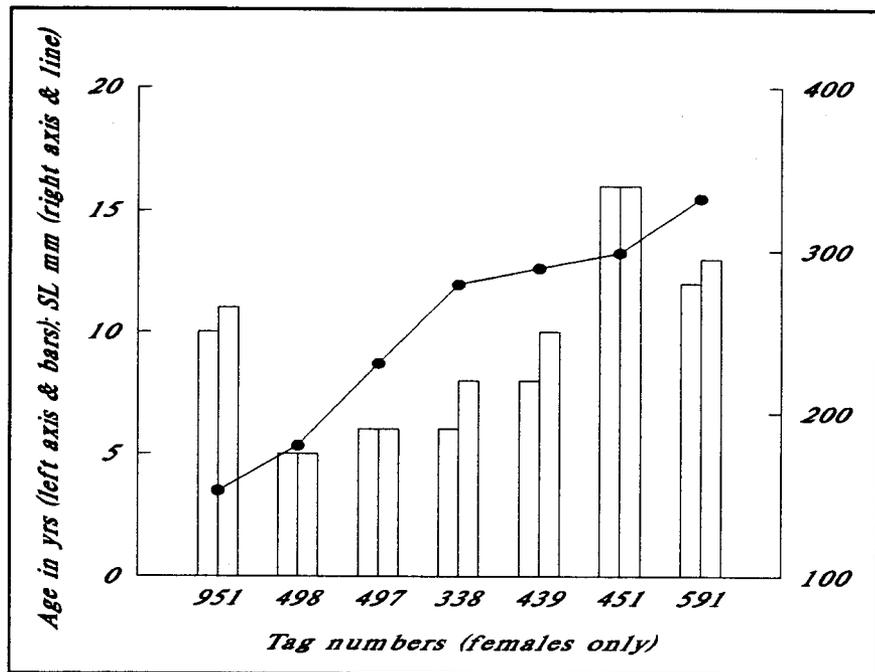


Figure 16. Minimum and maximum age estimates (bars) and Standard Length (dots) as determined from lapilli for all specimens verified to be females.

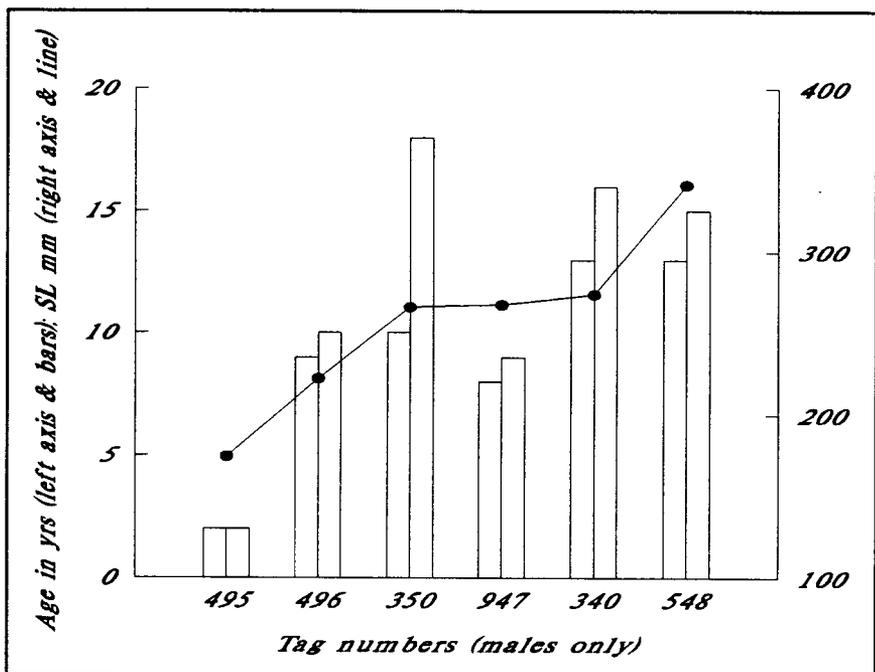


Figure 17. Minimum and maximum age estimates (bars) and Standard Length (dots) as determined from lapilli for all specimens verified to be males.

examined to determine dates of spawning in that river. Presumably specimens not yet processed, but listed in Appendix 1, collected in May, June and July of 1991, include at least some young-of-the-year, and if so, spawning dates in 1991 will be estimated in the next report. Similarly, since specimen 328 was analyzed blind shortly before preparation of this document, without knowledge of its capture location, no particular attention was paid to searching for increment patterns early in life which might support the hypothesis that it hatched and grew for some time in warm tributary waters before moving to the mainstream. Patterns presumed to depict this movement have been found in other specimens (e.g. Figure 4 or Figure 10). This hypothesis will now be investigated.

Hatching date estimates obtained to date, while based on relatively few specimens, indicate May and June hatches in 1992 (5 specimens - all from Colorado mainstream) and hatches in March and April in 1990 (9 specimens - all from the LCR). Interestingly, a single specimen taken about 5 miles below the LCR in the mainstream Colorado in October, 1990, was estimated to have hatched about May 30 of that year, nearly two months later than the latest estimated hatch date from the same year in the LCR. This may simply be an artifact of small sample size and/or sampling bias since young-of-the-year specimens, if such were present and collected in the LCR in late May or later in the summer of 1990, were not available to the author (Appendix 1).

ENVIRONMENTAL DATA

Though the magnitude of physical and chemical differences between the mainstream and LCR are obvious to even untrained observers, quantitative descriptors of chemical composition and physical attributes of these waters will be required for analysis of hypotheses that otolith composition reflects ambient water quality. Data on temporal and spatial variability in temperature in each river will be required, as will comprehensive water quality data. Since the otolith chemical analyses will be exploratory, data on as many water quality parameters as possible would be useful. This would include data on rare elements, heavy metals, isotopes, etc.. Any elements or isotopes which might uniquely characterize either river would be of particular interest. Precise identification of isotopes released in the Zuni River basin by an accidental spill a number of years ago would be of great interest, as would studies of its subsequent distribution downstream. Additionally, in order to analyze effects of discharge on growth rates and year-class strength, detailed discharge data will be required for each river. Ideally, chemistry and discharge data covering the past three decades might be provided. This period has been chosen to cover the entire estimated lifetime of the oldest specimens analyzed to date.

Temperature and discharge data covering the periods from which young-of-the-year specimens are available might prove especially valuable. It is likely that unusual spring or summer meteorologic events such as unusual cold spells during normally warm months, or dramatic floods, will produce event-specific, unique natural otolith banding patterns. These patterns could then be used as markers which would allow subsequent validation of both daily and annual ageing techniques, and future back-calculations of birth dates of adults in which such event-specific marks can be located. A few cases in which such unique, natural marks have proven valuable in management of commercial marine fisheries have recently been reported (1993 Otolith Research and Applications Conference).

GENERAL SUGGESTIONS

As discussed above, otoliths are clearly indicated by preliminary work to have considerable potential for humpback chub management applications in the Grand Canyon. It is hoped that this preliminary report will provoke comments from the management community which will assist the author in determining what future research pursuits are likely to provide the most useful contributions to those trying to make informed management decisions.

SUMMARY

Preliminary data obtained from otoliths of humpback chub from the Grand Canyon are provided. Age estimates with near daily precision appear to be easily obtainable from young-of-the-year specimens while in the Little Colorado River, yet the daily deposition of increment formation has yet to be rigorously validated in the lab or in field experiments. The conclusion that they are daily, however, is supported by evidence that hatch dates estimated from otoliths generally agree with field evidence of timing of spawning activity. Reliable resolution and counting of daily increments from periods spent in the cold, near constant-temperature waters of the mainstream Colorado River appears not to always be possible with standard light microscopy techniques, but might be attainable with Scanning Electron Microscopy.

Otoliths of humpback chubs appear to provide reasonable estimates of yearly ages of adult specimens. Up to about three years of age, length of the growing season can be estimated from daily increments between annuli.

Highly preliminary data from small samples analyzed to date provide interesting insights into the biology of humpback chub in the Grand Canyon. Growth rates in the mainstream Colorado River are strongly indicated to be much lower than those attained in the LCR. Some specimens from the mainstream appear to have spent several brief periods in waters much warmer than the mainstream, perhaps tributary mouths. Indications of very abrupt changes in growth rates have been found in many specimens, and is presumed likely to correspond to inter-habitat movements, such as passage from the LCR to mainstream Colorado and returns to the LCR. Back-calculated hatching dates indicate considerable variation in timing of reproduction among years, and relatively young ages of specimens taken far downstream of the LCR.

Very recent literature on temperature and salinity effects on elemental composition of otoliths indicate that it is very likely that at least some elements can be found that would provide a unique mark for time periods spent in the LCR or at least, non-mainstream Colorado River habitats. Though there is almost no literature on concentrations of elements expected in freshwater fish otoliths, they can clearly be expected to be near the detection capabilities of analytical equipment now commonly in use on the many studies being published on marine species. New techniques are quickly becoming available and analyses of micro-spatial distribution of elements across humpback chub otolith transects will be completed prior to the completion of the final report from this study.

ACKNOWLEDGMENTS

Dr. Ed Brothers provided training and general advice regarding otolith preparation and reading, as well as readings of all lapilli. Mr. Gary Scopetone graciously provided his estimates of ages from opercles, and Mr. Michael McCarthy mounted, ground and made age estimates from the asterisci.

APPENDIX 1

Tag numbers, capture locality and date, length, weight and sex of specimens collected and available for examination of otoliths but not yet analyzed.

APPENDIX 1 - SPECIMENS AVAILABLE FROM WHICH OTOLITHS HAVE NOT YET BEEN EXAMINED

TAG NO.	TAG TYPE	TAG COL.	RIVER	CAPTURE LOCALITY	DATE CAPTURED	N	SL	TL	WT (gm)	SEX
							(mm)	(mm)		
520		YE	LCR	5432/ SIPAPU	4/26/90	1	77.43	97.00		
523		YE	LCR	5432/ SIPAPU	5/2/90	1	78.29	98.99		
526	CAR	YE	LCR	5432/ SIPAPU	5/5/90	1	90.84	119.14		
527	CAR	YE	LCR	0/EXPERIMENTAL	4/26/90	1	82.74			
528	CAR	YE	LCR	5432/ SIPAPU	5/8/90	1	90.21	119.03		
529	CAR	YE	LCR	9650/ SALT TRAIL CAMP	5/15/90	1	27.52	36.54		
530		YE	LCR	5432/ SIPAPU	4/26/90	1	72.04	91.41		
537	CAR	YE	LCR	0/LCR WARM CONTROL	4/26/90	1	73.08			
539	CAR	YE	LCR		10/22/80	1	29.40	37.40		
540	CAR	YE	LCR	0/LCR WARM CONTROL	4/26/90	1	83.80			
541	CAR	YE	LCR	9650/ SALT TRAIL CAMP	5/15/90	1	22.05	29.29		
542	CAR	YE	LCR	9650/ SALT TRAIL CAMP	5/15/90	1	17.85	23.66		
544		YE	LCR	5432/ SIPAPU	4/26/90	1	58.25	75.28		
545		YE	LCR	5432/ SIPAPU	4/26/90	1	60.42	75.07		
551		YE	LCR	5432/ SIPAPU	4/26/90	1	78.43	98.72		
555	CAR	YE	LCR	9650/ SALT TRAIL CAMP	5/15/90	1	19.65	26.35		
556		YE	LCR	5432/ SIPAPU	5/2/90	1	87.88	82.81		
558	CAR	YE	LCR	0/LCR WARM CONTROL	4/26/90	1	82.44			
560		YE	LCR	5432/ SIPAPU	4/26/90	1	82.85	102.52		
562		YE	LCR	5432/ SIPAPU	5/2/90	1	84.41	106.84		
565	CAR	YE	LCR	1/4 MILE UP LCR	10/18/80	1		105.00		
568	CAR	YE	LCR	LCR - 1/4 MI. UP	10/18/80	1		94.00		
569		YE	LCR	5432/ SIPAPU	4/26/90	1	78.70	99.70		
571	CAR	YE	LCR	5432/ SIPAPU	5/8/90	1	83.92	110.18		
577		YE	LCR	5432/ SIPAPU	5/2/90	1	82.46	103.30		
579	CAR	YE	LCR	9650/ SALT TRAIL CAMP	5/15/90	1	26.36	34.34		
582	CAR	YE	LCR	0/LCR WARM CONTROL	4/26/90	1	81.12			
583	CAR	YE	LCR	5432/ SIPAPU	5/8/90	1	81.86	105.49		
587		YE	LCR	5432/ SIPAPU	5/2/90	1	74.79	93.91		
589	CAR	YE	LCR	LCR; AT MOUTH	5/6/89	1		370.00	368	M
62	CAR	BL	LCR	90/ ANGLING	5/10/90	1		390.00	490	U
749	CAR	YE	LCR	LCR; AT MOUTH	5/9/89	1		175.00	36	
864	CAR	OR	LCR	LCR; SALT CANYON	5/11/89	1		318.00	275	F
943	CAR	OR	LCR	100/ HOOP	5/9/90	1		246.00	141	U
962	CAR	OR	LCR	180/ NS D HOOP	5/9/90	1		287.00	174	M
965	CAR	OR	LCR	180/ NS D HOOP	5/9/90	1		302.00	226	M
976	CAR	OR	LCR	0/ PARA TRAM	4/20/90	1		385.00	476	F
984	CAR	OR	LCR	0/ PARA TRAM	5/1/90	1		415.00	644	M
986	CAR	OR	LCR	100/ HOOP	5/8/90	1		223.00	104	F
988	CAR	OR	LCR	192/ SS D HOOP	5/8/90	1		227.00		F
998	CAR	OR	LCR	5432/ SIPAPU	5/8/90	1		283.00	85	F
	NON		LCR	200/ HOOP	4/20/90	1		113.00	10	U
	NON		LCR	1200/ HOOP	4/20/90	1		106.00	11	U
	NON		LCR	1200/ HOOP	4/20/90	1		75.00	3	U
	NON		LCR	192/ SS D HOOP	4/21/90	1		123.00	16	U
	NON		LCR	180/ NS D HOOP	4/26/90	7				
	NON		LCR	5432/ SIPAPU	5/11/90	1		72.00		U
	NON		LCR	180/ NS D HOOP	5/12/90	1		52.00		U
	NON		LCR	13854/ HOOP	5/2/90	1		142.00	20	U
	LP2		LCR	9904/ HOOP	5/9/90	1		145.00		M
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	23.83	30.61		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	25.70	34.65		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	19.71	25.29		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	25.23	34.17		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	15.91	19.83		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	16.26	21.22		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	14.96	19.35		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	16.23	19.54		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	18.08	24.46		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	15.45	20.21		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	20.37	25.98		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	18.38	23.15		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	20.39	25.81		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	17.25	22.40		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	19.30	24.14		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	21.01	27.87		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	18.92	20.95		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	16.62	20.19		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	20.57	26.84		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	21.01	26.54		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	15.04	17.86		
	NON		LCR	9650/ SALT TRAIL CAMP	5/15/90	1	16.96	20.23		
	NON		LCR	380/ L SIDE MT	5/12/90	1		34.00		U
	NON		LCR	380/ L SIDE MT	5/12/90	1		37.00		U
	NON		LCR	550/ R SIDE MT	5/12/90	1		32.00		U
	NON		LCR	550/ R SIDE MT	5/12/90	1		34.00		U
	NON		LCR	550/ R SIDE MT	5/12/90	5				
	NON		LCR	592/ L SIDE MT	5/12/90	1		31.00		U
	NON		LCR	5432/ SIPAPU	5/8/90	1	85.19	111.41		
	NON		LCR	5432/ SIPAPU	5/8/90	1	81.32	103.98		
	NON		LCR	5432/ SIPAPU	5/8/90	1	74.36	97.70		
	NON		LCR	5432/ SIPAPU	5/8/90	1	93.57	116.51		
	NON		LCR	5432/ SIPAPU	5/8/90	1	75.73	100.88		
	NON		LCR	5432/ SIPAPU	5/8/90	1	71.46	95.11		
	NON		LCR	5432/ SIPAPU	5/8/90	1	73.58	98.41		
	NON		LCR	5432/ SIPAPU	5/8/90	1	78.42	106.38		
	NON		LCR	5432/ SIPAPU	5/8/90	1	84.09	109.47		

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5. Trout Studies

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This section summarizes research on rainbow trout (*Oncorhynchus mykiss*) in the Lee's Ferry reach from November 1989 through February 1993. During the past three years, a large amount of data were collected (*e.g.* > 18,000 length-weight records). To expedite data handling and analysis, these data (plus others) will be incorporated into a database management system. This report will briefly summarize data that have been collected plus indicate what types of data are still being collected. Intended methods of analysis will be discussed and some preliminary results will be presented. Detailed methods and materials have been described elsewhere (Angradi et al. 1992). Therefore, only a brief synopsis of the methods will be discussed. Additionally, new methods for the age, growth, and population dynamics portions of study are briefly described.

Organized by specific work items, the following is a summary of the progress to date on the trout studies portion of the GCES Phase II Studies.

Work item 2.1 - Determine the potential loss of trout spawning, defined as areal loss of spawning bars and exposure of redds, at various flows in the reach of the Colorado River between Glen Canyon Dam and Lee's Ferry.

Introduction

Phase I studies indicated that as many as 27% of the trout in the Lee's Ferry reach may be naturally reproduced within the system (Maddux et al. 1987). It is obvious that trout reproductive success can be affected by water level fluctuations. If water levels drop, trout can be forced out of suitable spawning sites and the eggs and/or fry can become desiccated by receding water levels. This portion of the study plans to identify the extent of suitable spawning gravels in the Lee's Ferry reach at various water levels and document the usage and behavioral response of spawning trout using these gravels for spawning at various water levels.

