

**GLEN CANYON DAM AND THE COLORADO RIVER:
RESPONSES OF THE AQUATIC BIOTA TO DAM OPERATIONS**

An Interim Glen Canyon Environmental Studies Report

T.R. Angradi, R.W. Clarkson, D.A. Kinsolving,
D.M. Kubly, and S.A. Morgensen

Arizona Game and Fish Department

Research Branch
GLEN CANYON ENVIRONMENTAL
STUDIES OFFICE

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Summary of Findings

The operation of Glen Canyon Dam affects aquatic ecosystem processes in the Colorado River including export of organic matter from Lake Powell to the tailwater, organic matter transport in Glen Canyon, periphyton resistance to disturbance, recolonization rate and standing crop.

The forebay of Glen Canyon Dam on Lake Powell was sampled quarterly. Our results indicate that volume of water released and penstock depth may influence the temperature, and the FPOM, chlorophyll, and nutrient concentration of the released water, and that the magnitude of the effects varies seasonally.

Organic matter transport at Glen Canyon Dam and Lee's Ferry was studied from September 1990 to October 1991. Diel variation in the concentration of coarse particulate organic matter (CPOM, >0.75 mm) was related to the daily hydrograph and to seasonal changes in primary productivity. Concentration was highest during the ascending limb of the hydrograph and lowest during the descending limb, and in spring and autumn. Diel and seasonal variation in fine particulate organic matter (FPOM, 0.0007-0.75 mm) were less pronounced than CPOM. Mean flow-weighted concentration of FPOM at Lee's Ferry (0.59 mg/l) was similar to the concentration at Glen Canyon Dam (0.53) 25 km upstream. We speculate that a combination of plankton inputs from Lake Powell and organic matter processing in Glen Canyon account for the lack of a net export of organic matter from the reach. CPOM quality (nutritional value) was generally high and influenced by flow. Material transported during the ascending limb of the daily hydrograph was of lower quality on most sample dates.

Experiments on periphyton resistance to disturbance were conducted in sluiceways at Glen Canyon Dam. Our findings indicate that periphyton has low resistance to dewatering disturbance. Daytime exposures of 12 h resulted in a 75% loss of chlorophyll *a*, an important determinant of algal productivity. Depth from which periphyton was collected and duration of exposure had little effect on the resistance to disturbance.

Rate of accretion of algal biomass on rock substrates in the zone of fluctuating flows was very slow compared to permanently inundated substrates. Complete recovery of periphyton following severe disturbance may require up to a year.

Dam operations affect rainbow trout spawning, stranding, and foraging in the tailwater. Rainbow trout in Glen Canyon spawned over a relatively long period of time, from December 1990 through April 1991 with the peak occurring in late March and early April.

The majority of rainbow trout spawning occurs between the 3,000 and 11,000 cfs discharge levels. Of the 586 redds mapped on three spawning bars, 90% were exposed at the 3,000 cfs discharge level, 83% were exposed at the 5,000 cfs discharge level, 59% were exposed at the 8,000 cfs discharge level, and 29% were exposed at the 11,000 cfs discharge level.

There is a general progression in the quality of spawning bar gravels from better at Lee's Ferry to poorer at Glen Canyon Dam. The bar at -14 mile had larger gravel, more fines and greater embeddedness than bars further downstream. Percent fines < 0.85 mm and < 3.35 mm were within acceptable limits for egg and alevin development. Spawning activity was less on the downstream end of spawning bars, where more fine sediments occur.

Spawning trout become stranded by fluctuating flows during the winter and spring months. Trout fry and some adults become stranded in the summer and fall. Eleven major stranding areas were identified. Most pools become isolated between 4,000 and 11,000 cfs discharge.

Rainbow trout have a high affinity for particular locations, as evidenced by repeated stranding of the same individuals in the same pools. Half of the fish equipped with radio transmitters (5) remained in the same area where they were originally caught. Rainbow trout traveled shorter distances during constant 11,000 cfs and "B" study flows (5,000-15,000 cfs), than during normal high fluctuations and 5,000 cfs constant flows. Rainbow trout experienced lower velocities at 5,000 cfs constant flows and moved greater distances. We suspect that trout do more random swimming at 5,000 cfs, either because they are forced out of their territories, or because the distribution of food (drift) is altered.

Three food categories, the algae *Cladophora glomerata*, the amphipod *Gammarus lacustris*, and Chironomidae accounted for 70-95% of the volume of material in trout stomachs. During constant flows of 5,000 and 15,000 cfs there was no variation in stomach content volume over the 24 hour period.

Studies of native fishes in the mainstem Colorado River and tributaries in Grand Canyon suggest that depressed water temperatures, in combination with daily flow fluctuations, prevent successful spawning in the mainstem by humpback chub and razorback sucker. Spawning by bluehead and flannelmouth suckers may occur in the mainstem to a limited degree, but most native fishes are dependant upon tributaries, especially the Little Colorado River (LCR), for successful life cycle completion.

Many larval and post-larval fishes enter the mainstem from tributaries, where they are exposed to conditions of flow and temperature that reduce growth and survival. However, mainstem backwater and tributary-mouth areas probably do provide significant

rearing habitat for juvenile fishes, at least in some sections of the canyon. Native fishes in the mainstem are not evenly distributed. Distance downstream from important tributaries influences the distribution of young native fishes at least as much as does distance downstream from Glen Canyon Dam.

Fish community structure in tributary streams varies widely. Shinumo Creek, Kanab Creek, and the Paria River are the most similar to the Little Colorado River in terms of community composition, and may be the most suitable streams for augmentation of humpback chub populations outside of the LCR. Water quality measurements made on the LCR suggest that humpback chub may be absent above Atomizer Falls because of physical rather than chemical barriers. Modification of travertine dams at Atomizer Falls might increase available chub habitat.

Although there are no data which indicate reductions of populations of humpback chub in the LCR, the range of chub in the mainstem appears to be shrinking. Razorback suckers are rare and may soon be extirpated from Grand Canyon if remedial actions are not taken.

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1. Introduction

Dennis M. Kubly

Purpose of the Report

The purpose of this report is to communicate our present understanding of the relationships between the operation of Glen Canyon Dam and the aquatic resources of the Colorado River in the Grand Canyon region (including Glen, Marble, and Grand canyons) to members of the Glen Canyon Dam Environmental Impact Statement (GCD EIS) writing team, fellow researchers, and other interested parties. We emphasize the term "present understanding" because our ongoing research under Phase II of the Glen Canyon Environmental Studies (GCES II) has been fully funded for slightly less than one year, since January 18, 1991, and many necessary data remain uncollected. Furthermore, there has been very limited opportunity to meet and discuss the results of our studies with GCES researchers in other disciplines. We recognize that an understanding of the biological processes in the domain of our research cannot be reached without better and more frequent communication with physical scientists investigating related phenomena in the same geographical setting.

Study Scope

The overall plan and objectives for this study were first articulated in the "Glen Canyon Environmental Studies Phase II Draft Integrated Research Plan" (Bureau of Reclamation 1990). Perusal of that document by the critical reader will reveal that not all objectives are covered in this report. Lack of coverage is attributable to insufficient time to analyze some data sets, the scheduling of research to satisfy some objectives at a time later in the project, or our inability to use proposed experimental designs with flows received during the study. Objectives not covered will be treated in later GCES reports.

Much of the research for this report was conducted during controlled flows initiated in June 1990 and ended in July 1991 (Figure 1.1, see Bureau of Reclamation 1990). The controlled flows may be placed in three sets: (1) steady flows of 11 days duration; (2) fluctuating flows of 11 days duration, and; (3) steady flows of three days duration. There were three steady flows in the first set--8,000 cfs, 11,000 cfs and 15,000 cfs. Fluctuating flows differed in minima, maxima, ranges, and rates of change. The second set of steady flows, all at 5,000 cfs, were juxtaposed between sets of controlled flows, "normal seasonal

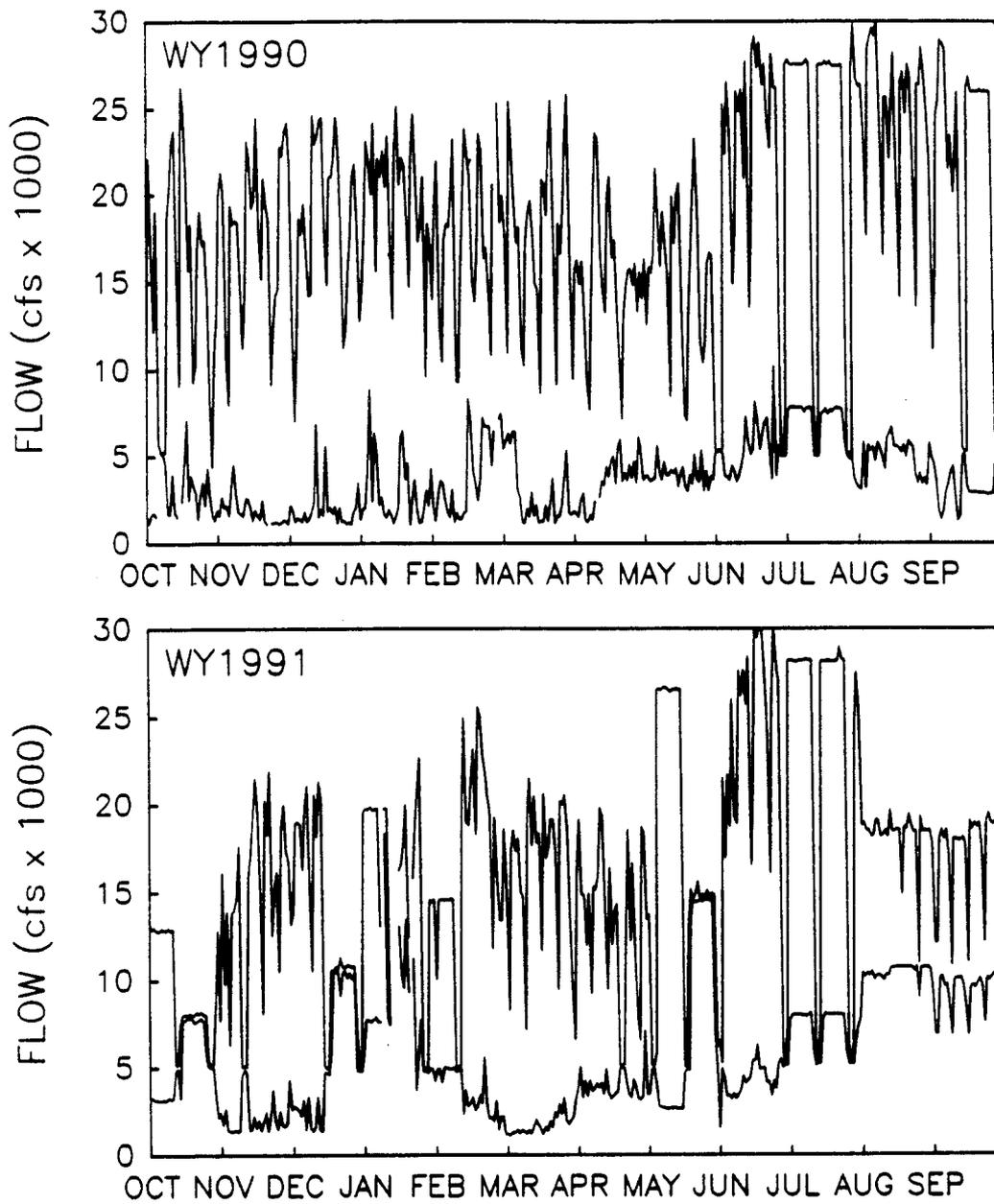


FIGURE 1.1.—Minumum and maximum daily flows during water years 1990-1991 at the USGS gaging station 2 km below Glen Canyon Dam.

flows" similar to 1989 flows, and largely unconstrained normal operations flows. During the 14-month period, flows were of the controlled type for 195 days, the normal seasonal flow type for 47 days, and the normal operations type for 184 days.

Since August 1, 1991, releases from Glen Canyon Dam have followed the interim flow criteria instituted by the Secretary of Interior. Minimum and maximum releases are restricted to 5,000 cfs and 20,000 cfs, respectively. Daily ranges vary dependent upon monthly total flows, but they may not exceed 8,000 cfs. Hourly increases are not to exceed 2,500 cfs, and decreases are limited to 1,500 cfs. Errors not to exceed 10% are allowed in recognition of difficulties in controlling releases. Exceptions have been granted for system emergencies, threats to human life, and economic considerations (forced power purchases).

Driving Variables--Much of our emphasis on dam operations is directed at regulation of flows into the Colorado River at temporal scales varying from hourly to annual. During development of the Phase II draft integrated research plan, the flow components were termed "driving variables" as a means of emphasizing their capacity to effect changes in Colorado River ecosystem resources and processes. Because controls on hydrology are receiving this emphasis in both GCES research and in the development and analysis of alternatives for the GCD EIS, it seems advisable to provide some detail on flow components and our perception of how variations in these components over different time scales may affect the Colorado River below Glen Canyon Dam.

There are four hourly to daily flow components whose effects are considered important to this investigation. Excepting periods when there are threats from floods or, to a lesser extent, drought, variation in these components is dictated by demands for hydroelectric power. Under "normal operations" prior to interim flows, the **range in daily discharge** potentially varied from 1,000 cfs or 3,000 cfs, depending upon season, to 31,500 cfs. Daily ranges of this magnitude, although seldom realized, produce changes in water surface elevation of 3 m or more depending on channel geometry. As water surface elevations fluctuate, nearshore zones are successively watered and dewatered, current velocities and flow hydraulics vary, light levels reaching the stream bottom increase and decrease, and water invades and retreats from within streambanks.