Methods and Progress

The experimental design was originally predicated on the assumption that most spawning occurred on 5 to 10 cobble bars that were subjected to daily dewatering. Direct observations of the trout during the 1990-1991 and 1991-1992 spawning seasons suggest that this may not be true. During the 1990-1991 and 1991-1992 seasons, the majority of the surface area of the various cobble bars was not used by spawning trout. Conversely, a large number of trout were

observed using other areas of the river for spawning; chiefly shoreline areas that appeared to offer an acceptable range of substrate size and current velocity. While these areas are also subjected to daily dewatering by fluctuating flows, a large number of trout were also observed using deep water spawning areas that were not subject to dewatering. These alternative habitat preferences greatly exacerbate the problem of quantifying suitable spawning areas and measuring the areal gain or loss due to fluctuating flows. As a result, an absolute areal measurement of spawning habitat in this reach may be an unobtainable goal. However, valuable information can still be collected as to what constitutes favorable spawning habitat and at which flow regimes some of the habitat becomes unusable. Also, it should be possible to use yearly redd surveys to develop a relative index of spawning success to compare against the changes in yearly flow.

A major goal for this portion of the study has been to generate detailed contour maps of each study bar so that a host of environmental variables could be measured and overlaid onto each map. The variables in this matrix include; cfs levels, water depth, current velocity, substrate size, imbeddedness descriptors, and redd placement data. It should then be possible to describe trout spawning habitat as being ideal, adequate, marginal, or unacceptable in the Lee's Ferry reach. [Each of the data sets resulting from these methods will be in the form of a matrix (x,y values) that areally describe the bar in terms of that particular variable. It is anticipated that each of these matrixes can be overlaid (along with the spawning gravel data set) onto surveyed elevations of the appropriate spawning bar. The results will be in the form of an x,y,z set of coordinates so that correlations can be calculated between elevation, gravel distribution, flow, and redd placement data.]

Towards this goal, cobble bars at river miles -4.0, -6.1, -8.9, -13.5, and -14.0 have been surveyed for elevation contours using Total Station surveying equipment. Steel rebar stakes spaced evenly along each bar were also surveyed. These stakes were used as reference points for determining transect locations, redd locations, and for fish locations required for a companion study using radio telemetry. Additionally, in February of 1993, GCES personnel surveyed benchmarks and backsights for each site and tied them into their system so that the surveyed bars could be tied to "real world" coordinates and ultimately into the AGFD GIS system.

Measurements of the wetted perimeter for each of the spawning bars were made from stakes placed along the high water line at 3,000, 5,000, and 8,000 cfs constant discharges. Cloth tapes and hip chains were used to measure the distance from the stakes to the waters' edge along a

magnetic compass bearing, perpendicular to the shoreline. These measurements will be combined with contour maps to correlate mean absolute elevations with flow discharges.

Extensive substrate samples have been collected along transects from each bar. Relative particle size distribution and degree of imbeddedness were measured. With the exception of the bar at -13.5 mile, the results were reported in Angradi et al. (1992). Gravel from -13.5 mile bar have been collected and the analysis is pending. Data have been collected in such a format that it would be feasible to construct a matrix of variable substrate particle sizes and degree of imbeddedness over maps of each the bars once these maps have been generated.

For the 1990-1991 and 1991-1992 spawning seasons, no spawning was observed on -14.0 mile bar and negligible spawning occurred at -8.9 mile bar. Because of the new "interim" flow regime, -6.1 mile bar can no longer be adequately surveyed for redds. Moreover, very few redds were observed there in previous years. For these reasons, the study of "traditional" cobble bars has been limited to -4.0 mile bar. This bar is unquestionably the largest and most significant for spawning in the Lee's Ferry reach. The additional study site at -13.5 mile bar was established to represent spawning habitat other than cobble bars. This littoral area was used extensively by spawning trout during the past three years.

In March 1992, extensive current velocity readings were taken along transects at -4.0 and -13.5 mile bar. Measurements were taken to construct a matrix of current velocities over contour maps. Velocities have been recorded at approximately 7,000 and 12,000 cfs. It is anticipated that this procedure will be duplicated for flows approximating 16,000 and 20,000 cfs.

In the past, redd placement data were collected at all spawning bars on a bi-monthly basis throughout the spawning season. Redds were identified, counted, and their geographical positions located by means of intersecting two compass bearings taken from known locations (surveyed stakes). However, an inherent problem with this methodology was the over estimation of the number of redds because of the inability to distinguish between previously counted ones and new ones during each consecutive survey. Colored rocks were placed in the counted redds but the trout displaced them and fishermen removed them between sampling times (Gamble, personal observation).

In March 1992, a new methodology was adopted that concentrates on -4.0 and -13.5 mile bars. To obviate the problems associated with duplicate redd counts, it was decided to locate redds only once a year thereby producing a "snapshot in time" of redd placement. [This technique

fails to document the progress of redd building activity throughout the spawning season. It also doesn't measure the absolute total of trout redds created during a particular season, but it should be very useful for establishing a relative index of spawning activity from year to year. Over time, this index could possibly be correlated with population levels of older year class trout, providing advance information to management about future population levels and the need for supplemental stockings.] This survey is conducted near the peak of the spawning season to allow for redd placement behavior that might be predicated on the relative positions of other redds. The peak of the spawning season is determined by counting and triangulating all of the redds at each study site once a month during the spawning season. For the purpose of predictive models, only the month that exhibits the highest redd count is selected as the peak month. Redds are located using the same compass bearing intercept method as described above and in Angradi et al. (1992).

Current Problems and Solutions

A large portion of this study depends on generating maps in an appropriate format so that data on spawning gravel size, embeddedness, and redd placement can be superimposed on maps of discharge contours. Although surveying has been completed, it was done in small segments by three different survey crews. Consequently, the data exists in several different formats that needs to be standardized and collated. Current project personnel lack the appropriate expertise necessary to accomplish this task. The GCES coordinator at AGFD is trying to provide an outside consultant to organize these data who will also work with GCES personnel to generate maps and to integrate the data with the GIS System.

Complicating the study, this was an atypical period for trout spawning with some of the problems possibly generated by the research flows themselves. For example, during 1990-1991 and 1991-1992, spawning activity was delayed for a couple of months and apparently never reached the levels associated with a "normal" year (1991-1992 appeared to be an improvement over the previous year). Possibly, the research flows may have aggravated a food supply problem which then led to the appearance of a large number of sick, emaciated trout that were too stressed to spawn normally. Additionally, the entire population was also infected with an intestinal parasite (see section 2.3 for details). To what extent this nematode affects trout growth and reproduction is unknown.

The present spawning season seems more typical. That is, spawning activity started earlier and is occurring at a greater intensity than in previous years (Gamble, personal observation). This

survey should be continued over the next several years to obtain more data for the purpose of developing a relative index of spawning.

Work item 2.2 - Determine the rate of stranding and mortality of naturally reproduced and stocked trout under different flow regimes in the Glen Canyon tailwater.

Introduction

It was observed during the Phase I studies that as water levels declined in the Lee's Ferry reach, some trout became stranded in isolated backwaters. Little was known about the degree of stranding and the mortality of these fish. This portion of the study identifies major stranding areas and determines the mortality of adult fish relative to season and flow levels.

Methods and Progress

During the months of January and February 1990, the river from Glen Canyon Dam to Lee's Ferry was surveyed several times at low flows to identify major and minor stranding pools. It was determined at what discharge levels these stranding pools were no longer connected to the mainchannel causing fish to become stranded. At this juncture, it was determined that surveys would have to be conducted at night to avoid biases caused by predation and anglers. Ten major stranding areas at river miles -0.5R, -4.0R, -8.2L, -8.9R, -9.7R, -11.0R, -11.7R, -11.9L, -13.0R and -14.8R were identified (R= river right, L= river left). These areas were surveyed four times a month from March through August 1990 and twice a month during the periods of "fluctuating flows" (as opposed to "steady" research flows) from September 1990 through February 1991. Sites were also surveyed bimonthly from September 1991 through May 1992 and monthly from September 1992 to the present. It was not necessary to survey during the summer months since the minimum daily flows (summer interim flows) exceeded the levels necessary to strand trout.

Detailed methods and materials were reported in Angradi et al. (1992). It was anticipated that all stranding sites could be periodically surveyed for dead trout and that a total number of dead trout per year could be calculated by multiplying the results over the number of nights per year that the flows duplicated conditions that existed on survey nights. A seasonally corrected version of this method was used to determine that approximately 15,000-20,000 adult trout ($\bar{X}_{TL}=437$ mm, $SD=53$) were lost due to stranding from February 1990 to February 1991 (Bagley et al. 1991). As the study progressed, several complicating factors were identified:

1) When exactly do fish become stranded in these pools? Direct observation of fish in stranding pools showed that fish become effectively isolated before the pool itself actually closes off from the main channel. For example, in June of 1990, observers watched 286 adult trout die in a backwater that reached water temperatures of 25° C. Although the trout would have had to negotiate about 100 meters of 10-15 cm deep water to escape, this backwater was never isolated from the main channel. Predator avoidance behavior possibly prevents trout from crossing shallow water bridges. How deep the water needs to be for passage, and whether the depth varies with the length of the passage, or whether trout are willing to traverse shallower water at night, remain unanswered questions. For this study, the cfs level at which the physical separation of the backwater from the main channel was determined for each of the stranding sites and it was assumed that the trout had freedom of movement until this occurred.

2) Prior observations showed that sites dewater at different rates. Three major factors that influence dewatering rates have been identified. i) Bank retention--water from the river bank tends to "feed" the stranding pools at rates proportional to the water level (*i.e.* the higher the daily maximum flows, the more pronounced this "feeder" effect is and the longer it takes for the pool to dewater). ii) The ultimate minimum daily low also influences dewatering rates. The lower the ultimate minimum flow, the faster the dewatering rate. iii) The down ramping rate of the flows effects dewatering rates both directly and indirectly. Indirectly, it has effects on the first two factors. Directly, the lower the down ramping rates, the less time a pool is subjected to dewatering before the water comes up the next morning.

3) Should a distinction be made between the research flows themselves and the operating flows they were attempting to mimic? A significant finding of this study suggests that water quality parameters (temperature, dissolved oxygen, *pH* and conductivity) rarely reached lethal limits in any of the stranding pools and that trout were killed either as a direct result of dewatering or predation. However, during the research flows on 5,000 cfs weekends, fish perished in some sites as a result of high temperatures or oxygen supersaturation on the second or third day of constant 5,000 cfs flows. During the spring of 1990, before the research flows went into effect, there was an interruption of the power grid and the river was lowered to 3,000 cfs on a warm spring day. This resulted in the mortality of 88 adult trout at site -11.9L; presumably due to water temperatures exceeding 25°C. Discounting these unusual summer low flow events, water quality had little or no effect on stranding mortalities.

4) Two different habitat types are evident from the stranding sites. Only sites -11.9R and -14.83, which both isolate at 4,000 cfs, appear to be located where trout actually "live" and

presumably would be subjected to stranding mortalities throughout the year. These two sites were usually inundated and had dense standing crops of *Cladophora* on the cobble substrate. Apparently, this must be good habitat for resting and feeding because trout are often observed there. All of the other sites are shallow water areas with moderate currents and cobble/gravel substrates. The trout show an affinity for these sites only during the spawning season. Being shallow in the daytime, these areas are dewatered at night. The spawning instinct may account for the trouts' strong affinity for these areas. It could be that trout do not want to vacate their redds and are thus more susceptible to becoming trapped by receding water levels. For instance, 13 adult trout in spawning condition were taken from a stranding pool at -13.0 mile, Floy tagged, and released into the mainchannel on February 24, 1991. On March 5, 1991 the area was resurveyed and five of the marked trout had returned and perished when the pool dewatered.

River areas in the zone of fluctuation were not very productive (Angradi et al. 1992). These areas seem to offer little to the trout except during the spawning season. Therefore, stranding of trout is chiefly a spawning related phenomenon. When they are not spawning, only extreme and prolonged low flows during the summer would have serious consequences on the population.

It should be noted that during extended periods of high flows, the particular sites surveyed could become productive *Cladophora* beds. Sites at higher cfs levels would be in the zone of fluctuation and would become future stranding sites. Water levels may vary, but the phenomena of stranding will probably remain consistent if water levels are allowed to fluctuate dramatically during the spawning season.

1,692 stranded adult trout were found during 22 river surveys conducted from February 1990 to February 1991 (Angradi et al. 1992). Using the methods described above, it was estimated that approximately 15,000-20,000 adult trout ($\bar{X}_{TL}=437$ mm, $SD=53$), in spawning condition, died due to stranding during this period (Bagley et al. 1991). This estimate must be accepted with caution. However, even within wide limits, losing this magnitude of mature, breeding fish would have deleterious impacts on the population, especially if it is small. In stark contrast, data from 17 surveys conducted in 1991-1992 and four surveys in 1992-1993 indicate that a total of four stranded adult trout have been found during this period, and three of these trout would have survived until the river level came up in the morning. Clearly, some combination of the new minimum flows and reduced ramping rates have virtually eliminated stranding as a cause of mortality of adult trout in this reach.

A fishery can withstand a higher mortality rate among juveniles than among mature, adult fish. Stranding of trout fry was previously reported (Angradi et al. 1992). Fry become stranded but probably in equal or fewer numbers than adults (Angradi et al. 1992). Under the new flow regime, when fry are most vulnerable (in the late spring and summer), water levels have tended to remain high enough to eliminate stranding as a major mortality factor. Future flow conditions that are significantly different from the present ones could, however, adversely impact trout fry.

As stated in work item 2.1, this has not been a typical period of trout reproduction and growth. The impacts of the research flows are largely unknown and many sick fish plus a delay of peak spawning have been observed. A second problem was the lack of confidence in determining the origin of fish (wild v. hatchery).

Addendum to Work Item 2.2. Conduct a literature review of trout strains. This should include an assessment of the relationship between trout strains and their interaction with flows, growth, survivorship and movement.

Introduction

Over the years, several strains of rainbow trout were stocked at Lee's Ferry. Unfortunately from 1963 through the early 1980s, records were not kept on which strains were stocked. Stocked trout accounted for 73% of the total adult population in 1984 and 1985 during a period of high steady flows (Maddux et al. 1987). The yearly recruitment of stocked trout to the fishery is unknown and probably highly variable. Genetic origins are largely unknown, consequently, there is some speculation that other strains might exhibit higher level of fitness.

Two studies were added to the AGFD's obligation to provide this information. First, a literature review of available trout strains and their fitness characteristics was undertaken. The scope of the work included compiling information on the fitness characteristics of commercially available strains and the identification of tailwater fisheries that are similar to Lee's Ferry and their associated strains. The ultimate goal was to evaluate strains that could potentially prosper in the operating regimes at Lee's Ferry. Second, trout populations in the Colorado River and its tributaries, as well as hatchery stocks, were analyzed by allozyme electrophoresis to determine their genetic cohesiveness and contribution to the fishery.

Methods and Progress

These work items have been completed. The literature review was completed November 1991. (Davis 1991) Electrophoretic samples were analyzed at the Illinois Natural History Survey (Claussen and Philipp 1991). Dr. Mike Musyl, a recent staff addition at AGFD who has expertise in allozyme electrophoresis and population genetics, intends to review the genetics report and study and make recommendations.

Work item 2.3 - Determine the effects of fluctuating flows on age and growth relationship of stocked trout in the Glen Canyon Dam tailwater downstream of Lee's Ferry.

Introduction & Methods

To obtain data for age and growth information, three techniques were used to collect fish. They were electrofishing, seining isolated backwaters, and trammel net "seining" of cobble bars. Although almost 6,000 trout were captured, tagged, and released using seines during the first year of the study, this method is no longer feasible due to the new interim flows. Minimum daytime water levels are too high to effectively seine and most backwaters never become isolated.

In May 1992, 89,000 rainbow trout fingerlings (50-125mm) were tagged with binary coded wire tags (BCWTs) at Page Springs Hatchery. Seventy thousand of these trout were subsequently stocked in May and June of 1992. Additionally, 8,000 BCWT trout were allowed to grow in the hatchery for four months and were stocked in September and October of 1992. Tag retention was checked one to two weeks after implanting and just before stocking and found to be 95%-96%. This new technology will make it possible to distinguish wild trout from hatchery trout.

AGFD has been electrofishing the Lee's Ferry reach on a quarterly or semiannual basis for a number of years. These data have been used to generate length frequency histograms and relative weight comparisons. The results are presented below.

Direct observation suggested that a variety of habitats and microhabitats were present in the reach. Particularly evident was the longitudinal zonation of the river from the upstream to the downstream section. Although a complete breakdown and analyses of habitats and microhabitats was beyond the scope of the study, it was nonetheless profitable to rank the habitat types for

future comparisons. To this end, the river was broken down into three main habitat types which were analogous to the classic riffle, run, and pool.

Habitat #1 is analogous to the riffle and comprises those portions of the reach associated with cobble bars. Characteristics of this habitat are; i) high current velocities and shallow water, ii) steep longitudinal gradient, iii) pronounced "tidal" effect from fluctuating flows, iv) cobble or boulder substrate with less sedimentation and v) large portions of continually inundated substrate covered with *Cladophora*.

Habitat #2 is analogous to the run and it is an intermediate habitat between habitats #1 and #3. It resembles habitat #1 but has slower current velocities. Characteristics of habitat #2 are; i) intermediate current velocities with some deep water, ii) intermediate longitudinal gradient, iii) largely sand substrate with some silt, iv) less "tidal" fluctuations with the areas of fluctuation typically sand beaches and v) some rooted emergent macrophytes but typically a "shifting sand" substrate which discourages vegetation.