The combination of channel geometry and range of daily fluctuation determines the area affected at a given transect on the river (Figure 1.2). Wider segments of stream with gradual lateral slopes have larger areas affected by the same range of flows than do narrower, deeper segments with steeper slopes. The range of flow fluctuations is determined

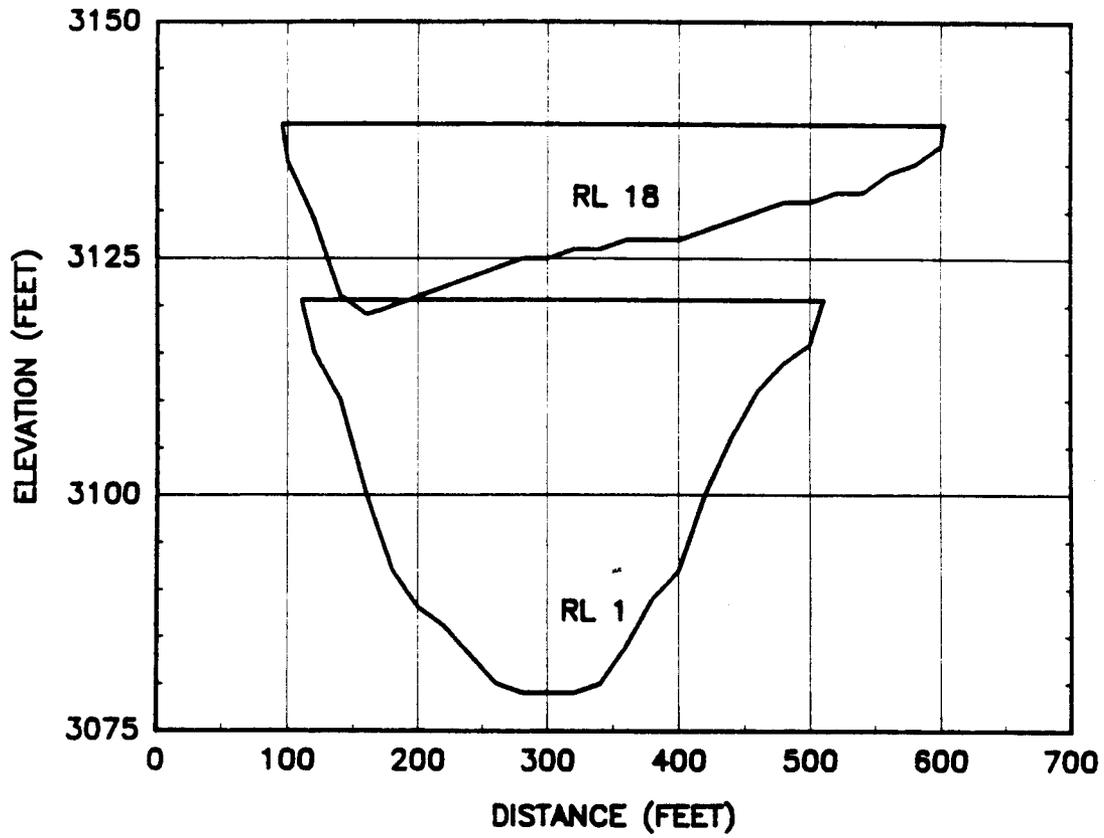


FIGURE 1.2.--Cross-sections of Colorado River at Range Line 1 and Range Line 18 below Glen Canyon Dam.

by the **minimum and maximum releases** for the day and, disregarding changes in tributary inputs, by distance from the dam. Downstream distance acts through attenuation of the release wave to reduce the maximum discharge and increase the minimum discharge. Just where the affected area is located on the stream bottom, i.e. its elevational limits, is dictated by the minimum and maximum flows during the daily cycle.

The rate at which water surface elevation changes is determined by the rate at which discharge changes, termed the **ramping rate**, the magnitude of discharge, distance downstream from the release source, and the extent of bank storage return to the river. Ramping rate is calculated as the hourly rate of change, but in practice changes in discharge most often are effected by dam operators during 10-minute periods on either side of the hour. In a single discharge cycle, the release pulse attenuates as it travels down the canyon. Waters released at higher discharges travel at greater velocities, however, and in overtaking lower, slower flows downstream they steepen the ramping rate on the rising stage. Pulse attenuation is exaggerated on the falling stage and, when coupled with the effect of return flows from bank storage, acts to diminish the rate at which stage declines. In this manner, interactions between two flow cycles increase the downstream ramping rate on the rising stage and decrease this rate on the falling stage (Dawdy 1991).

Prior to impoundment of Lake Powell, the seasonal pattern of the Colorado River hydrograph in Grand Canyon was determined by the temporal distribution of precipitation and temperature in northern mountains high in the watershed. Tributaries providing local inflows then, as now, typically produced less than 10% of the flow passing through the canyon (Thomas et al. 1963). The hydrograph was unimodal with minimum monthly flow typically occurring in January and maximum flow in June. There was an order of magnitude difference for median total flows in these months at Lee's Ferry for the period 1922-1962 [$\sim 318,000$ - 3 MAF (million acre-feet), Parker et al. 1990)].

The seasonal pattern of releases from Glen Canyon Dam is dictated by the level of Lake Powell, the forecasted amount of runoff, the annual storage targets, the annual release requirements, and, to a lesser extent, demands for hydroelectric power (Department of Interior 1988). Unless errors in forecasted runoff force changes to be made, monthly releases follow the Annual Operating Plan for Colorado River Storage Project reservoirs and Lake Mead. For the period 1963-1990, median monthly total flows differed by less than a factor of two, from ca. 556,000 acre-feet in February to ca. 903,000 acre-feet in August. A Spearman's rank correlation of median monthly total flows for the pre- and post-dam

periods ($r_s = 0.531$, $P > .05$) suggests that, in addition to extreme reduction in differences among months, the pattern of monthly flows also has been changed by dam operations.

Pre-dam total annual flows at Lee's Ferry were determined by the same set of climatic factors affecting seasonal releases, but with greater emphasis on the amount of precipitation. Median total flow for the period 1922-1962 was nearly 12 MAF, with extremes of just over 4 MAF to nearly 20 MAF (Parker et al. 1990). Following construction of Glen Canyon Dam, climatic factors affecting runoff have remained important, but a combination of congressional actions and court decisions presently guides the decision by the Secretary of Interior for the amount of water delivered from the Upper Colorado River Basin to the Lower Basin in most years. The effect of regulation on annual releases appears to be less than that of hourly, daily, or monthly time scales. Median total flow for the period 1963-1989, which includes the period of filling for Lake Powell, was slightly more than 8.3 MAF, and the extremes were from approximately 2.1 MAF to 20.5 MAF (Parker et al. 1990). An aspect of annual flows that may be affected by regulatory control to a greater extent, the sequencing of low and high total flow years, has not been determined, but autocorrelation has been demonstrated for the pre-dam period (Leopold 1959, Dawdy 1991).