Habitat #3 is analogous to the pool and comprises those portions of the river that are most like a lake. Characteristics of this habitat are; i) deep water with slow current velocities, ii) shallow longitudinal gradient, iii) almost no "tidal" effect, iv) sand or silt substrate, v) area of greatest sedimentation, vi) large numbers of rooted aquatic macrophytes are common and vii) some of the habitat is relatively deep and habitat characteristics are largely unknown.

The river was divided into these three habitat types. Habitat #1 comprised approx. 34% of the reach as did Habitat #2. Habitat #3 comprised approx. 32% of the reach.

Within each habitat type, the river was broken down into 640 m transects. For the sampling design, a table of random numbers was used to select three sites from within each habitat type (50-100 fish were desired and a 640 m site allowed the whole sample to be taken in one pass, thereby avoiding depletion passes). From empirical trials, it was decided that the fishing effort would be standardized at 2000 seconds per site.

Five sites are sampled on each of three consecutive nights each quarter. Sites are marked prior to each night's sampling with cyclamen glow sticks to avoid confusion for the boat operators. All sampling takes place after dark to enhance visibility for the netters and to allow the trout to move into shallow water areas. The shocking boat operator works the shallow areas of each site (typically the shoreline in areas less than 1.5 m deep) from upstream to downstream for 2,000

seconds as netters gather stunned fish and placed them in electrically shielded side cars. After the sample is collected, the fish are transferred to a workup boat and placed in a live car beside the boat (a 6 mm mesh bag, 2 m deep suspended from a float with a 2 m square opening). The shocking boat is then released to sample the next site.

The fish are processed "assembly line style" by a crew of four or five technicians. To prevent handling injuries, trout are first anesthetized in a solution of MS 222 at a 50-125 mg/l concentration for 2 to 5 minutes. They are then tagged with numbered Floy spaghetti tags, weighed to the nearest gram and measured (TL) to the nearest mm. An effort is made to determine sex, degree of sexual maturity, and to note any hooking injuries or other abnormalities. Since August 1992, fish in appropriate size classes are examined with a magnetic detection wand for the presence of BCWTs.

Preliminary Results & Discussion

Past evaluation of the age and growth relationships of stocked trout in the Lee's Ferry reach has been problematical and largely restricted to the use of Petersen (Ricker 1975) length-frequency distributions. However, for this to be an effective method to infer the age structure and/or growth relationships between cohorts, three assumptions must be satisfied. First; the spawning season must be relatively short, second; growth among cohorts must be uniform, and third; stocked trout must be reliably distinguished from naturally reproduced trout.

Because of the artificially created ecosystem in the tailwaters downstream from Glen Canyon Dam, it is apparent that the first two assumptions have been compromised. For example, trout have been documented to spawn from August through May (Gamble, unpublished results), and growth (in terms of relative weight) has been sporadic (see below).

Steps are now currently underway to rectify the last assumption. Since 1989, stocked trout were marked with an external fluorescent pigment or through the use of tetracycline feeds at the hatchery. Both methods proved unreliable due to variable pigmentation rates and difficulties in detecting marker in older age classes.

Since May 1992, all stocked trout (*ca.* 78,000) in the tailwater have been tagged with BCWTs in an attempt to distinguish hatchery trout from wild trout. Each year class is given a different code. This practice will allow AGFD personnel to estimate vital parameters such as: 1) growth rates between hatchery trout vs. wild trout, 2) mortality of stocked trout, and 3) the contribution of hatchery trout to the total fishery.

For effective management of the trout fishery at Lee's Ferry, it is essential that reliable methods to age trout (or estimate the age with a high degree of confidence) be further explored. Information about the age structure and dynamics of the trout population will allow estimates of various parameters (e.g. instantaneous growth, mortality, recruitment and yield). These parameters, as influenced by fluctuating flows, are necessary to base future policy concerning stocking rates, slot limits and/or bag limits. Conventional methods for aging trout in the tailwaters by the examination of annuli in scales and otoliths was apparently ineffectual possibly due to the consistency of cool water temperatures in the tailwaters (Angradi et al. 1992). Whether this initial observation represents a true phenomenon or a sampling artifact needs further investigation. Therefore, other bony structures (e.g. cleithrum, operculum, sagittal otoliths, and vertebral centrum) plus scales from "key" areas will be re-evaluated for annuli using different methods (including weighing and baking otoliths; clearing and staining opercula). Approximately 15 to 20 trout representing a wide size range (and presumably ages) will be collected from an upcoming electrofishing trip in March 1993 and evaluated by experienced personnel in Phoenix.

In the event that trout cannot be aged using conventional bony structures and techniques, their ages will also be estimated using a computer simulated growth model from length-frequency distributions. This method, 'MULTIFAN', finds the "best" match between the theoretical and observed length-frequency distributions with either maximum likelihood or chi-square methods (Fournier et al. 1991, Terceiro et al. 1992). This program also generates von Bertalanffy growth coefficients (K) that can be used to compare growth rates between sampling locations and cohorts. In addition, it is possible that a cohort could be tracked through time to test the effects of fluctuating flows on such dependent variables as growth, mortality and age structure. It is planned that length-frequency data from 1984 to the present (over 80,000 records) will be analyzed by this method.

In the absence of reliable methods to distinguish stocked trout from wild trout, it is nevertheless useful to examine the growth and presumptive age patterns of trout in the fishery to search for general trends. Preliminary results using relative weights (W_r), length-weight relationships and length-frequency distributions, from both creel and electrofishing data, are discussed below. However, a possible vitiating factor regarding trout growth must be briefly mentioned. A parasitic nematode *Buldodacnitis ampullastoma*, probably adversely affecting the growth of trout in the fishery, was identified in the pyloric caecae from virtually all of trout collected in 1990 (see below). As yet, there is no clue to the etiology or epidemiology of the parasite but experiments are underway.

Recent concerns about the condition of trout at Lee's Ferry prompted an examination of the data from 1984 to the present. Length-weight data were separately analyzed from the electrofishing catches and creel data to assess the relative condition of trout in the reach. We also explored the use of the Relative Weight Index (W_r) (Murphy et al. 1990) as a better method to quantify condition rather than traditional condition factor (K) indices (see Lagler 1956).

The logarithms of the length-weight regression equations were also used to compare the relative condition of fish from different populations. The logarithmic relationships of the length-weight regression were computed and plotted for each year.

Relative Weight (W_r) is calculated as $100 \times W/W_s$, where W is the weight of an individual fish and W_s is the "standard" weight of a fish for a given length. With this correction factor, relative weight is not dependent on length and W_r can be used as an unbiased estimate to compare populations. The standard weight is defined such that a mean W_r of "100" (from a wide range of lengths) may reflect the ecological and physiological optimality for a population (Anderson and Gütreuter 1983).

W_s was calculated using the algorithm of Murphy et al. (1990). The log length-weight regression equations were used to predict the lengths and weights of trout in the Ferry from April 1984 to August 1990. From empirical study (Persons, unpublished data), outliers in the data were excluded from the regression analyses if $0.2 > K > 1.5$. The predicted weights of fish in 1 cm length intervals were calculated from the regression equations. The 75th percentile of weights in each of the intervals were regressed upon length to determine the parameters of the W_s equation.

Lastly, the historical data base will be re-analyzed in an effort to quantify the effects of fluctuating flows against dependent population variables. Because the degree, nature and duration of the flows has varied significantly from the onset of the study in 1984 until the present, it may be possible to model this temporal variation. Next, time permitting, a corollary study of flannelmouth suckers (*Catostomous latipinnis*) in the reach will allow a direct comparison with results from the current trout study and will provide useful management information. Further, when GCES personnel provide accurate maps of the spawning bars, it is feasible that a predictive model of redd density and relative abundance could be generated using regression analyses. Lastly, some of the recapture data may be used to estimate population abundance (and variances) with the Lincoln Index or the "open" fishery models of Seber-Jolly and Zippen as described in Ricker (1975).

Length-Frequency Distributions

Length-frequency distribution scatterplots for the 1989 to 1992 electrofishing samples are presented in Fig. 5.1. In 1989 and 1990, the distributions were predominately unimodal with some evidence of a smaller cohort around 100 to 300 mm (Fig. 5.1). However, in 1991 and 1992, the distributions were distinctly bimodal with two cohorts readily apparent in the population (Fig. 5.1).

Breaking the distributions down by season are presented in Fig. 5.2. Although there was some evidence for presence of two cohorts in the years 1989 and 1990, the indication of this trend was clearly evident in the years 1991 and 1992. However, although it appeared that 100 to 300 mm fish were recruited into the population, it was not known whether this cohort represented hatchery or naturally spawned trout. Moreover, the presence of two modes or cohorts could be misleading. For example, the first mode at approx. 100 to 300 mm could be composed of one year old fish but it also could be composed of slower growing two year olds. The second mode at approx. 300 to 525 mm likewise could be composed of more than one age group, which is likely.

General growth, in terms of mean total lengths between the samples, appeared to have significantly declined since 1989 (Fig. 5.3a) [A oneway ANOVA comparing total lengths was significantly different between the sampling years ($F_{(3,10610)}=389$, $P < 0.001$)]. The \bar{X}_{TL} were; 397 ± 5.29 (SE) in 1989, 407 ± 3.11 (SE) in 1990, 302 ± 1.99 (SE) in 1991 and 285 ± 3.13 (SE). For the combined sampling years between 1989 and 1992, growth was not evenly spaced among river mile intervals (Fig. 5.3b; $F_{(4, 9533)}=249$, $P < 0.001$) and the mean TL \pm SE were as follows for each of the river mile intervals (RMI); 308 ± 3.02 for RMI '0-3', 314 ± 2.78 for RMI '3-6', 379 ± 3.22 for RMI '6-9', 397 ± 2.11 for RMI '9-12' and 380 ± 2.06 at RMI '12-15'. Significantly larger fish were captured from the mid-portion of the river. Whether this observation can be correlated to a greater abundance of food needs further investigation.

Not surprisingly, all of the winter seasons from 1989 produced significantly larger fish (Fig. 5.3c; $F_{(3, 10610)}=212$, $P < 0.001$) which is probably the result of trout in spawning condition. The mean TL \pm SE for each of the combined seasons since 1989 were; 304 ± 3.91 for spring, 290 ± 2.34 for summer, 353 ± 2.91 for fall and 378 ± 3.08 for the winter season. However, until the contribution of hatchery fish can be reliably determined, it is not known whether they represent a significant portion of the breeding population. For example, after 30+ years stocking different strains into the system, intuitively, it seems reasonable to speculate that natural selection may have favored certain combinations of alleles that constitute a resident 'wild'

population and, consequently, a majority of spawners. As an alternative stocking strategy, the selection of broodstock from the reach may prove beneficial.

Relative Weight

Traditional condition factors (K) can be meaningfully compared only among individuals of similar lengths. Therefore, if growth in the population is allometric, condition factors linearly decrease with increasing length (Fig. 5.4). The standard length-weight equation determined by this regression line percentile (RLP) technique was:

$$\log W_s(g) = -4.600 + 2.856 \log TL \text{ (mm)}, r^2=0.0004,$$

where log is the logarithm to the base 10, and TL is the total length. Relative weights (W_r) calculated for fish collected by electrofishing from 1984 to 1990 appear to provide a better index of fish plumpness than traditional techniques because they do not vary significantly with fish length (Fig. 5.4). Table 5.1 provides W_r and 95% confidence intervals for trout collected from 1984 to 1991 and Fig. 5.5 provides the floating histogram of the data.

It was evident that there has been a significant stepwise degradation of W_r from 1984 to 1991 in the reach. The result was considered significant at $P = 0.05$ if the 95% confidence intervals of the floating histograms did not overlap. Relative weight was significantly different between 1989 and 1992 (Fig. 5.6a; $F_{(3, 10608)}=19$, $P < 0.001$). Mean $W_r \pm SE$ were; 83 ± 4.14 for 1989; 79 ± 2.43 for 1990, 64 ± 1.56 for 1991, and 82 ± 2.45 for 1992. Although W_r was significantly different between the seasons since 1989 (Fig. 5.6b; $F_{(3, 10608)}=11$, $P < 0.001$), it was not significantly different between river mile intervals (Fig. 5.6c).

The decreasing trend in W_r since 1984 was also apparent in the creel data (Fig. 5.7). Table 5.2 lists the summary of the creel data from 1977 to 1992. In almost every category, there was a precipitous decline from 1977 to 1992. In particular, the creel per hour and mean weight has declined markedly indicating that perhaps the relative number of "plump" fish has declined in the fishery, which is supported by Table 5.1 and Fig. 5.5. Another possible explanation is that there are fewer numbers of catchable trout in the reach. Creel catch per hour (and the harvest) has likewise declined from previous highs in the mid-1980s. Although the number of angler hours has dropped decidedly in 1992 from 1991, this may be an indication that the fishery has steadily declined from 1990 since there are fewer anglers seeking fewer fish that are in poor condition. However, the trend in W_r for 1992 appears to be on the incline from 1991 (Fig. 5.6a). Whether this trend will continue for the 1993 season has yet to be determined. Appendix 5.1 presents initial analyses of relative weight and several independent flow variables.

Length-Weight Relationships

The log length-weight relationships of the electrofished catches remained relatively consistent over the period from 1984 to 1992 in the reach (Fig. 5.8). However, it was empirically tested that this method was an ineffective gauge of growth due to its size dependency and allometric characteristics (Fig. 5.4). Therefore, we plan to recalibrate our W_r equation and compare it to recently developed national standards. It is anticipated that this method will more accurately reflect growth patterns than traditional length-weight equations.

Growth of BCWT Trout

Length-frequency distributions of wire-tagged and untagged fish in the reach for August, 1992 are given in Table 5.3. The composition of wire tagged fish relative to the catch of all trout <200mm was 22%. This estimated 78% of natural reproduction is opposite to what Maddux et al. reported [27%] in 1987 (*cf.* Page 5.1). The breakdown of wire-tagged fish stocked into the reach and hatchery of origin are given in Fig. 5.9.

Total length was significantly different between stocked (PS) and 'wild' (LF) trout ($F_{(2,453)}=893$, $P < 0.001$). Trout held in hatchery conditions at PS to 8/92 had significantly greater growth rates (mean TL 180 ± 2.36 SE) than compared with ex-hatchery stock (147 ± 2.12 SE) captured at Lee's Ferry on 8/92. These initial stockings occurred in May 1992, and these fish, from PS, had a mean TL of 92 ± 0.74 SE. Not surprisingly, the growth of trout fingerlings was significantly better under controlled hatchery conditions than in the wild.

From this baseline experience, staff at AGFD will wire-tag each subsequent stocking with a unique code thereby making it possible to track different hatchery cohorts through time to estimate their growth patterns and contribution to the fishery. It is anticipated that BCWTs will be a prominent fixture in the long term monitoring plans of the fishery.

Nematode Infestations

During the fall of 1990, trout from Lee's Ferry appeared to be emaciated and suffering from malnutrition. The marked decline in relative weights in the fishery from 1988 to the present seems to support this observation (Fig. 5.6a). In that same time frame, the number of creel fish per hour, catch per hour, mean lengths and weights, and harvest has also dramatically declined (Table 5.2).

In order to investigate this occurrence and quantify (if possible) the presumptive causative agent, a health survey of trout was initiated in December, 1990. During that survey, it was discovered

that all of the 60 trout sampled were suffering from a nematode infestation. Additionally, approximately 1500 trout viscera have been collected from 1990 through 1993 for a companion diet study. Detailed analysis of these data are pending, however, it does indicate that virtually 100% of the trout in this reach were infected with the nematode.

This nematode was found in the pyloric caeca and in the junctions between the lumen of the intestines and openings to the caeca. Other parasites were discovered on the skin and gills, *Gyrodactylas* sp. and *Ambiphya* sp., respectively, but only in a few cases. Further, bacterial and viral assays indicated only a few cases of *Yersinia ruckeri* (ERM-1) in the sample. Lastly, in virtually all of the 60 trout sampled, none of them appeared to contain any body fat reserves. Given the emaciated condition of these trout, called "snakes" by the local fishermen, it was possible to speculate that the parasite interfered with nutrient absorption. Because Lee's Ferry is completely artificial (e.g. trout and their simultaneously introduced food base *Gammarus lacustris*, are exotics) it is believed that the nematode is also an (unwittingly) exotic introduction.

Preliminary taxonomic identification indicated that the nematode was *B. ampullastoma* (Maggenti 1971) which was later confirmed (A. Maggenti, personal communication, 1991). The type locality of this species is the California Fish and Game's Hot Creek State Fish Hatchery, Modoc County, CA. To further gain insight into this problem, the digestive tracts were excised out of preserved adult trout from 1984. The parasite was found in all of the samples. With the aid of Carothers and Assoc., the nematode was present in all adult trout sampled from Lee's Ferry to Lake Mead during routine surveys in 1989/90. As a preventative measure in 1991, trout from Arizona's state fish hatcheries were screened for this parasite but none were found.

Historical records indicate that the endoparasitic nematode was not a "recent" invader. Interviews with a former biological assistant that worked at the Ferry years ago revealed that the nematode was present as early as 1980. Specifically, he remembered large numbers of nematodes in the intestines of a few "skinny" fish (Don Randall, personal communication, 1993). Although no further data are available, anecdotal comments by other biologists from the same period (1980/81) likewise indicated that "skinny" trout were present, but not common.

Previous laboratory experiments investigating the effects of *B. ampullastoma* infestations on growth of rainbow trout have been conducted (Hiscox and Brocksen 1973). In their study, Hiscox and Brocksen (1973) reported that when infected trout were maintained on a normal diet, only slightly reduced growths rate were observed. However, they also suggested that the reduced growth rate was not due entirely to uptake of nutrients by the nematode. Moreover, they

speculated that the nematode may mechanically interfere with fat absorption or enzymatically convert it to an unusable form.