The effects of Glen Canyon Dam on the Colorado River and its aquatic resources are not limited to regulation of hydrology. Since Glen Canyon is a deep hypolimnial release dam with penstock depth of ~ 70 m at full stage, its outflow is perennially cold ($\sim 7-10^\circ\text{C}$). Unlike many tailwaters carrying lesser volumes of water and receiving inputs from major tributaries, the Colorado River maintains near constancy of temperature throughout its more than 400 km distance in the Grand Canyon region. Thus, the seasonal warming and cooling common to unregulated streams in the Southwest, including the pre-dam Colorado, are largely absent. The contribution of these perennially cold waters to extirpation of native fishes from Grand Canyon has been suspected for some time (Holden and Stalnaker 1975, Fish and Wildlife Service 1978), although the effects of introduced fishes cannot be ignored (Minckley 1991). Studies on other tailwaters below hypolimnial release dams have revealed restrictions in species diversity at lower trophic levels, and perennially cold waters are typically implicated as a causative factor (Ward and Stanford 1979, Rader and Ward 1988).

Waters drawn at great depth from Lake Powell also differ from near-surface waters in both inorganic and organic chemistry (Potter and Drake 1989, Stanford and Ward 1991). These depth-related differences occur as a result of seasonal thermal and chemical stratification, incomplete mixing during periods of turnover, advective and convective

circulation, progressive mineralization of organic matter, light limitations on primary productivity, and vertical migrations of planktonic organisms in the reservoir water column. In totality, these differences produce major changes in the chemical character of release waters that are dictated by the depth of withdrawal from Lake Powell.

The great length (300 km) and depth (mean = 51 m) of Lake Powell combine to provide a basin that retains more than 90% of the 40-140 million ton annual suspended sediment load entering the reservoir from its tributaries (Iorns et al. 1965, Evans and Paulson 1983). One effect of this sedimentation, the extreme clarity of release waters from Glen Canyon Dam, is apparent to even the most casual observer. Much less evident is the loss of sediment-bound nutrients necessary to sustain downstream primary productivity. Based on flow-weighted mass balance calculations, 74% of the dissolved phosphorus and 96% of the total phosphorus entering Lake Powell are retained by the reservoir (Gloss et al. 1981, Miller et al. 1983). There has been little investigation of nutrient limitation in the tailwater, but phosphorus has been implicated as the limiting nutrient for primary productivity in both Lake Powell and Lake Mead (Paulson and Baker 1983).

Sediment removal in Lake Powell increases the competency (sediment-carrying capacity) of waters emanating from Glen Canyon Dam. By 1975, the clear release waters had removed about 9.87 million cubic meters of finer-grained sediments from the 25 km reach between the dam and Lee's Ferry (Pemberton 1976). This armoring process substantially changed the particle-size distribution and stability at higher flows of bottom sediments. Transport of finer sediments from the reach has complemented the effects of reservoir sedimentation in reducing turbidity and has effected major changes in an important habitat component for algae, invertebrates, and fishes in the tailwater. The implications of decreased sediment and nutrient inputs with concomitant increase in water clarity and sediment particle size are many, and they form central issues for the studies contributing to the GCD EIS.

Response Variables--There are three major research elements, with subdivisions classified as response variables in the development of the Phase II draft integrated research plan, for which the Arizona Game and Fish Department has responsibility under GCES II: (1) ecosystem processes and lower trophic levels; (2) trout, and; (3) native fishes. Potential effects of dam operations on these elements are both direct and indirect, and interactions exist among them.

Our use of the term ecosystem follows that of Odum (1971):

Any unit that includes all of the organisms (i.e., the "community") in a given area interacting with the physical environment so that a flow of energy leads to clearly defined trophic structure, biotic diversity, and material cycles (i.e., exchange of materials between living and nonliving parts) within the system is termed an ecological system or *ecosystem*.

Boundaries of the Colorado River ecosystem (unit) have been defined by the Bureau of Reclamation as the reach from Glen Canyon Dam to Separation Rapids for the purposes of this study. We acknowledge the necessity of setting geographic limits on any study, yet we recognize rivers are open systems that import and export water, nutrients, sediments, and organic substances within geographical boundaries set by their watersheds. Dams interrupt the flow of these materials and affect rivers in both upstream and downstream directions. Therefore, to fully understand the relationships between dam operations and the functioning Colorado River ecosystem, we may be compelled to extend our research beyond the geographic limits set for this study.

The ecosystem processes referenced in our study objectives are those which effect the provisioning of food resources to the fishes for which the Department and other resource management agencies have legislatively mandated responsibilities. In a generic sense, these food resources are organic matter in the form of different-sized particles. In some instances these particles occur as a complex of non-living detritus and colonizing bacteria and fungi. Often they are the species of algae and invertebrates that form the lower trophic levels of the stream ecosystem. Where piscivores are involved, the organic particles occur as other fishes. How the operation of Glen Canyon Dam affects the origin, behavior, and fate of these particles is a central concern of this study.

Division of our study into trout and native fishes components also reflects resource agency responsibilities and management priorities. Trout are but one group in a larger set of nonnative fishes inhabiting the Colorado River in the Grand Canyon region. They differ from other members of the nonnative fish community, however, through a combination of their extended inhabitation in the river, their suitability to environmental conditions in the tailwater, and their desirability by the sportfishing public.

The native fishes of the Grand Canyon region, including three catostomid and two cyprinid species, are surviving members of a larger pre-dam community with eight species. Three of the extant species are relatively common in the study area, but the remaining two--the humpback chub, *Gila cypha*, and the razorback sucker, *Xyrauchen texanus*, are federally listed as endangered. Preservation of these indigenous species, and particularly those federally listed, is a recognized priority of the Arizona Game and Fish Department, National Park Service, Fish and Wildlife Service, and other cooperating agencies.

Although the emphasis of our studies is directed at the effects of dam operations on downstream resources, we recognize that the limnology and fisheries of Lake Powell and Lake Mead also are affected by Glen Canyon Dam. The depth and magnitude of releases, through their control of the position and thickness of the intake plume (Johnson and Merritt 1979), may affect heat, salinity, and nutrient budgets in both release and receiving reservoirs (Gloss et al. 1981, Paulson and Baker 1981, Paulson 1983). The extent to which these effects are presently realized or to which they would change with different operations including changes in the withdrawal depth is unknown. It is apparent, however, that changes in evaporation losses and salinity have important economic implications, that primary productivity of the reservoirs is nutrient limited (Paulson and Baker 1983b, Watts and Lamarra 1983, Stanford and Ward 1991), and that the existing sport fisheries are unstable (Paulson and Baker 1983a, Gustaveson et al. 1990).

Study Area

The reach of the Colorado River in the study area has been described by many authors, including most recently Carothers and Brown (1991), and there is little justification for duplicating those efforts. Therefore, only select elements pertinent to this study will be detailed.