Hiscox and Brocksen (1973) also indicated that at accelerated feeding regimes, both parasitized and non-parasitized trout had fast growth rates but that the parasitized trout exhibited significantly slower growth rates. Next, under simulated conditions of starvation, parasitized trout had a 60% higher mortality than non-parasitized trout. For the sake of argument, if one can extrapolate the results from Hiscox and Brocksen (1973) to the present study, it seems plausible that under severe or prolonged periods of physiological stress (such as dramatic fluctuations in flows and/or reduction of the food base), parasitized trout in Lee's Ferry might experience an abnormally high mortality rate.

A second general fish health survey at the Ferry was undertaken during November, 1992. The primary objectives of this survey were to monitor the health of trout and to screen for various pathogens, including the parasitic nematode. Summary results of the 1992 survey are provided below.

The yellow grub *Clinistomum minimum* was observed in few fish. Next, the nematode *B. ampullastoma* was found in 88% of the fish in moderate to heavy concentrations. Records indicated that fish stocked into the system three months prior to sampling (August 1992) appeared to be nematode free. These stocked trout had the greatest amount of estimated body fat in the entire sample (ratings of 70 to 90%, Table 5.4). Next, trout examined from an earlier stocking in May 1992 were infected by the parasite and exhibited greatly reduced fat storages. Of the May stockings, 42% exhibited no estimated fat reserves and another 33% had less than 50% estimated fat (Table 5.4).

In comparing the 1990 and 1992 fish health surveys, a few general observations can be made. Firstly, it appears that the occurrence of *Y. ruckeri* (ERM-1) in the trout population(s) from Lee's Ferry is extremely rare. Secondly, and more importantly, of the trout surveyed from 1990 and 1992, the amount of body fat found in the 1992 samples was slightly higher than the amount found in 1990 samples. Although it is perhaps too premature to draw any valid conclusions regarding this result, it is nonetheless an encouraging sign. Finally, until the etiology and epidemiology of the parasite *B. ampullastoma* is understood, it probably will continue to infect the trout population(s) at varying concentrations. Possible control measures can be evaluated when the intermediate host(s) and/or vector(s) of the parasite is identified.

Work item 2.4 - Determine the behavioral responses of trout in the Glen Canyon Dam tailwater to different steady and fluctuating flow regimes.

Introduction

Changes in river stage, current velocity, and wetted area, that accompany fluctuating flows, have the potential to affect the behavior patterns of adult trout during reproductive and feeding activities. This may result in increased stress levels and/or energy expenditures. Project biologists attempted to document movements and other behavioral responses using radio telemetry.

Methods and Progress

Radio telemetry was used to evaluate the behavioral responses of adult trout in regard to constant and fluctuating flow regimes. Five adult trout (40-50 cm TL) were implanted with radio transmitters in November 1990 and five more in December 1990. Detailed methods have been reported (Angradi et al. 1992).

Limitations of the experimental design prevented accurate measurement of small scale movements. The design used surveyed stakes along the riverbank for triangulations. It was hoped that by using these stakes, more accurate measurements could be made and the resulting x, y coordinates could be more accurately plotted on maps. However, the flaw in this design was that it required taking bearings at greater distances from the fish, particularly during low flows. Angular errors increased proportionally with distance from the surveyed stakes. Accuracy tests confirmed that it was only possible to triangulate within 5 m of the fish 66% of the time, and the remaining measurements often showed gross errors.

By using different antennas, repeated measurements, and triangulating fish locations from a boat, technicians were able to pinpoint the location of a fish to within 5 m 95% of the time. This level of accuracy was acceptable for fish movement, but possibly not for microhabitat preferences. Without using surveyed stakes, the difficulty with this method is that it was hard to plot successive movements of fish to within 5 to 10 m. While it is possible to be accurate to within 5 m of a fish presently being triangulated, it is exceedingly difficult to determine where the fish was four hours ago, 24 hrs. ago, etc., without being able to accurately map these small movements.

An appropriate radio telemetry study plan is a major goal of this study. It is intended that trout movements be accurately measured and mapped to within 5 m. Modifying past methods,

measuring behavioral responses of trout as influenced by the new flow regime will be attempted. Radio telemetry accuracy tests may be repeated and explained in more detail for the final report.

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Table 5.1. Mean relative weight (W_R) and 95% Confidence Interval by year and season, Lee's Ferry rainbow trout 1984 to 1991.

Season	Year	Mean	STD	n	95% Confidence Interval
Spring	1984	99	13	171	97 - 101
Fall	1984	100	14	841	99 - 101
Spring	1985	94	12	414	93 - 95
Summer	1985	98	10	584	97 - 99
Fall	1985	92	12	211	90 - 94
Winter	1985	89	14	442	88 - 90
Spring	1986	96	10	415	95 - 97
Winter	1986	87	13	531	86 - 88
Spring	1987	87	11	268	86 - 89
Fall	1987	88	18	343	86 - 90
Spring	1988	93	14	498	91 - 94
Fall	1988	90	16	283	88 - 92
Winter	1988	92	13	77	89 - 95
Fall	1989	83	14	293	81 - 84
Spring	1990	83	12	241	81 - 84
Summer	1990	74	15	345	72 - 76
Fall	1990	76	13	451	75 - 77
Spring	1991	75	13	629	74 - 76
Summer	1991	69	12	290	68 - 70
Fall	1991	74	13	743	73 - 75
Winter	1991	74	15	877	73 - 75

Spring = March - May
 Summer = June - August
 Fall = September - November
 Winter = December - February

Table. 5.2. Summary of creel survey statistics from Lee's Ferry, 1977 to 1992.

	NPS Angler Days	Angler Hours	Creel per Hour	Catch per Hour	Mean Length (mm)	Mean Weight (g)	Estimated Harvest	Percent Released
1977	10,613	72,202	0.24	n/a	398	735	17,320	n/a
1978	9,990	67,932	0.20	n/a	445	1,015	13,586	n/a
1979	22,085	150,178	0.15	n/a	431	926	22,527	n/a
1980	18,986	129,105	0.09	0.13	465	1,153	11,619	30
1981	28,784	195,731	0.14	0.22	436	957	27,402	36
1982	49,000	333,200	0.13	0.19	449	1,024	43,316	31
1983	52,725	358,530	0.15	0.27	431	926	53,780	44
1984	40,174	273,183	0.16	0.37	370	595	43,709	57
1985	27,572	183,630	0.23	0.60	370	548	41,115	64
1986	18,927	122,803	0.14	0.39	426	827	16,071	67
1987	32,103	212,706	0.18	0.68	416	770	36,754	75
1988	34,780	241,029	0.17	0.78	412	731	39,726	80
1989	32,537	222,438	0.14	0.76	395	663	30,133	81
1990	38,789	267,904	0.05	0.80	385	514	11,783	94
1991	32,928	242,432	0.04	0.56	380	503	10,076	93
1992	14,682	110,392	0.03	0.41	371	499	3,216	92

n/a = not available

Table 5.3. Rainbow trout catch by river mile location, August 1992.

Mile	All	All < 200 mm	All < 100 mm	No Wire < 100 mm	All Wire
1	90	73	7	7	6
1.9	62	53	15	15	10
3	95	67	25	25	8
4	126	98	48	47	10
5.2	91	78	41	41	2
2.7	57	46	9	9	7
7.1	26	17	1	1	8
9.2	85	36	5	5	16
9.7	43	21	3	3	11
10.2	42	23	7	7	13
12.5	29	13	0	0	4
13.5	39	21	1	1	9
14.2	95	31	2	0	19
14.7	48	12	4	4	8
TOTAL	928	589	168	165	131

Table 5.4

Estimated body fat of rainbow trout taken between Glen Canyon Dam and Lee's Ferry. A score of zero equals no estimated body fat. A score of 1 indicates <50% estimated body fat and a score of 2 indicates >50% estimated body fat. A score of 3 represents a full complement (100%) of estimated body fat.

EstimatedBody Fat	1990	1992
0	60	18
1	0	14
2	0	10
3	<u>0</u>	<u>0</u>
	60	42

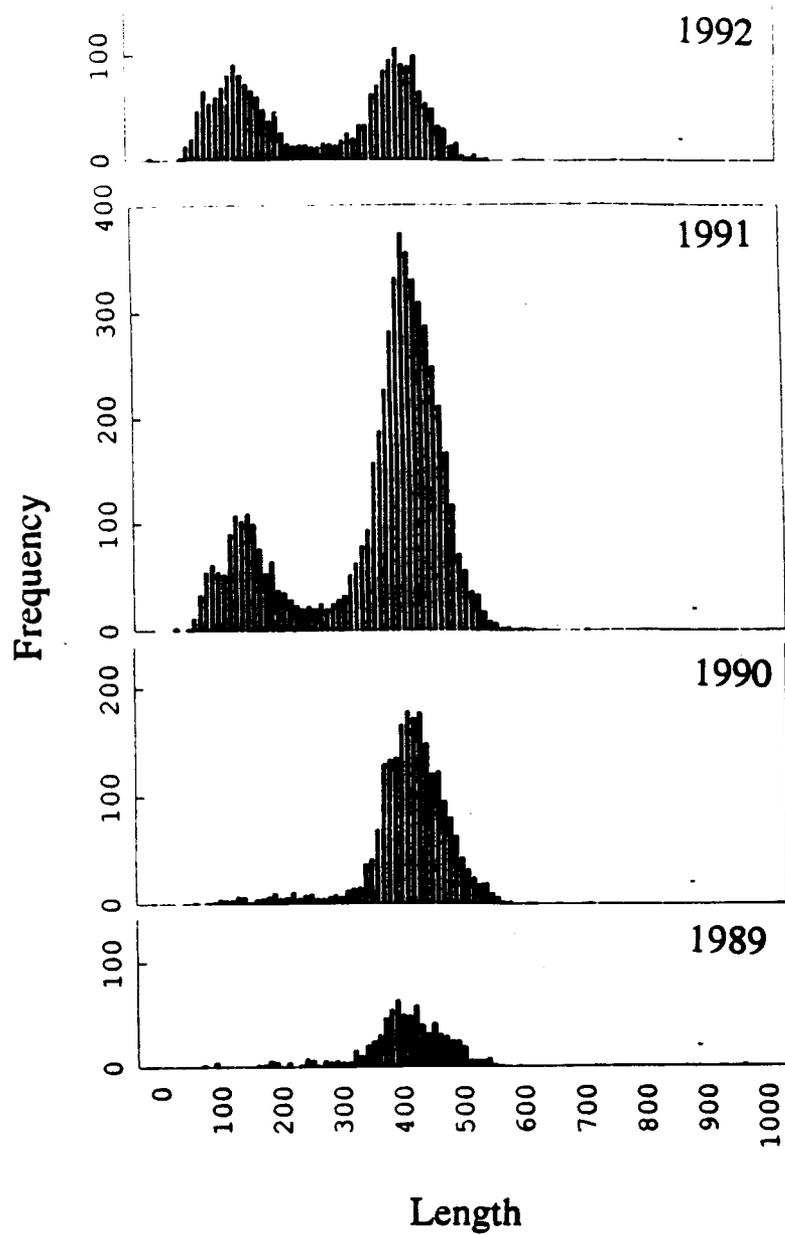


FIGURE 5.1. Length-frequency histograms of rainbow trout *Oncorhynchus mykiss* collected by electrofishing from the tailwaters of Glen Canyon Dam downstream to Lee's Ferry from 1989 to 1992. Length is the total length measured in 10 mm intervals.

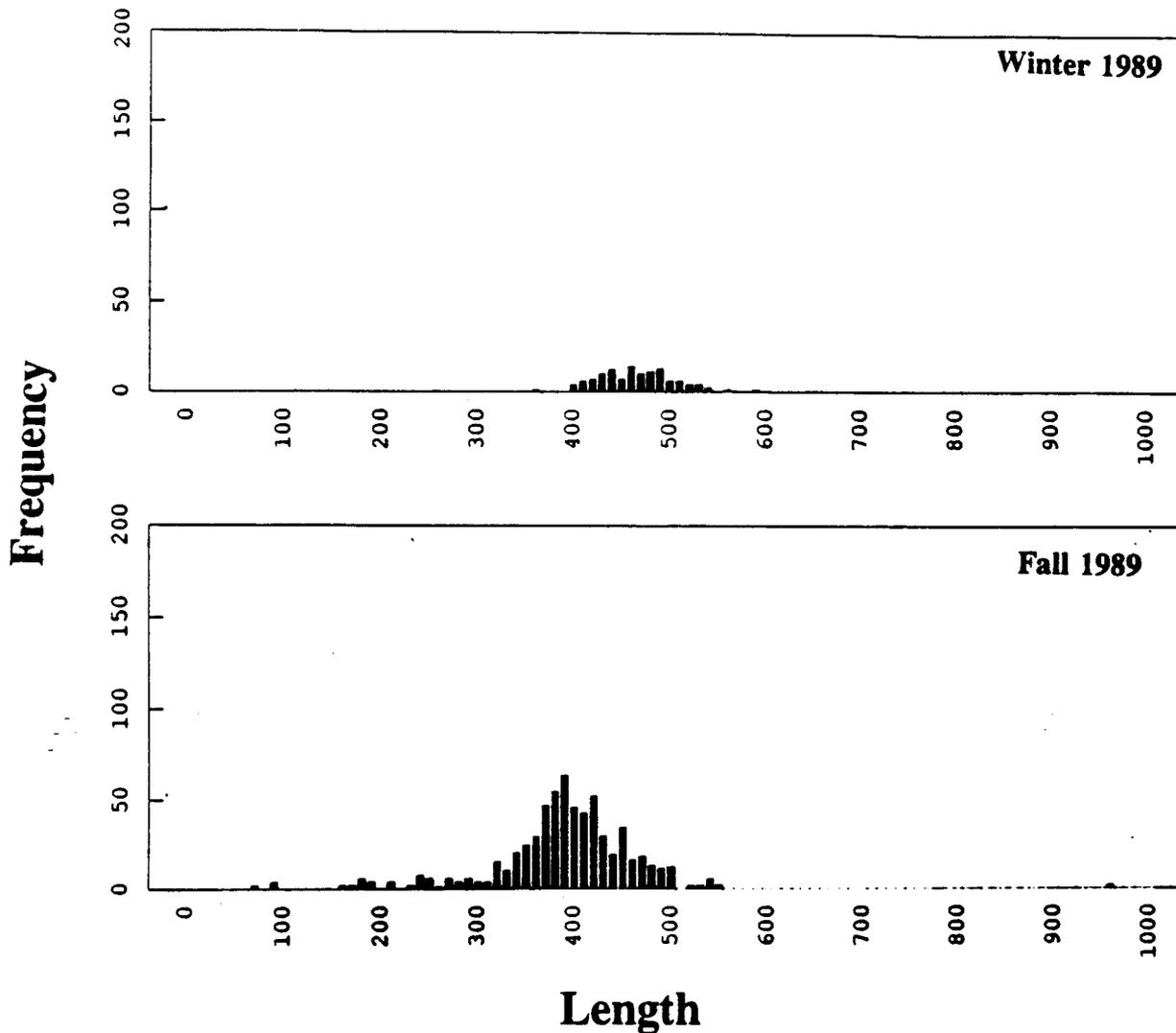


FIGURE 5.2. Seasonal length-frequency histograms of rainbow trout *Oncorhynchus mykiss* collected by electrofishing from the tailwaters of Glen Canyon Dam downstream to Lee's Ferry from 1989 to 1992. Length is the total length measured in 10 mm intervals.

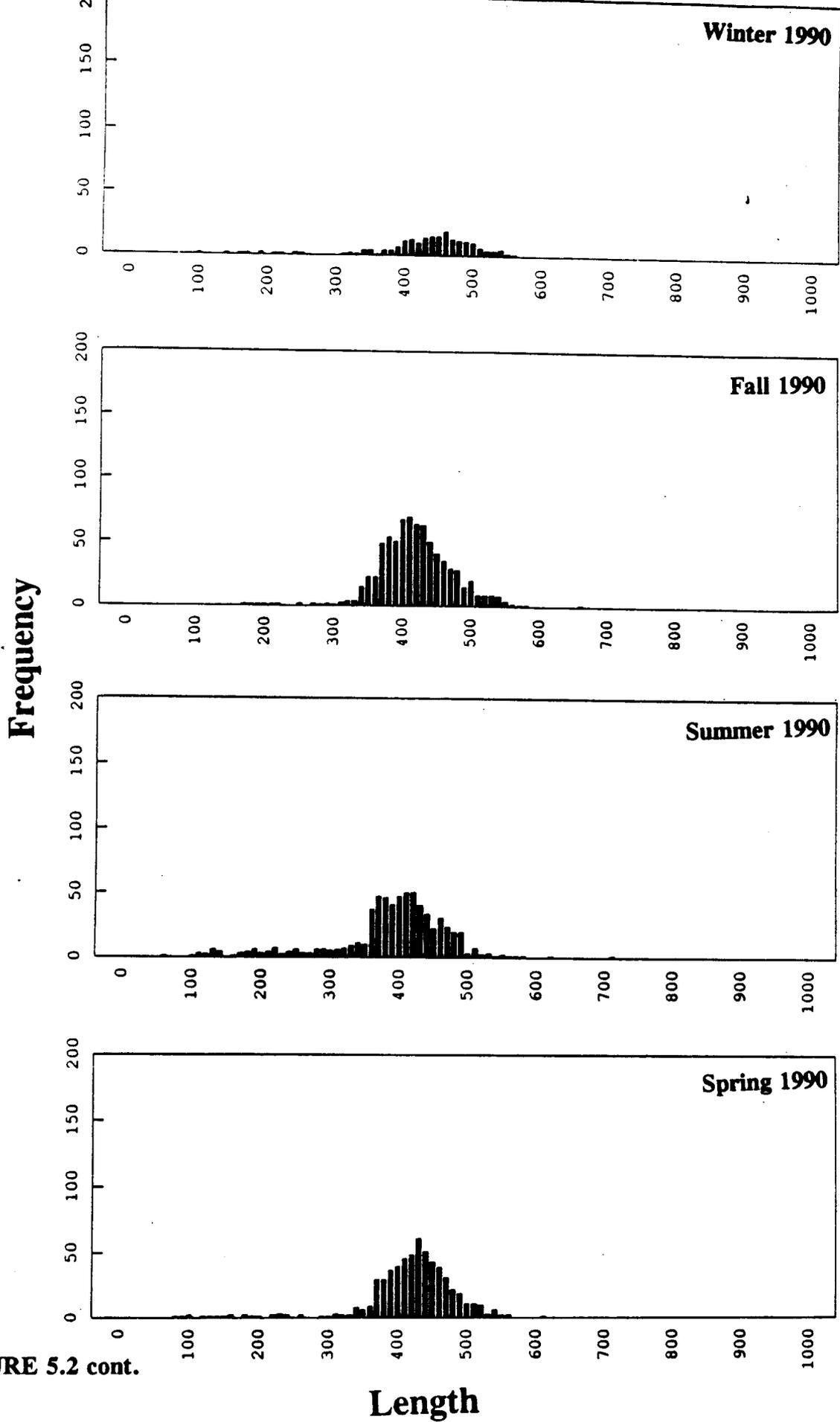


FIGURE 5.2 cont.

Frequency

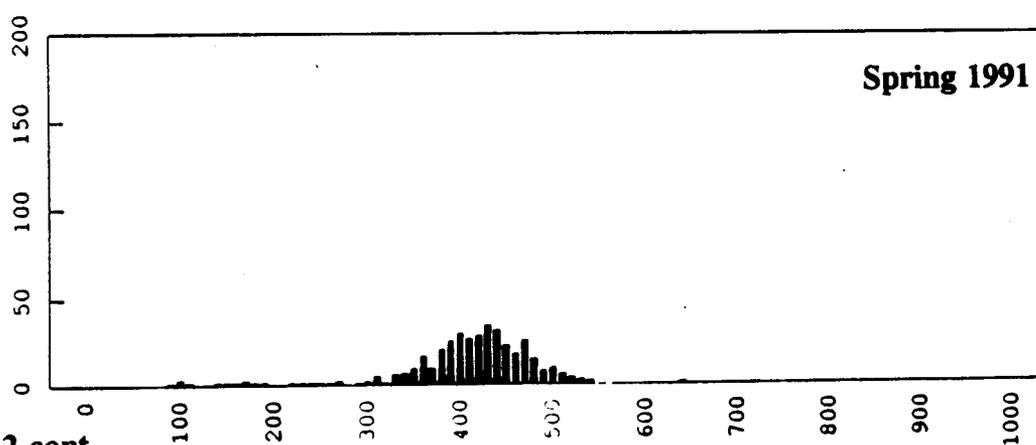
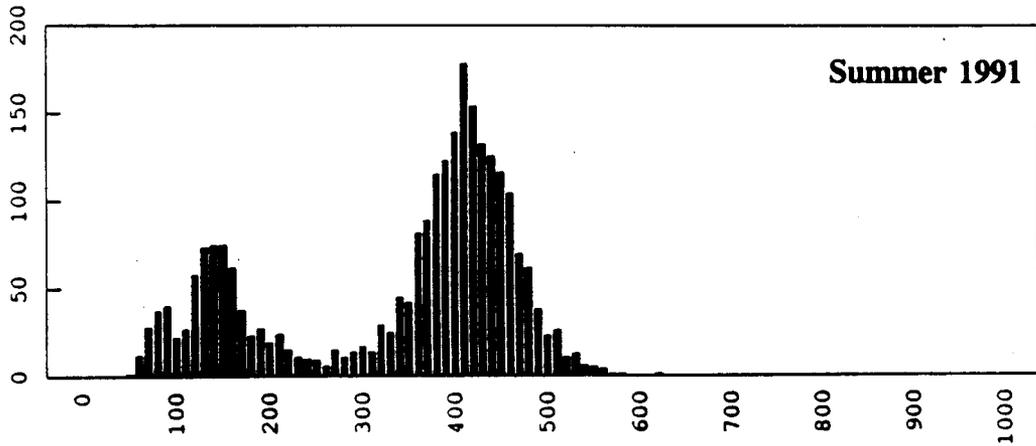
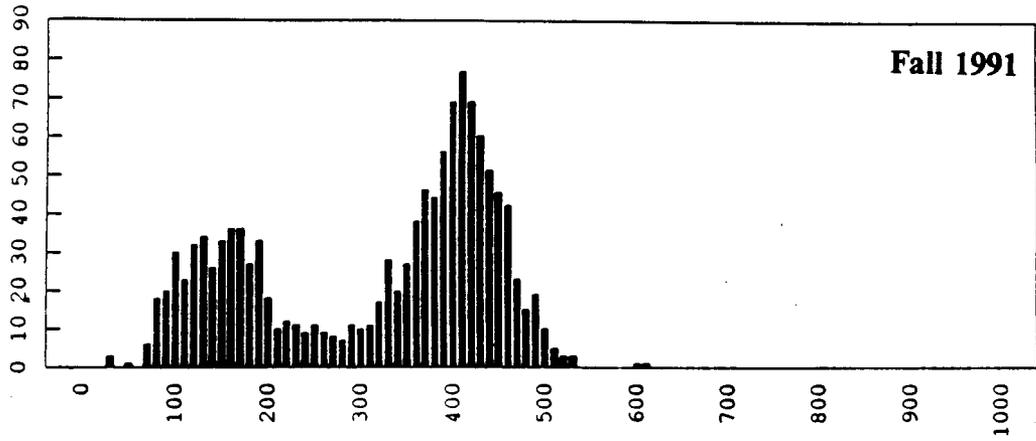
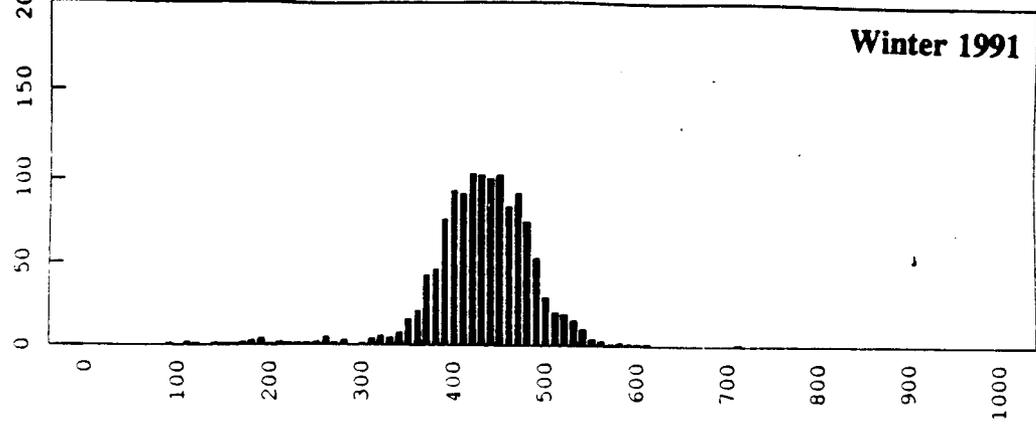


FIGURE 5.2 cont.

Length

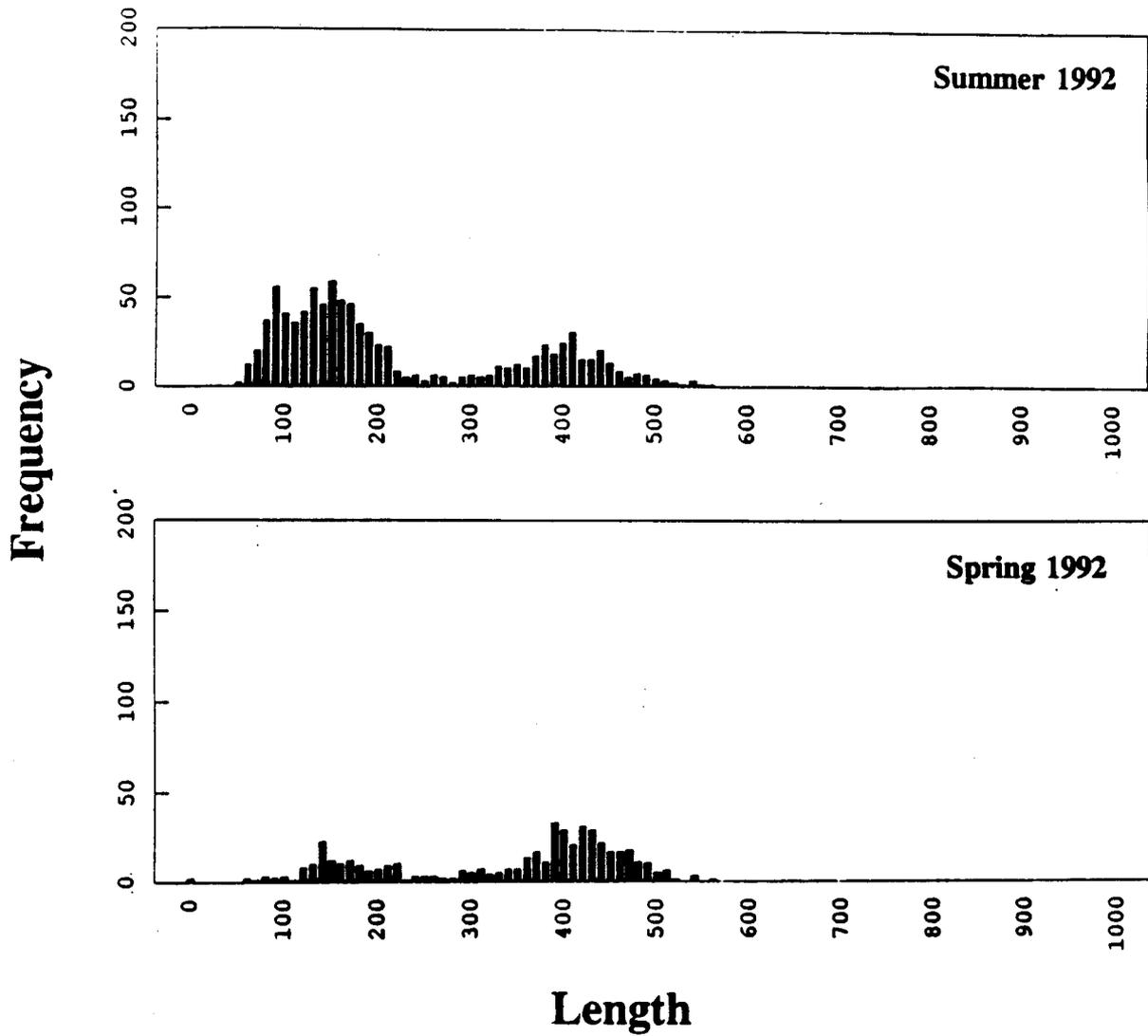


FIGURE 5.2 cont.

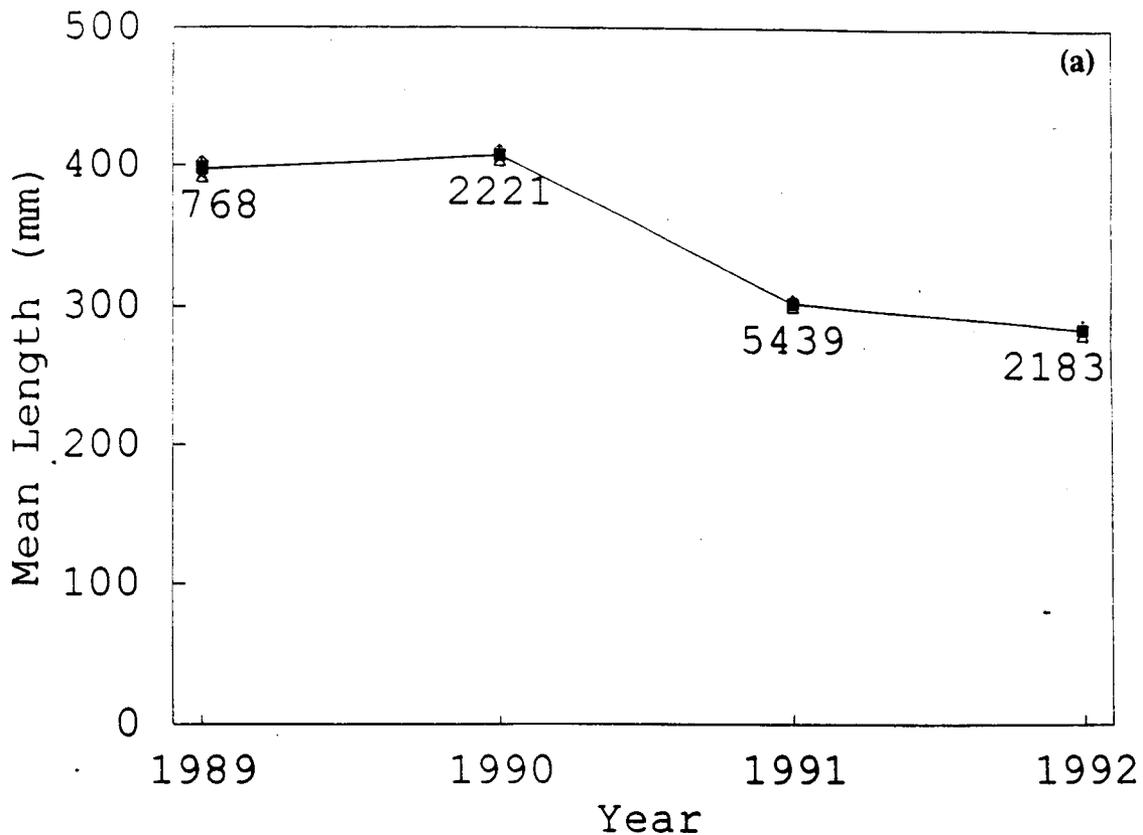


FIGURE 5.3a. Mean length of rainbow trout *Oncorhynchus mykiss* collected by electrofishing from the tailwaters of Glen Canyon Dam downstream to Lee's Ferry from 1989 to 1992. Length is the total length measured in mm. (a) Mean length arranged by year, (b) mean length arranged by season (*i.e.* individuals collected from 1989 to 1992 were categorised by season of capture), and (c) mean length arranged by river mile location (*i.e.* individuals collected from 1989 to 1992 were categorised by location of capture). Numbers = *n*. The darkened area represents \pm SE, the bisecting line is the mean and the upper and lower 95% confidence intervals ($P = 0.05$) are represented by a diamond and open triangle, respectively.