Data for this report were collected in the Lake Powell forebay above Glen Canyon Dam and in the Colorado River and several of its perennial tributaries from the dam to Diamond Creek, a distance of approximately 385 km (Figure 1.3). Research on ecosystem processes and lower trophic levels covered in Chapter 2 is being conducted in the reservoir and in the 25 km reach of the tailwater between the dam and Lee's Ferry. With the exception of trout collections made for the genetics study of Claussen and Phillips (1991), all trout research (Chapter 3) also is being carried out in this reach. Native fish research (Chapter 4) is being conducted under two subprojects. The first includes the mainstream from Lee's Ferry to Diamond Creek and the confluence zones of a subset of the perennial

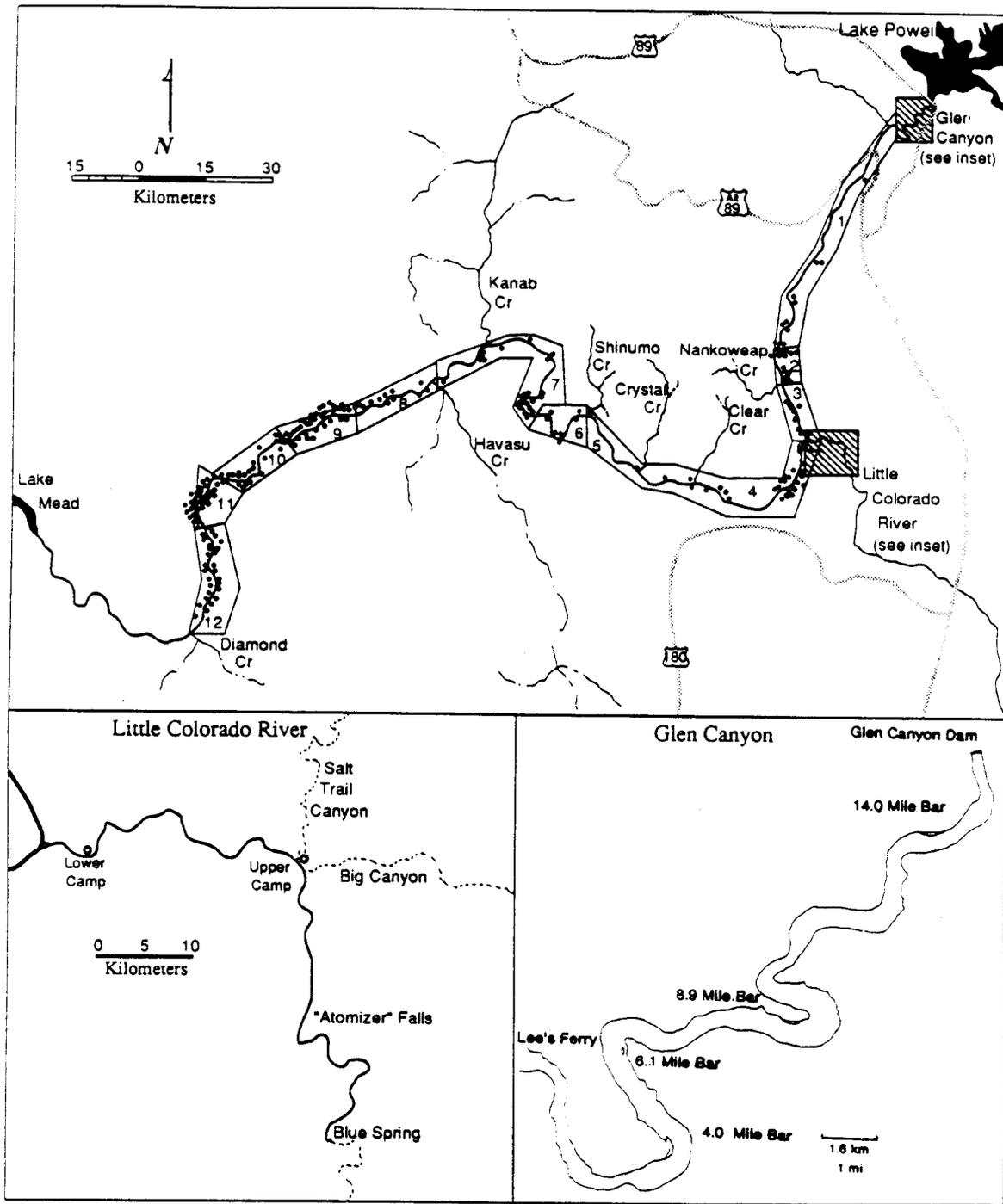


FIGURE 1.3--Map of the study area showing Colorado River sections used for native fish studies (top). Lee's Ferry reach of the Colorado River below Glen Canyon Dam with locations of study spawning bars (lower right). Perennial lower 21 km reach of the Little Colorado River (lower left).

tributaries entering the Colorado River (Paria River, Nankoweap Creek, Clear Creek, Crystal Creek, Shinumo Creek, and Kanab Creek). The second native fish study is the perennial lower 21 km reach of the Little Colorado River (LCR).

Mainstem Colorado River--The mainstem was divided into five reaches corresponding to those used by the Department during Phase I studies (Maddux et al. 1987) and 21 sections of approximately equal length with boundaries at perennial tributaries whenever possible. Because of small sample sizes at present, a number of the original sections were merged to form 11 final sections. The study area, reaches, sections, and the location of sites sampled are shown in Figure 1.3.

The study reach is situated in the middle portion of the Colorado River's 2,250 km traverse from the Rocky Mountains to the Gulf of California. By far the majority of water flowing from the river's 632,000 sq km drainage basin has reached the Colorado prior to its entry into Glen Canyon. Before the construction of Glen Canyon Dam, when the mean annual sediment load passing Phantom Ranch (RM 87.5) exceeded 100M tons, the same statement held true for inputs of sediment. Since 1963 sediment passing that point has declined precipitously to an annual mean of 12M tons with two tributaries, the Paria River and Little Colorado River, contributing 75% of the total (Andrews 1991).

The sheer-wall canyons cut through sedimentary, metamorphic, and igneous rocks by the Colorado River tower above the stream at heights reaching a kilometer or more. Through most of the study reach the river channel, which varies in width between approximately 55 m and 120 m, is bounded by bedrock or by talus slopes which give way to canyon walls (Schmidt and Graf 1988). This combination of relatively narrow channel and high canyon walls restricts solar insolation and limits energy inputs contributing to warming of the river and primary productivity.

River elevation declines nearly 550 m in the 385 km study reach, and most of this descent occurs in short, steep, turbulent rapids. The rapids typically form where debris fans from tributary canyons constrict the river (Kieffer 1987). Debris fans also modify flow hydraulics above and below the rapids such that sediment sorting and deposition create alluvial deposits, e.g. separation and reattachment bars, of finer sediments (Schmidt and Graf 1988). These bars or beaches form topographical highs which have associated topographical lows, the primary eddy return channels, at their interior (streamside) margins. At discharges low enough to pond water in the primary eddy return channels and restrict exchanges with

the mainchannel, these streamside areas become low velocity rearing habitats, herein referred to as backwaters, for early life stages of Colorado River fishes.