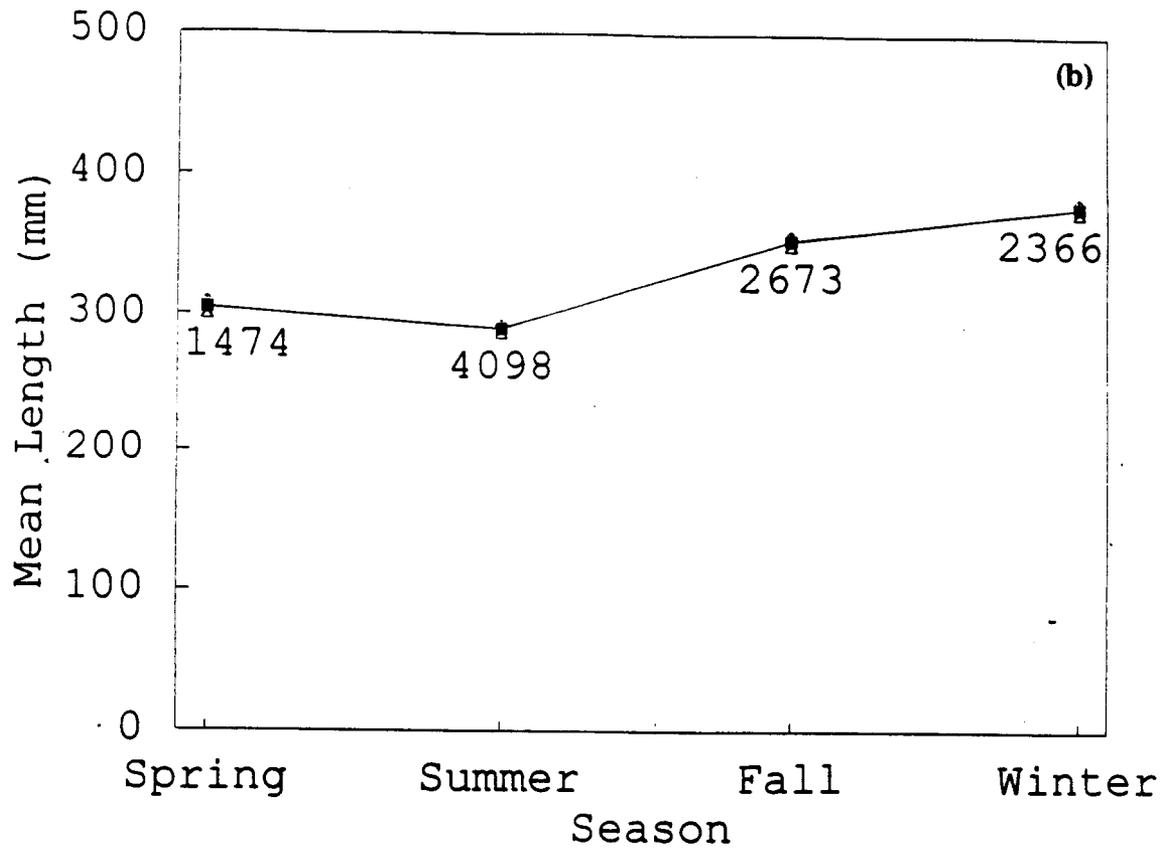


FIGURE 5.3b

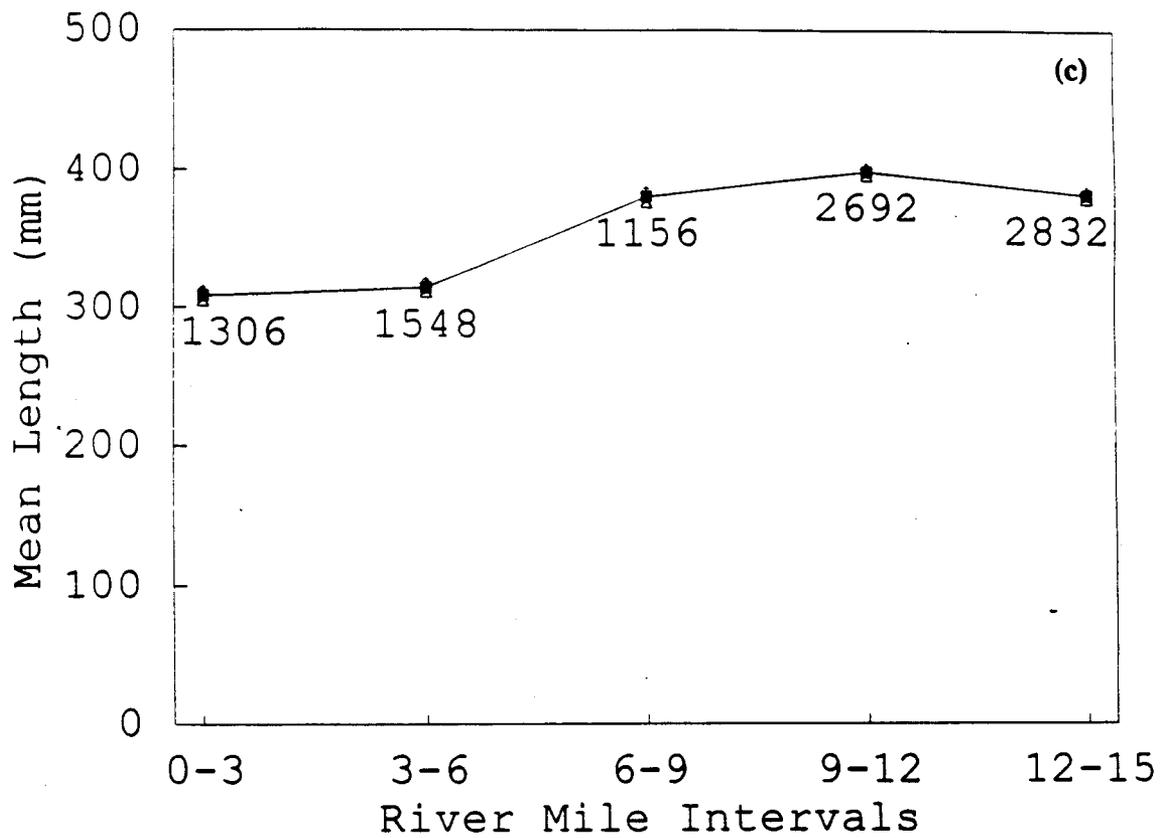


FIGURE 5.3c

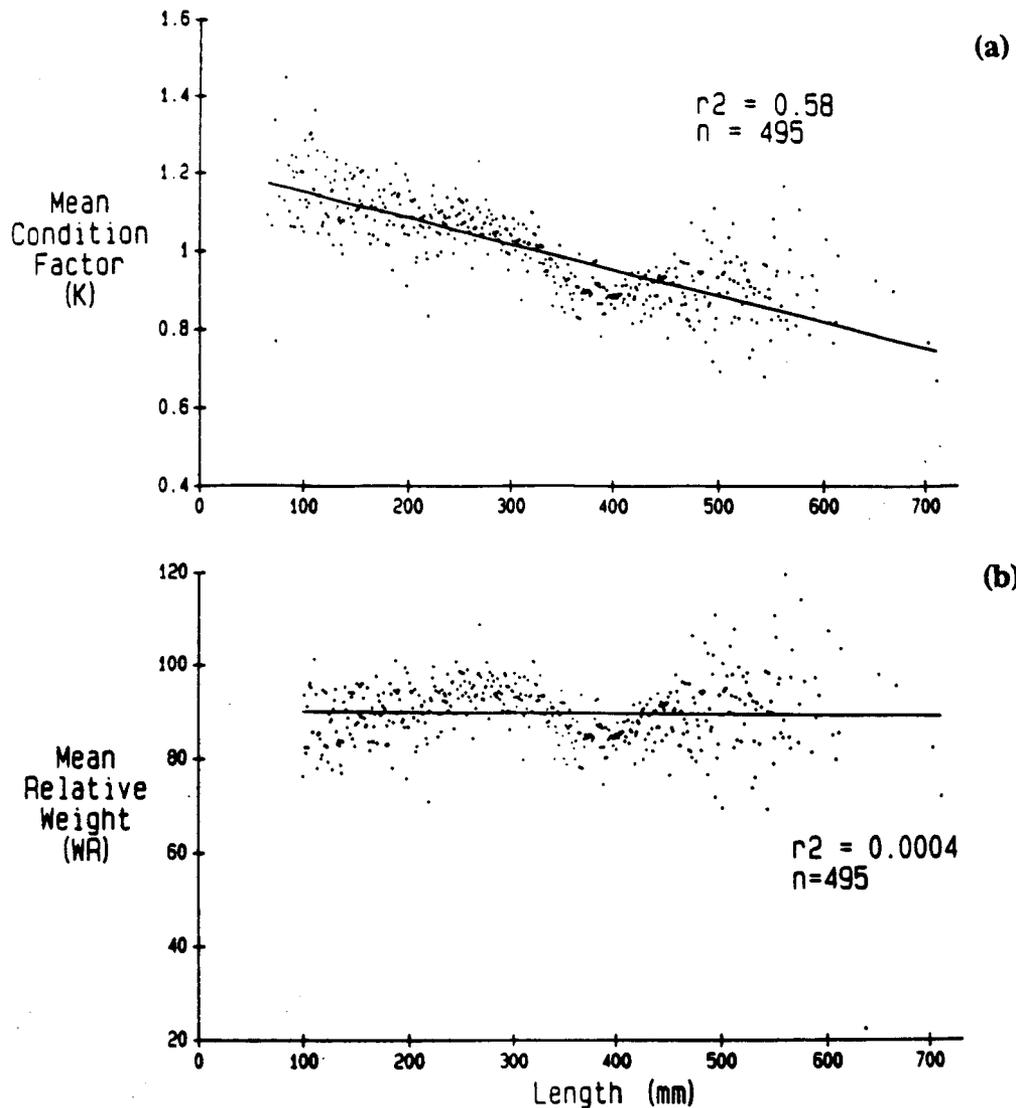


FIGURE 5.4. Regressions of condition factor K (a) and relative weight W_r (b) on length of rainbow trout *Oncorhynchus mykiss*. Length is the total length measured in mm. Regression lines were fitted by least squares. (a) condition factor K was calculated as $K = W/TL^3 \times 100$; where W is the wet weight (g) and TL is the total length (mm). (b) the formula to calculate W_r is provided in the text.

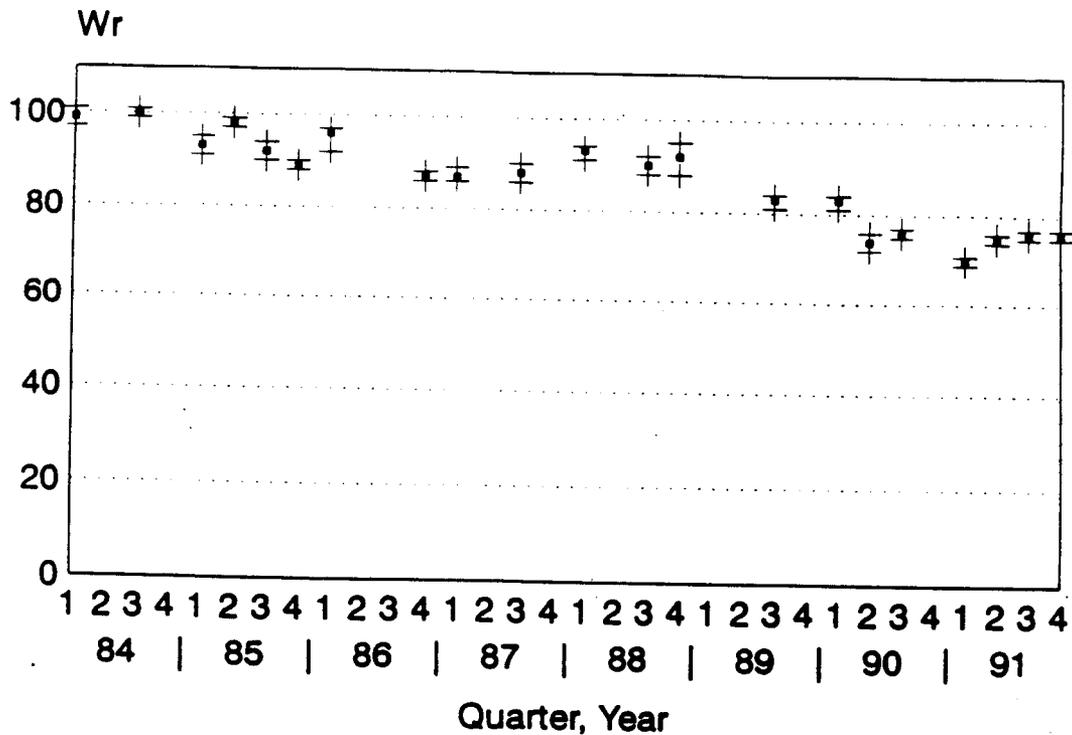


FIGURE 5.5. Mean relative weight W_r of rainbow trout *Oncorhynchus mykiss* collected by electrofishing from the tailwaters of Glen Canyon Dam downstream to Lee's Ferry from 1984 to 1991 arranged by quarter. The darkened squares represent the mean, vertical lines the range, and perpendicular lines represent the upper and lower 95% confidence intervals at $P = 0.05$.

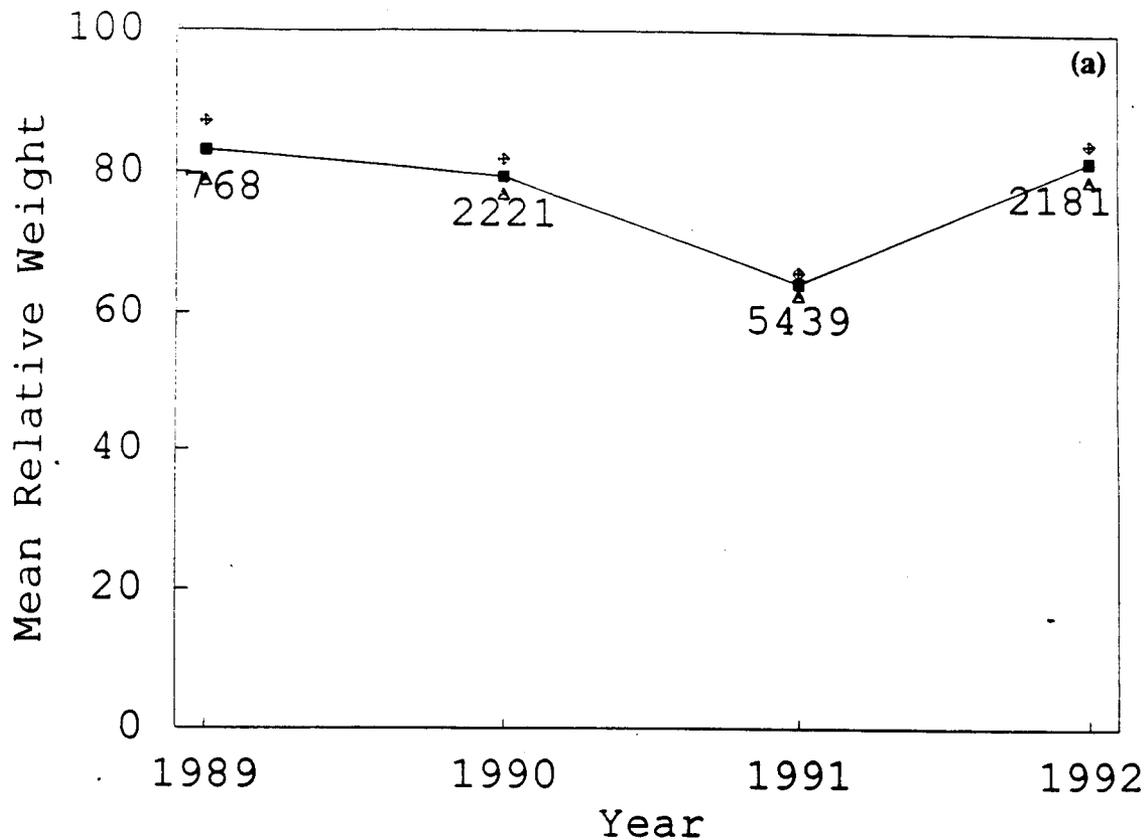


FIGURE 5.6a. Mean relative weight W_r of rainbow trout *Oncorhynchus mykiss* collected by electrofishing from the tailwaters of Glen Canyon Dam downstream to Lee's Ferry from 1989 to 1992. (a) Mean W_r arranged by year, (b) mean W_r arranged by season (*i.e.* individuals collected from 1989 to 1992 were categorised by season of capture), and (c) mean W_r arranged by river mile location (*i.e.* individuals collected from 1989 to 1992 were categorised by location of capture). Numbers = n . The darkened area represents \pm SE, the bisecting line is the mean and the upper and lower 95% confidence intervals ($P = 0.05$) are represented by a diamond and open triangle, respectively.

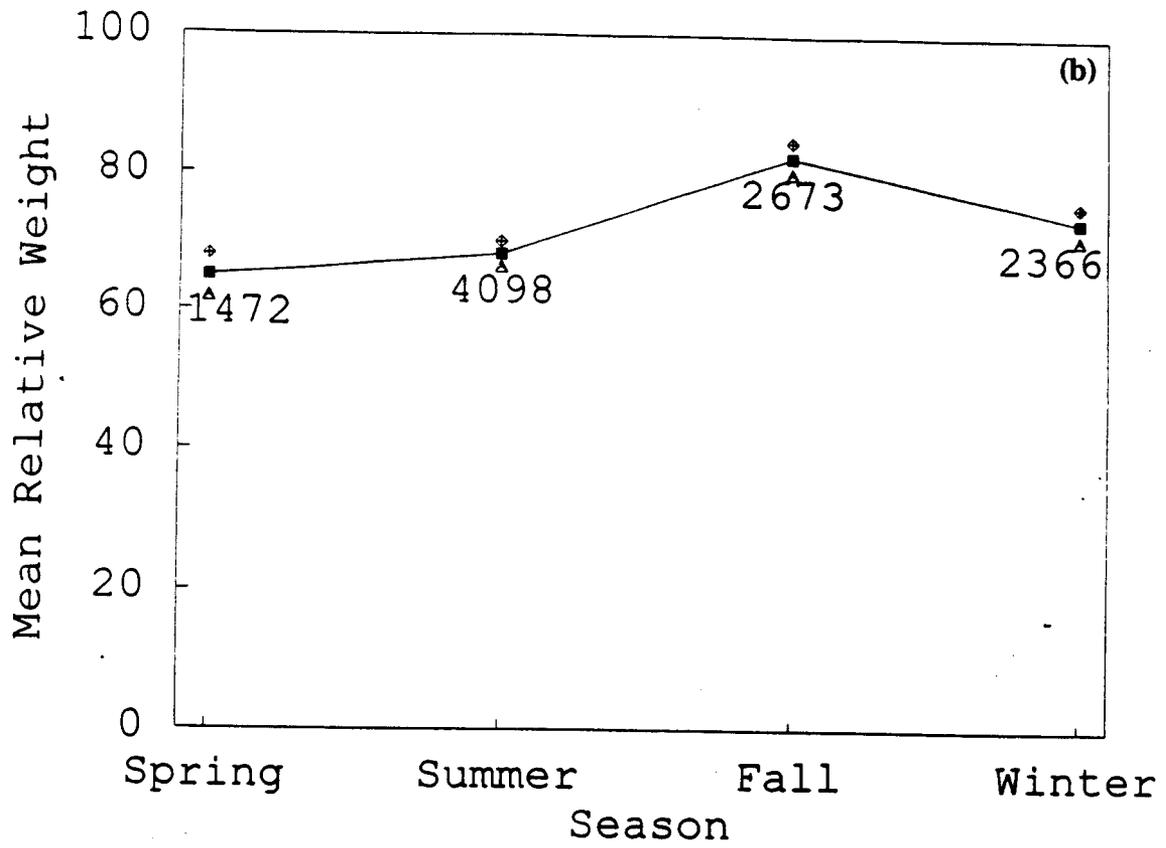


FIGURE 5.6b.

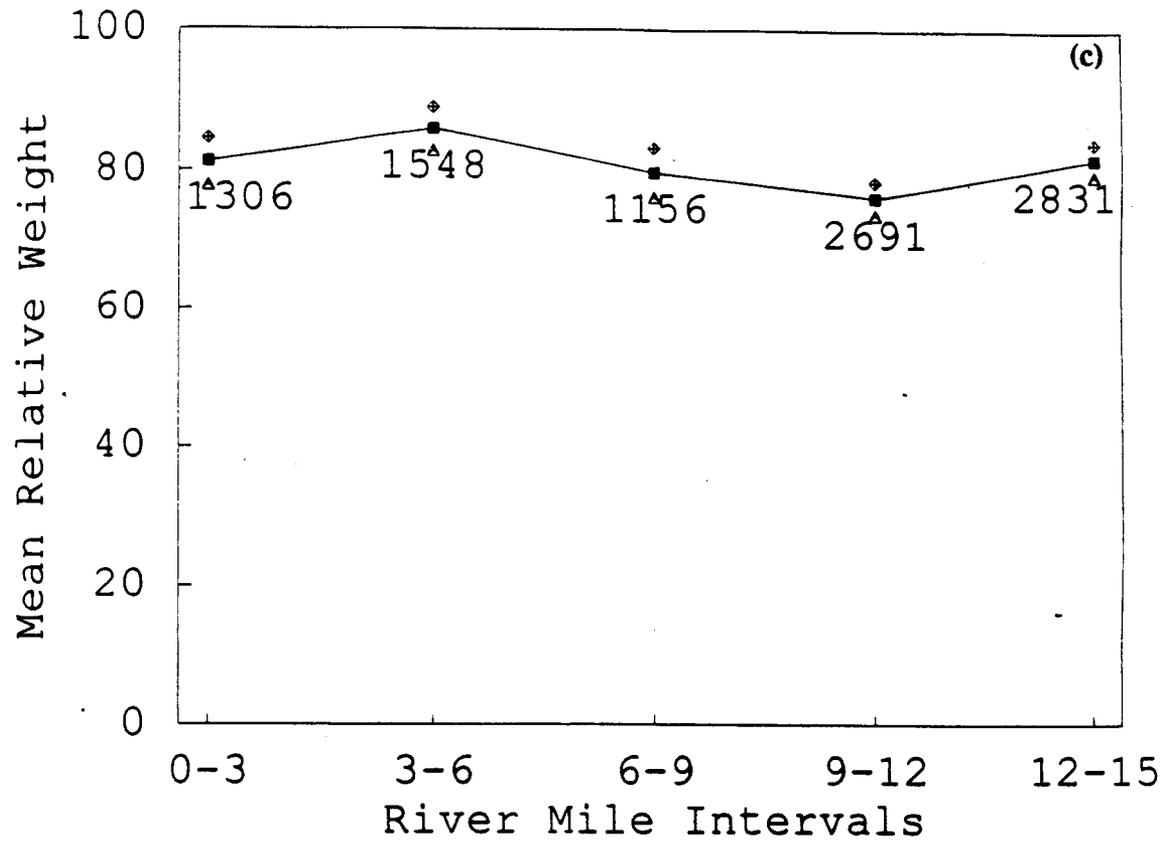


FIGURE 5.6c.

LEE'S FERRY 1982 - 1992 WR FREQUENCY FROM CREELED FISH

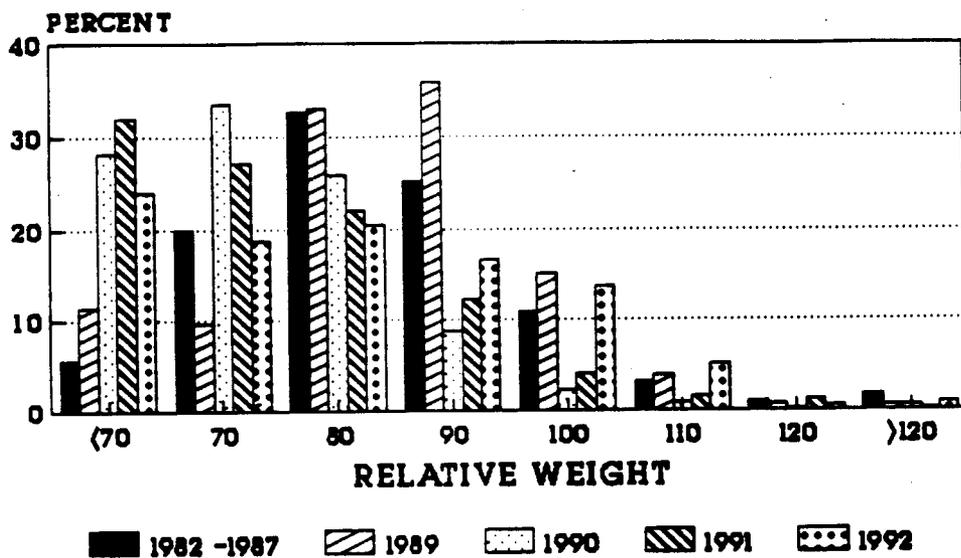


FIGURE 5.7. Relative weight W_r by percentage of rainbow trout *Oncorhynchus mykiss* crested from the tailwaters of Glen Canyon Dam downstream to Lee's Ferry from 1982 to 1992. Consult Table 5.2 for details.

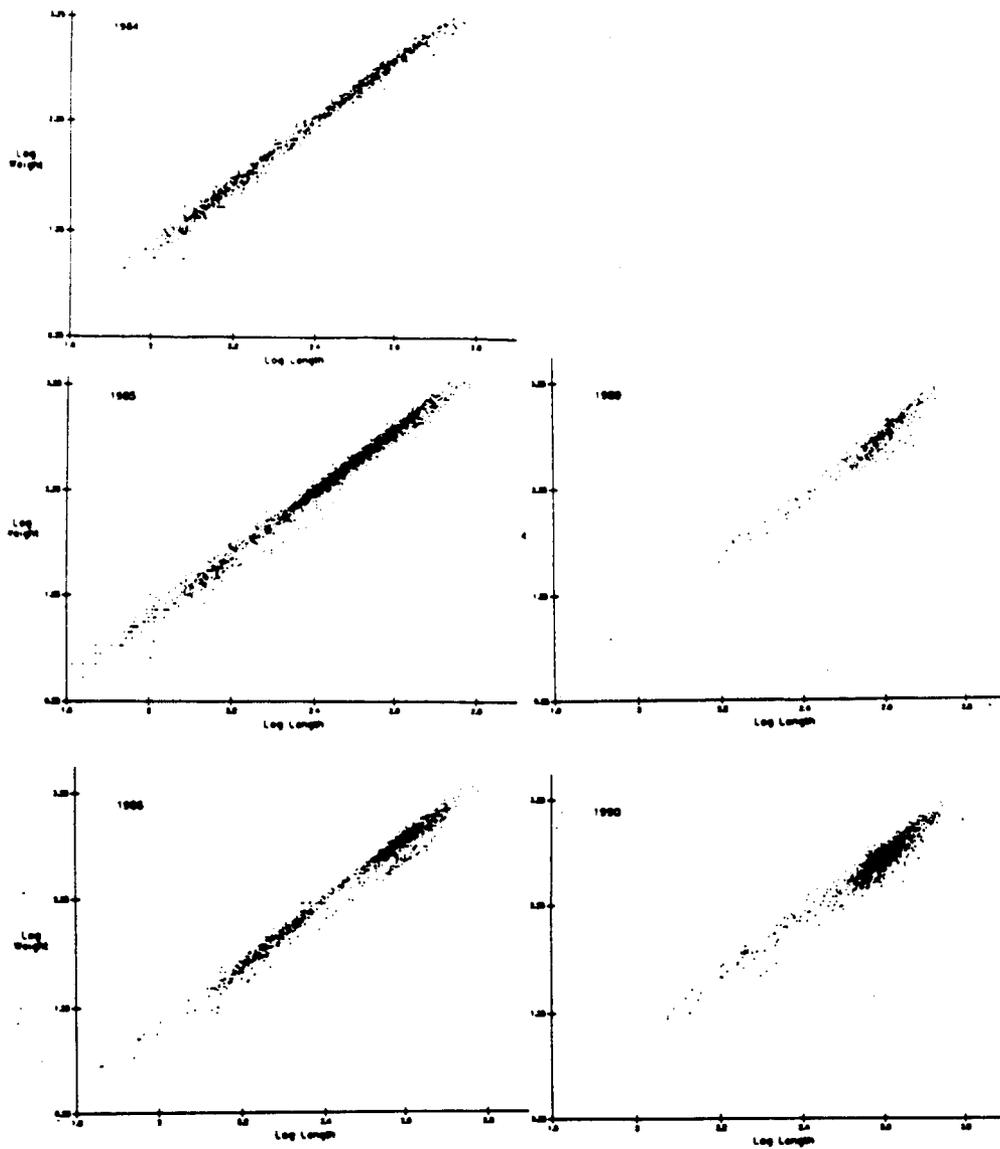


FIGURE 5.8. Logarithmic (base 10) length-weight relationships of rainbow trout *Oncorhynchus mykiss* collected by electrofishing from the tailwaters of Glen Canyon Dam downstream to Lee's Ferry from 1984 to 1992. Weight is in g and length is TL in mm.

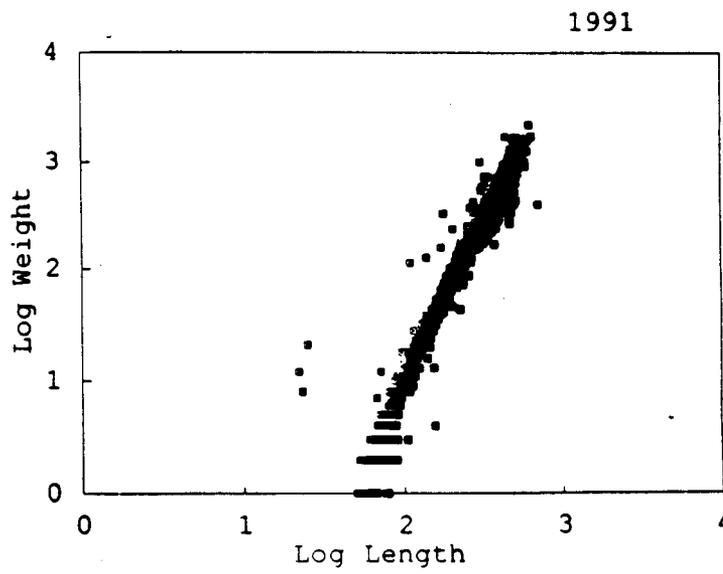
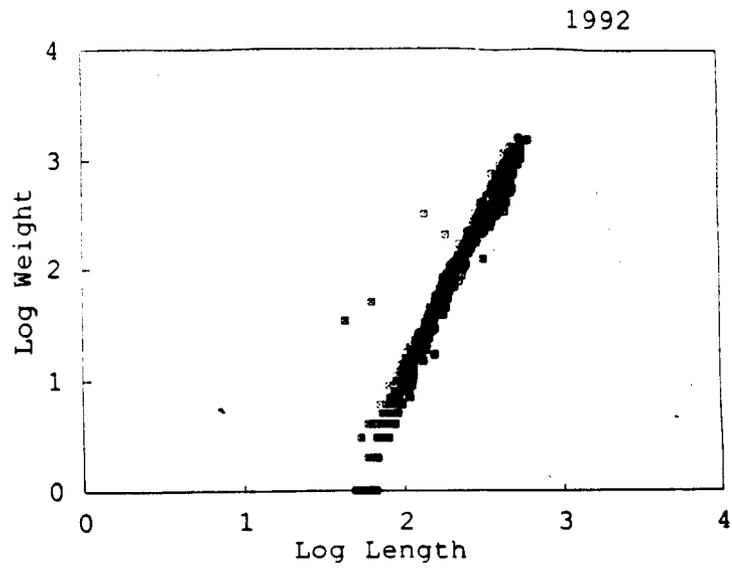


FIGURE 5.8.

Page Springs Hatchery Trout

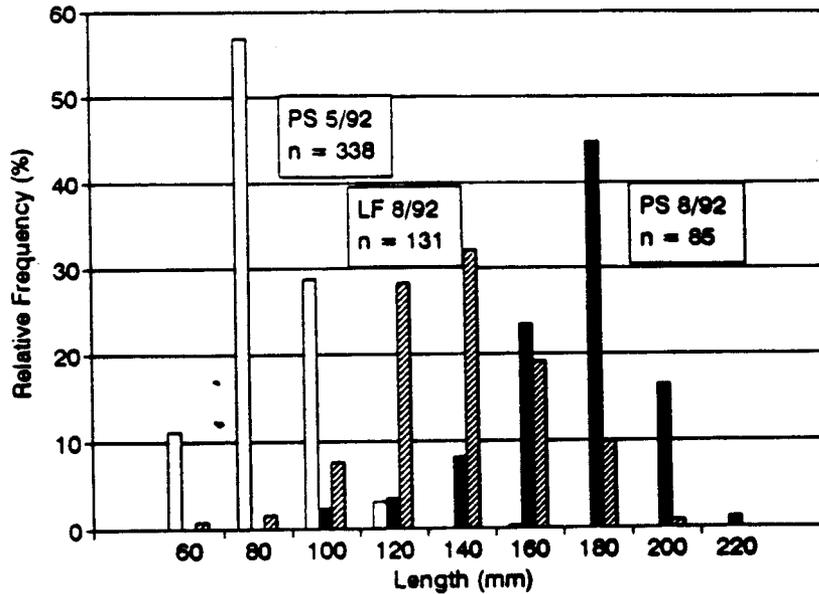


FIGURE 5.9. Length by percentage of binary coded wire tagged (BCWT) and untagged rainbow trout *Oncorhynchus mykiss*. Length is the total length measured in mm. BCWT trout arranged by date of hatchery release (PS = Page Springs Hatchery and LF = Lee's Ferry). PS (8/92) [darkened bars] is the length of trout fingerlings held at the hatchery to that date. PS (5/92) [open bars] is the initial length of those hatchery trout in May. LF 8/92 [hatched bars] is the length of trout fingerlings planted into Lee's Ferry (LF) from PS 5/92.

APPENDIX 5.1

Appendix 5.1

A Preliminary Parametric Examination Of The Relationships Between Relative Weight In Rainbow Trout And Time, River Section, And Water Flow Parameters From Lee's Ferry To The Glen Canyon Dam On The Colorado River

Carl R. Gustavson

The purpose of this appendix is to describe an initial attempt to evaluate the suitability of a large amount of data for parametric analysis. The data in this analysis were selected from a larger set of data collected on many species of fish at many locations on the Colorado River over the past five years by the Arizona Game and Fish Department, and from U.S.G.S. measurements of water flow in the Colorado River taken at Lee's Ferry in one half hour intervals from January 1, 1987 through December 1, 1992. The reader is referred to other sections of this document for the details of the methods used to obtain the fish related measures. For this initial evaluation, only the length and weight of rainbow trout, and only samples taken by electrofishing methods between Lee's Ferry and the Glen Canyon Dam from 1988 through 1992 were included in the analysis. No attempt to draw conclusions from the analysis of these data will be reported here, as the intent of this report is to describe the operational procedures of the analytical approach.

Dependent Variable

The dependent measure for this analysis was the Z score (Zar 1984) of the calculated relative weight (W_r) of each rainbow trout for which a length and weight had been recorded ($n=11,749$ fish). Relative weight was calculated by dividing the weight of each fish by the calculated standard weight (W_s), and then multiplying by 100. The standard weight of each fish was calculated by taking the \log_{10} of a figure equal to the sum of -4.6 and the \log_{10} of the length of each fish multiplied by 2.856. (full procedure under work item 2.1).

Fixed Independent Variables

Three categorical (fixed) independent variables were used in the analysis. The first fixed variable was the year in which the fish sample was taken. This variable was coded as "Research Year" with 1988 = 1 and 1992 = 6. The second fixed variable was the "season" in which the fish sample was taken. This variable was coded as "Research Season" with October 1, through April 30 = 1, May 1 through July 31 = 2, and August 1 through September 30 = 3. The third fixed variable was the section of the river from which each fish sample was taken. This variable was coded "River Section" with the first five miles from Lee's Ferry toward the dam coded = 1, the second five miles coded = 2, and the last five miles coded = 3.

Continuous Independent Variables

Ten continuously variable independent variables were constructed to represent different aspects of changes occurring to the water flow in the Colorado River at Lee's Ferry.

Flow

Flow scores were constructed by calculating the Z score of the each measure taken at Lee's Ferry from January 1, 1987 through December 31, 1992.

Low Flow

Low flow scores were constructed by calculating the Z score of the each measure taken at Lee's Ferry from January 1, 1987 through December 31, 1992, for only those scores less than the mean of the overall flow scores

High Flow

High flow scores were constructed by calculating the Z score of the each measure taken at Lee's Ferry from January 1, 1987 through December 31, 1992, for only those scores greater than the mean of the overall flow scores

One Hour Ramping

One hour ramping scores were constructed by calculating the Z score for deviation scores constructed by subtracting the flow values for each measure from the flow value one hour earlier beginning January 1, 1987 through November 14, 1992.

One Hour Low Ramping

One hour low ramping scores were constructed by calculating Z scores for only those one hour ramping values in which the change in the target measure was less than the measure taken one hour earlier.

One Hour High Ramping

One hour high ramping scores were constructed by calculating Z scores for only those one hour ramping values in which the change in the target measure was larger than the measure taken one hour earlier.

Six Hour Ramping

Six hour ramping scores were constructed by calculating the Z score for deviation scores constructed by subtracting the flow values for each measure from the flow value obtained six hour earlier beginning January 1, 1987 through November 14, 1992.