Riparian vegetation in the study reach consists primarily of introduced species that line the shore in two strips, the new and old high water zones (Turner and Karpiscak 1980). Width of the nearshore new high water zone varies from one to 10 meters, with areas of greatest width occurring on slopes of low relief. Density of the new high water zone vegetation is highest on alluvial sediment deposits that form beaches and sandbars. The role of this vegetation in the trophic economy of the river has not been investigated. Shading of the channel is not appreciable, but local inputs of organic matter in the form of leaves, pollen, or wood may be very important to rearing habitats of native fishes.

Little Colorado River and Other Tributaries--Hamblin and Rigby (1968) categorized tributaries of the Colorado River in Grand Canyon into two major geomorphic groups. Tributaries with relatively large drainage areas, low overall stream gradients, high sinuosity and entrenchment, and predominantly fine-grained sediments constitute one group, which is represented by the LCR, Paria River, and Kanab Creek (Fig. 2.1). Excepting stream segments fed by springs, flows of this group are intermittent and highly variable. When in flood they deliver large quantities of sediment to the Colorado River. Waters of the Paria River and Kanab Creek are dominated by sulphate ions, while the LCR is a saline, sodium chloride stream in the 21 km perennial reach below Blue Spring (Kubly and Cole 1979).

The other tributary class of Hamblin and Rigby (1968) contains short, relatively straight (low sinuosity), first or second order streams that arise from springs and have less variable flows. These streams generally have steeper gradients, and consequently larger substrates. Those that arise from the karstic groundwater system of the north Kaibab Plateau (e.g. Bright Angel, Shinumo, Tapeats, Deer; Fig. 2.1) were classified calcium-magnesium bicarbonate by Kubly and Cole (1979). Havasu Creek and other streams that enter the Colorado River from the south rim of Grand Canyon contain more sulfate, chloride, and sodium, with magnesium levels exceeding calcium.

The LCR has characteristics of both tributary classes. The study area (Fig. 1.3) encompasses the reach from Blue Spring, which provides the bulk of the perennial flow in the lower reach, to the confluence with the Colorado River (RM 61.3) 21 km downstream. The channel is deeply entrenched in an often vertical-walled canyon that in places narrows to less than 50 m. Recorded base flow in the lower perennial reach ranges from 217-232 cfs, whereas the reach above varies temporally between dryness and large-scale floods

(maximum recorded 50,000 cfs, Johnson 1976). The spring water is highly charged with free carbon dioxide. Precipitation of CaCO_3 occurs downstream in the form of an unconsolidated white floc or as travertine. The 6 km reach immediately below Blue Spring to "Atomizer" Falls, a series of precipitous drops in stream elevation just below RKM 15, exhibits relatively little CaCO_3 precipitation and deposition as evidenced by water clarity and scarcity of travertine. Substrates in this reach are predominantly sands and small gravels.

The major reach of travertine formation occurs between Atomizer Falls and the confluence with Salt Trail Canyon at RKM 10.8. Travertine formation often occurs as a series of vertical or undercut dams that may completely span the width of the river. Other bottoms in this reach are mostly fine-grained, although boulder-dominated areas also occur. The LCR canyon below Salt Trail Canyon widens and the river has fewer deposits of travertine and is more boulder-dominated. Thick deposits of flocculent CaCO_3 occur everywhere current velocities slacken.



2. Ecosystem Processes and Lower Trophic Levels

Ted R. Angradi

The operation of Glen Canyon Dam may affect downstream ecosystem processes and lower trophic levels in a variety of ways. We know or suspect that these processes have high relevancy to ecological resources of human concern such as native fishes and trout, but many of the linkages among processes within and among trophic levels are poorly understood. Only when an ecosystem perspective is adopted with an appropriate spatial scale (Minshall 1988) can the impacts of dam operations be accurately assessed.

The discharge regime of a dam may influence the quality, concentration, and loading of seston (entrained particulate organic matter) imported into and exported from the tailwater reach. Seston dynamics are a critical feature of stream ecosystem function (Cummins et al. 1983); changes in the spatial and temporal distribution of particles through the system may precipitate effects at several trophic levels (Petts 1984, Ward 1976, Sedell et al. 1978, Soballe and Bachmann 1984, Kondratieff and Simmons 1984, Rader and Ward 1988, 1989, Ross and Wallace 1981).

Three ways in which the operation of Glen Canyon Dam may affect seston-mediated ecosystem-level processes downstream are to alter the quality (nutritional value), concentration (mass per unit volume), and loading (mass per unit time) of organic matter in transport. Animals that rely on a spatially and temporally predictable concentration of seston of sufficient quality on which to feed are compromised--they must adapt, die or leave--if the concentration is altered beyond their limits of tolerance.

Loading determines the amount of seston exported from Glen Canyon to Grand Canyon in a given time interval. Flux between these reaches may be especially important, since turbidity from entrained sediments may limit primary productivity below Lee's Ferry in some seasons. Organic matter imported from Glen Canyon may fuel heterotrophy in downstream reaches during those periods. If dam operations alter the amount of organic matter exported from Glen Canyon trophic effects may occur far downstream.

Phenomena occurring in Lake Powell are included in our ecosystem perspective. The surface elevation of Lake Powell determines the depth at which water is withdrawn from the reservoir (Merritt and Johnson 1977). Reservoir elevation and flows interact. In the short-term, the volume of water withdrawn at a given time influences the size and orientation of the intake plume, which determines the level from which water is actually withdrawn. In the long-term, the amount of water stored in the reservoir determines the penstock depth.

In ecology, disturbance is defined as an event which kills, displaces, or damages enough individuals such that space is created that can be colonized by new individuals (Sousa 1984). In unregulated streams, disturbance usually results from episodes of drought, flood, or chemical toxicity; episodes may vary greatly in magnitude, duration, and frequency (Gore et al. 1990). Stream periphyton communities (epilithic algae and microfauna) are thought to have low resistance (ability to persist) and high resilience (ability to recover) to disturbance (Steinman and McIntire 1990, Grimm and Fisher 1989).

Lotic organisms adapted to stressful environmental conditions are most likely to withstand disturbance (Peterson 1987). In most respects, lotic conditions in Glen Canyon are very moderate: water chemistry and temperature do not vary much (Maddux et al. 1987); natural floods and draughts are very rare; light levels are high; herbivory is low. Indeed, conditions are ideal for algae growth (Petts 1984), and periphyton biomass in the upper tailwater is at the high end of the range of reported values (Angradi et al., unpublished manuscript, Steinman and McIntire 1990).