Six Hour Low Ramping

Six hour low ramping scores were constructed by calculating Z scores for only those six hour ramping values in which the change in the target measure was less than the measure taken six hours earlier.

Six Hour High Ramping

Six hour high ramping scores were constructed by calculating Z scores for only those six hour ramping values in which the change in the target measure was larger than the measure taken six hours earlier.

Stability

Stability scores were constructed by calculating the square of Z scores of the means of each flow measure and the flow measures for both the preceding and following six hours. (It was the intent of the author to use the square root of the squared Z scores. However, this step was inadvertently omitted from the calculation procedure. This error changes only value of the measure used, not the relationship to other measures.

In order to relate these variables to the dependent measure, fish measurements were divided into twenty three collection periods, coded as "Samples" with the first period = 1 and the last period = 23. For each water flow variable, the mean value of the flow measures starting with the first measure in the first day after the prior "Sample" and ending with the last measure of the last day of the current "Sample" was used to represent the value of the independent variable that would have independent influence on the fish taken during any given period.

The independent variables constructed from the U.S.G.S. data in this report are exploratory, and we plan to continue to evaluate these scores, and other values that may capture different aspects of changing water flows such as the durations of flow levels).

Data Analysis

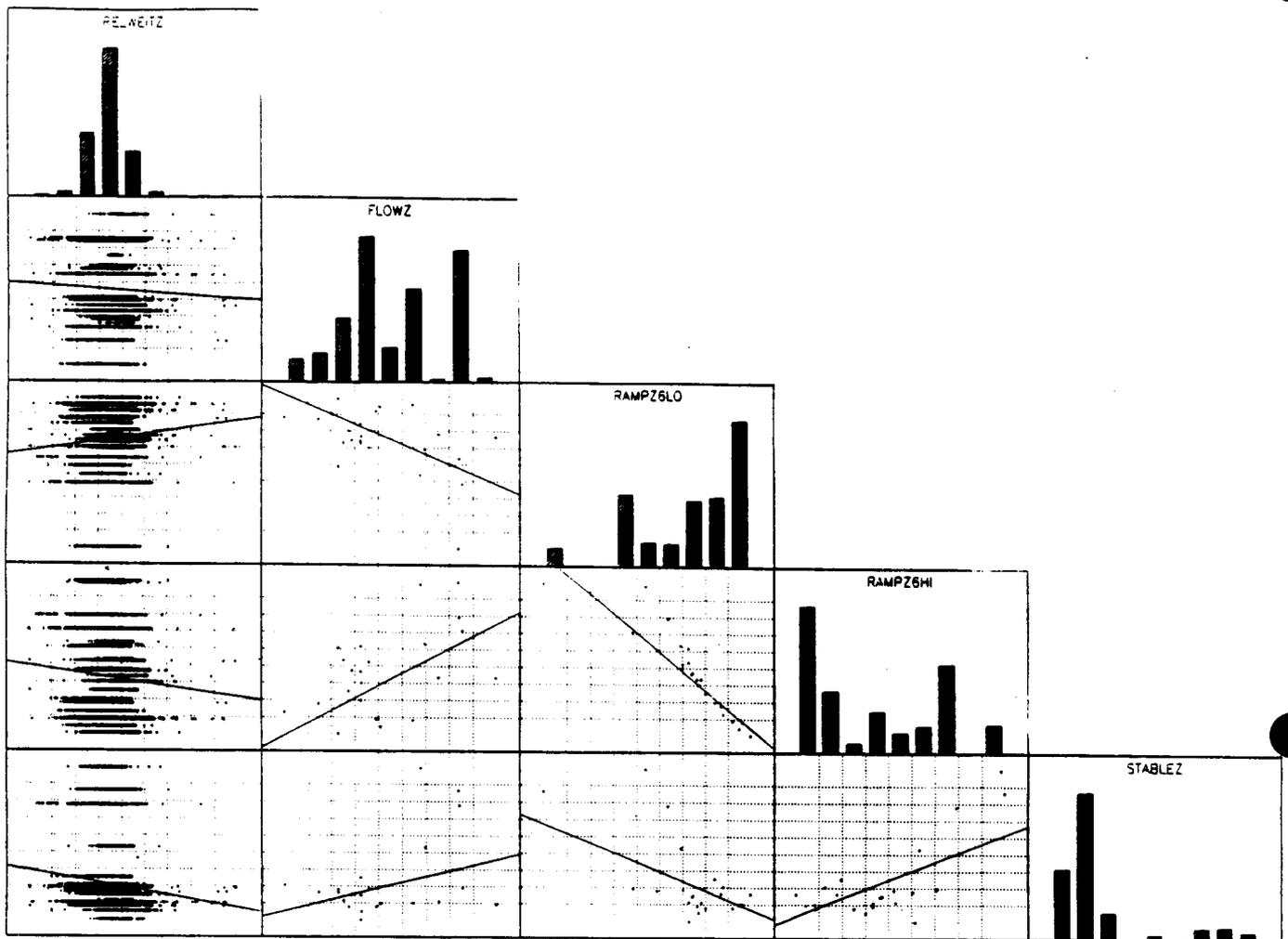
Multiple linear regression was used to evaluate relationships between relative weight and the ten different water flow variables. Flow, six hour low ramping, six hour high ramping and stability were shown to be reliably related to relative weight ($P < .05$) [Fig. 5.A].

A three way analysis of covariance procedure was used to explore the relationships between the fixed independent variables (variates); research year, research season, river section, and the continuous independent variables (covariates); flow, six hour low ramping, six hour high ramping, stability and the dependent variable, relative weight. The main effect of research year was shown to be reliable (Fig. 5.B), as was the main effect of river section (Fig. 5.C). Interactions of both research year and river sections (Fig. 5.D), and river sections and research season (Fig. 5.E) was shown to reliably influence the relative weight.

The reader is cautioned to be very conservative in any interpretation of the data presented in the figures accompanying this report because the intent of this exploration was to evaluate the viability of using parametric procedures for investigating this large data base. As an example of the need for caution, one assumption underlying the use of an analysis of covariance procedure is that the slope of the relationship between a covariate and the dependent measure must be in the same direction. The analysis reported here has not been examined for meeting this requirement.

Literature Cited

Zar, J.H. 1984. *Biostatistical Analysis*. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718pp.



230 **FIGURE 5.A:** Interactions of standardized variables; W_r (RELWEITZ), flow (FLOWZ), low 6 hr. ramping rate (RAMPZ6LO), high 6 hr. ramping rate (RAMPZ6HI), stability scores (STABLEZ). See Appendix 5.1 for descriptions of the variables.

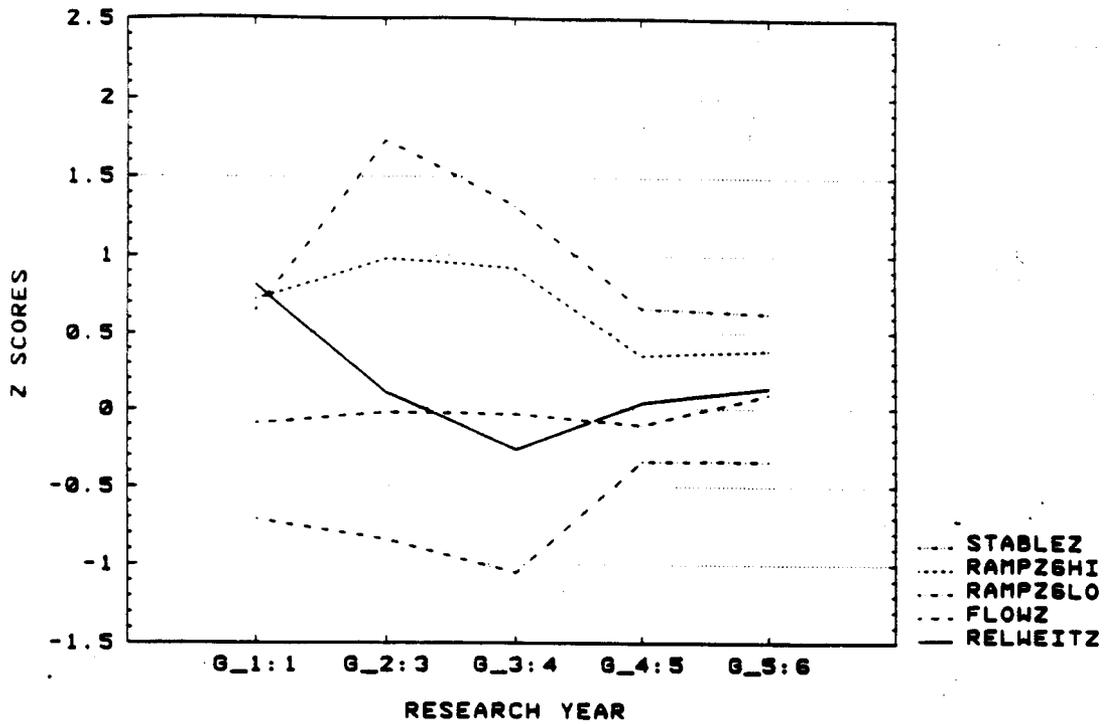


FIGURE 5.B Research year main effect, $F_{(4,11748)}=120$, $P<0.001$. G_1:1=1988, G_2:3=1989, G_3:4=1990, G_4:5=1991, G_5:6=1992.

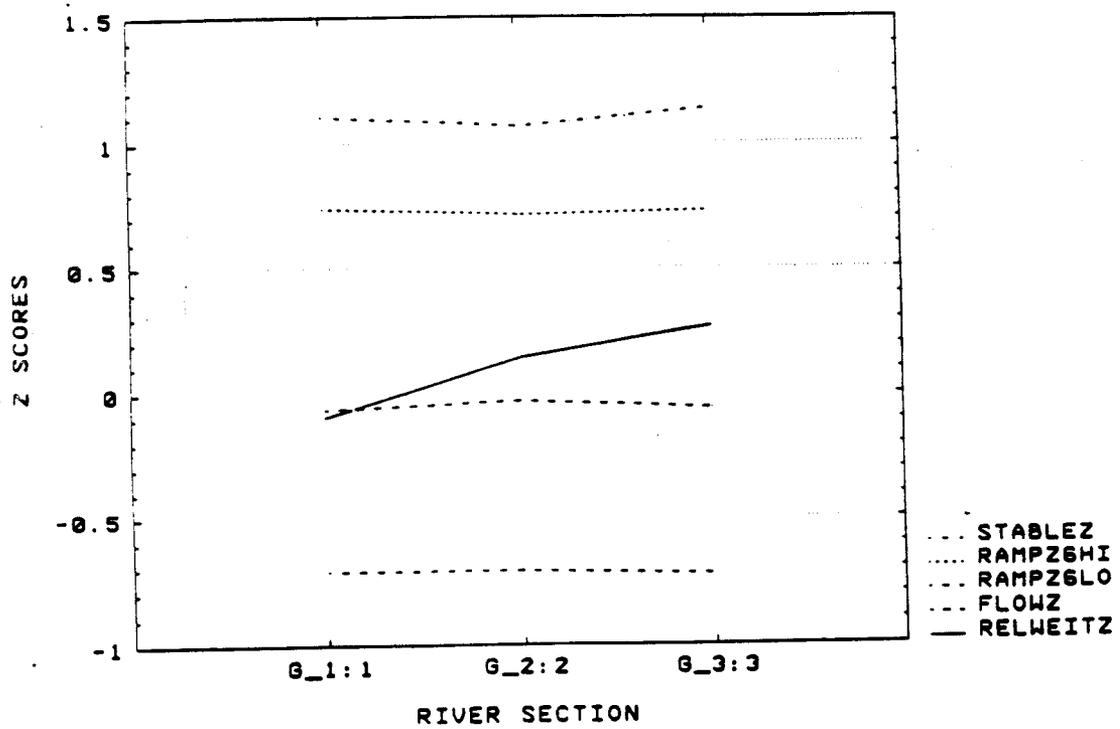


FIGURE 5.C River section main effect, $F_{(2,11748)}=51$, $P<0.001$. G_1:1=RM -5 to -1, G_2:2=RM -10 to RM -6, G_3:3=RM -15 to RM -11.

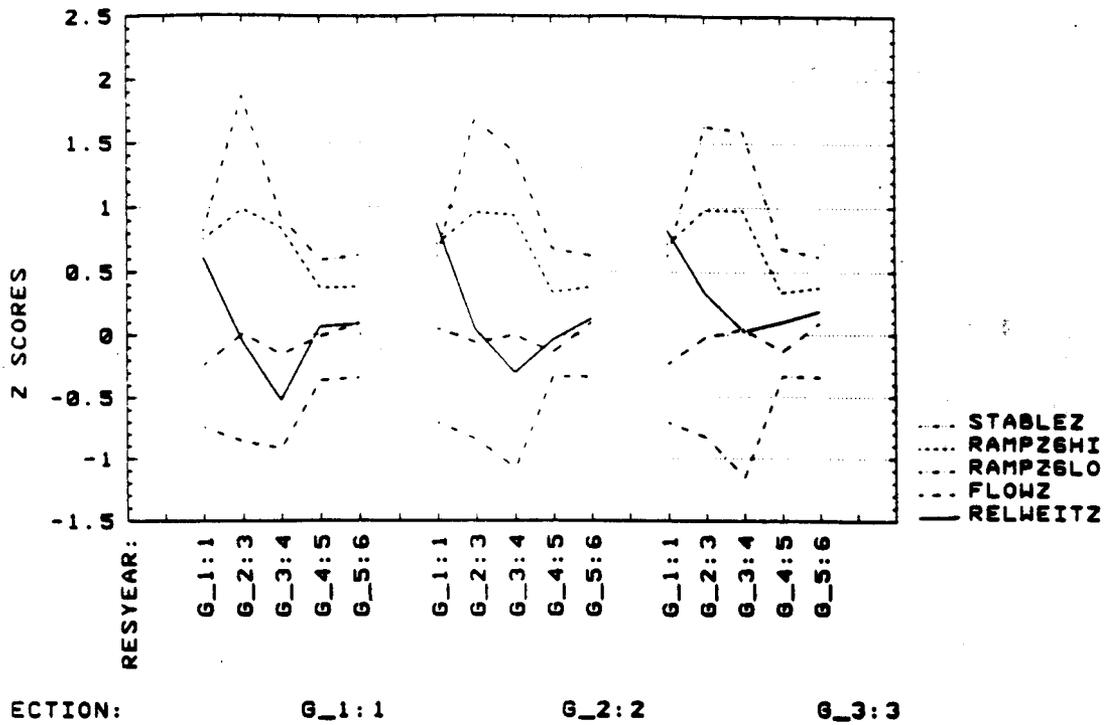


FIGURE 5.D Research year by river section interaction, $F_{(8,11748)}=15$, $P<0.001$.
 G_1:1=1988, G_2:3=1989, G_3:4=1990, G_4:5=1991, G_5:6=1992. G_1:1=RM -5 to -1,
 G_2:2=RM -10 to RM -6, G_3:3=RM -15 to RM -11.

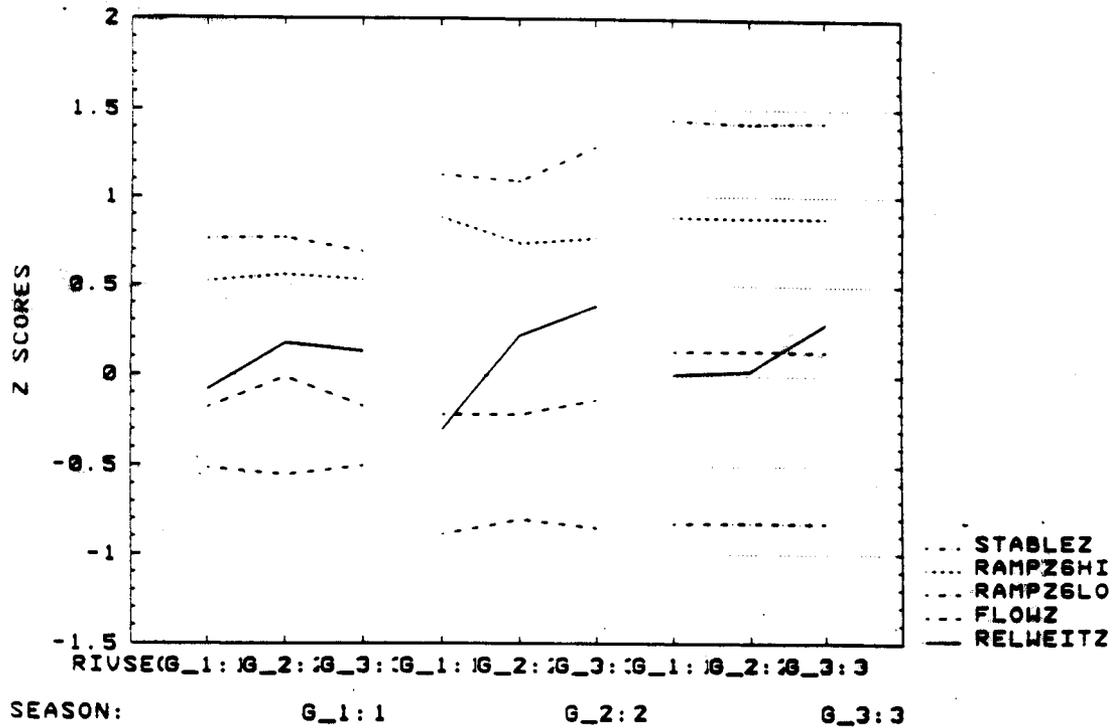


FIGURE 5.E River section by season interaction, $F_{(4,11748)}=9$, $P<0.001$. G_1:1= October-April, G_2:2=May-July, G_3:3=August-September.