Daily fluctuations in flow below the dam are a chronic, low intensity phenomenon, to which the existing community is acclimated. However, prolonged exposure at low flows, particularly during periods of extreme ambient air temperatures, can exceed the threshold of tolerance and result in wide-spread algal mortality (i.e., a disturbance). Usher and Blinn (1990) demonstrated that *Cladophora glomerata*, the most conspicuous component of the periphyton, is devastated by even relatively brief (12 h) day-time exposure. *Cladophora* may have some adaptations which allow individual thalli or propagules to persist beyond virtually every disturbance, even if the structure and function of the periphyton assemblage is destroyed (Usher and Blinn 1990, Steinman and McIntire 1990, and papers cited therein). In general, however, protracted dewatering is devastating to periphyton (e.g., Neel 1963, Waters 1964, Kroger 1973).

Resistance to disturbance of periphyton in Glen Canyon is probably a function of disturbance magnitude and seasonality, whereas resilience is linked to frequency of disturbance (Grimm and Fisher 1989). Not much is known about the resiliency of Colorado basin rivers (Minckley 1991), but post-disturbance recovery of smaller streams in the region is often very rapid (Meffe and Minckley 1987, Grimm and Fisher 1989). Algal recolonization dynamics in Glen Canyon are not well understood. Formation of an organic film on substrates may precede algal sere (Korte and Blinn 1983), or may not (Hamilton and Duthie 1984, Steinman and McIntire 1986). Conditions in the zone of daily fluctuation

readily tolerated by the mature assemblage (which may modify its own microenvironment) may be too severe for the rapid establishment of a post-disturbance replacement assemblage.

In most unregulated streams, there is often sufficient functional redundancy within the biota so that effects on specific taxa do not have widespread ecosystem-level consequences (Kelly and Harwell 1990). The epilithic periphyton in Glen Canyon has low functional redundancy. *Cladophora glomerata* is, by any measure, the dominant aquatic plant in the reach (Blinn and Cole 1991). Four or five species comprise ~90% of the epiphytic diatoms (Pinney 1991). Aquatic macrophytes are restricted to only a few sites. Thus, exposure-disturbance of a large area of *Cladophora* and its epiphytes would likely have consequences for organisms and process that require an intact periphyton community.

There is some evidence (Pinney 1991; D. Kubly, unpublished data) for non-disturbance, flow-related effects on the periphyton assemblage. For example, water surface elevation may influence the rate of algal photosynthesis via light limitation and light inhibition effects. Measurements of periphyton metabolism may reveal the potential magnitude of this effect (Uelinger and Brock 1991).

Rainbow trout (*Oncorhynchus mykiss*) in rivers are diurnal, usually opportunistic, drift feeders (Angradi and Griffith 1990, and papers cited therein). In most unregulated streams invertebrate drift density is usually highest at night when light levels are too low to allow efficient foraging by trout (Allan 1981, Bisson 1978). Diel changes in flow below Glen Canyon are thought to alter the daily drift pattern, and thus the availability to trout of drifting invertebrates, particularly the amphipod *Gammarus lacustris* (Leibfried and Blinn 1986, Maddux et al. 1987). There is much anecdotal evidence that trout foraging activity is or was, in the past, closely linked to the daily hydrograph to the benefit of trout; scientific data are lacking. On the other hand, if the pattern of release from the dam is such that nocturnal drift is enhanced relative to and at the expense of the rest of the diel cycle, trout growth may decrease as a direct result of a lowered daily ration or, indirectly, if trout switch to a less calorific diet.

The purpose of this chapter is, therefore, to draw together the scientific information now at hand, and to speculate on the potential effects of the operation of Glen Canyon Dam on ecosystem processes and lower trophic levels. The specific objectives of this study were to: (1) examine Lake Powell forebay limnology and to relate forebay water quality parameters to tailwater processes; (2) examine the daily and seasonal variation in seston quality, concentration, and loading in Glen Canyon, and to relate sestonic and dissolved parameters to flow and within-reach processes; (3) examine the effects on periphyton of

dewatering, and to relate those effects to exposure duration in a semi-natural setting; (4) examine periphyton colonization in Glen Canyon, and to relate colonization rates and trajectories to flow fluctuations; and (5) examine the effect of the daily hydrograph on trout foraging.

Methods

Organic Matter Transport and Lake Powell Forebay Limnology

Dissolved and particulate organic matter (POM) were collected at Lee's Ferry, Glen Canyon Dam, and on Lake Powell in the forebay of the dam. Water for fine particulate organic matter (FPOM; 0.7-750 μm) and dissolved nutrients was collected with a boat-mounted diaphragm pump at Lee's Ferry and Lake Powell. At Lee's Ferry a depth integrated sample was collected by raising and lowering the pump inlet hose while the boat was maneuvered back and forth normal to flow on a transect located 1 km upstream of the boat launch area. At Glen Canyon Dam, samples were collected by withdrawing water from the draft tubes. In the Lake Powell forebay, samples were collected at six depths: surface, 6.1, 12.2, 36.6, 45.7, and 61 m, at a single station using a diaphragm pump. At Lake Powell, Hydrolab data were collected (temperature, conductivity, pH, dissolved oxygen) on or near organic matter sampling dates as well as on several additional dates.

Coarse particulate organic matter (CPOM; $> 750 \mu\text{m}$) was collected at Lee's Ferry by towing a pair of high-speed Miller tubes (10-cm diam. mouth, 750- μm mesh, integral flow meter), behind a boat moved across the transect. Tubes were raised and lowered for a depth integrated sample. CPOM samples were frozen prior to analysis.

Lee's Ferry and Glen Canyon Dam were sampled at irregular intervals (usually monthly) between September 1990 and October 1991. Lake Powell was sampled in December 1990, and in April, August, and November 1991. At Lee's Ferry, samples were collected at approximately 1000, 1600, 2200 h, and at 0400 and 1000 h of the following day in an attempt to capture ascending, steady, and descending portions of the daily hydrograph. At the dam the second 1000 h sample was not collected. Lake Powell forebay samples were collected at 1200 and 2400 h.

Water samples for analysis of total $\text{NH}_4\text{-N}$, organic N, $\text{NO}_2\text{+NO}_3\text{-N}$, PO_4 , and orthophosphate were transferred directly to amber bottles, preserved with HgCl_2 , and chilled. Samples for chemical oxygen demand (COD) and organic carbon (TOC, DOC) were transferred to glass bottles, preserved with H_2SO_4 , and chilled. Samples for analysis of

DOC and dissolved NH_4 , $\text{NO}_2 + \text{NO}_3$, NO_2 , PO_4 and orthophosphate were prefiltered (750- μm mesh), vacuum filtered through a 0.45- μm nucleopore filter, transferred to amber bottles, preserved with HgCl_2 , and chilled. Dissolved silica samples were filtered as above but were not preserved. Sample processing and preservation followed Sylvester et al. (1990).

FPOM was collected by filtering prefiltered (750- μm) aliquots through tared, preashed, 0.7- μm glass-fiber filters (GF/F). Separate filters were used for FPOM COD, Kjeldahl nitrogen, phosphorus, chlorophyll, and ash-free dry matter (AFDM). Filters were frozen prior to analysis. Prior to submission for C,N and P analysis, CPOM samples were dried for 24 h at 60 °C, and ground to a powder in a Wiley mill.

Ash-free mass of CPOM and FPOM samples was determined gravimetrically. Samples were dried in tared crucibles for 24 h at 105 °C; the samples were then desiccated, weighed ($\pm 0.0001\text{g}$), ashed for 2 h at 550 °C, desiccated and reweighed (APHA 1989).

Chlorophyll *a* and pheophytin *a* content of samples was determined by spectrophotometry. CPOM samples were homogenized in a blender with 150-200 ml of water. An analytical pipet was used to withdraw several 5-ml subsamples (Biggs 1987) from which the water was removed through a glass fiber filter (GF/F). Filters containing CPOM and FPOM were ground in a round-bottomed tube with a teflon pestle (Kontes Instruments) in buffered 90% aqueous acetone, transferred to a 50-ml centrifuge tube, and refrigerated at 4 °C for 24 h. Pigment concentrations were determined using a Spectronic 21 spectrophotometer. The concentration of chlorophyll *a* corrected for pheophytin *a* and the concentration of pheophytin *a* was determined using monochromatic equations (APHA 1989).

Seston and sestonic chlorophyll concentration data were transformed [$\log_{10}(x+1)$] to correct for non-normality. Two-way ANOVA was used to determine the effect of time of day and season on seston concentration at each site and to determine the effect of site (Lee's Ferry versus Glen Canyon Dam) on FPOM and FPOM plant pigments. One-way ANOVA was used to determine the effect of sample date on concentration. Only data for the first four samples in the diel cycle were used in the ANOVA models, i.e., the second 1000 h sample from Lee's Ferry was omitted. The Tukey honestly significant difference test (SPSS Inc. 1990) was used to make multiple comparisons among times of day and dates. Spearman rank correlation was used to examine relationships among seston components. Nutrient concentration samples that were below detection limit (DL) were set to DL/2. This method may produce biased estimates of the mean and variance (Newman et al. 1989).

Periphyton Exposure

Two experiments (I-II) were conducted under semi-natural conditions in the sluiceways at the base of Glen Canyon Dam. All periphyton (colonized cobbles) used in the experiments was collected at -14 mile bar from either the 6,500-5,000 ($= > 5,000$) cubic feet per second (cfs) level or the $< 5,000$ cfs level. Periphyton on cobbles from the 6500-5000 cfs zone was partially exposed at flow of 5,000 cfs. The gradient of -14 mile bar is low and sufficient water remained in depressions among the cobbles to allow the algae above 5000 cfs to persist, presumably by "wicking up" water. Steeper cobble bars nearby lacked algae above the 5,000 cfs level. Cobbles from the deeper zone were collected from transects of equal elevation at a depth < 1 m. In all cases, cobbles were collected at dawn and transported to Glen Canyon Dam in ice chests filled with river water.

The sluiceways convey seepage from within the dam to the river. They have a trapezoidal profile, are 0.5 m deep, 0.65 m wide at the bottom and 0.9 m deep at the top. Base flow in the 31 m section of the sluiceway used in the experiments was $0.03 \text{ m}^3/\text{s}$. Every 16 minutes, a sump inside the dam is evacuated and flow increases to $0.2 \text{ m}^3/\text{s}$ for 2.5 minutes. A 0.2-m high weir was installed at the halfway point and at the downstream end of the study section. This created two sections of nearly equal depth and velocity. Prior to experiments, the sluiceways were drained and attached algae were removed by scraping and wire-brushing.

Photosynthetically active radiation (PAR) reaching exposed cobbles was measured at the sluiceways in both experiments with a LI-COR 190 quantum sensor. Incident PAR was recorded at 15 minute intervals (average minute readings) with a Campbell Scientific CR21 data logger.

Experiment I was begun on July 3, 1991. Forty-eight cobbles were collected: 24 each from the deep ($< 5,000$ cfs) and shallow zones ($> 5,000$ cfs). Cobbles were held overnight in the sluiceways and then transferred to open-sided plastic boxes (35 x 35 x 9 cm). Four cobbles from the same level were placed in each box. Five boxes for each level were removed from the sluiceways and placed next to the sluiceways. Two boxes from each level remained inundated as controls, but were subsequently lost. Geometric mean diameter of the cobbles used was 162 mm, and did not differ between treatments.

Cobbles were sampled immediately (0700 on July 4, 1991), and 10, 34, 58, 130, and 336 h after removal from the sluiceway. At each sample period a single randomly selected sample was collected from each cobble using the method described below for colonization of natural cobbles.

Experiment II was begun on July 6, 1991. Ninety-six cobbles were collected, 48 each from the deep and shallow zones. Cobbles were placed in boxes as in experiment I and held in the sluiceways, twelve in each section. Boxes were randomly assigned to one of three treatments: continuously inundated controls, 24-h exposure, and 48-h exposure. The experiment had a randomized block design with two factors; one with three levels (exposure time), one with two levels ($>5,000$, $<5,000$ cfs), and two blocks (sluiceway sections). Each treatment was replicated four times (twice in each block). Measurements of individual cobbles were later pooled to produce a mean for each box (the experimental unit) and date. Geometric mean diameter of cobbles used in experiment II was 147 mm, and did not differ between levels of the depth treatment.

All cobbles were sampled initially on July 11. At 1900 h the boxes assigned to the 24 and 48 h exposure treatments were removed from the sluiceways and placed on platforms above the sluiceways. Boxes were returned to the sluiceway after 24 or 48-h (approximately 12 and 24 h of daylight, respectively) according to treatment. Cobbles were sampled at 24, 168, and 336 h after reinundation. Periphyton samples were frozen prior to analysis.

To evaluate algal colonization in the sluiceway channel during experiment II, an array (5 x 5) of sandstone tiles (described below) was placed just upstream of the cobbles in each section. The tiles were installed five days before the first cobble sample. Every five days thereafter for 25 days, five tiles were randomly collected from each section. Tiles in section two were lost after day 15. Collected material was processed as described below for the spring 1991 colonization study.

Samples were thawed and the water was extracted by vacuum over a glass fiber filter (GF/F). The algae and filter were ground in 90% acetone, extracted and read as described above for CPOM. In addition to chlorophyll *a* and pheophytin *a*, chlorophyll *b* was determined using monochromatic equations (APHA 1989). Diatoms contain chlorophyll *a* and lack chlorophyll *b* (Jeffrey 1974). We used the ratio of chlorophyll *a*:*b* as an index of the degree of epiphyte colonization in periphyton samples. Following spectrophotometry samples were transferred to crucibles and dried to obtain AFDM.

Repeated-measures ANOVA was used to examine the effects of treatments (between-subjects effects) and their interactions. In experiment II, two repeated measures ANOVA models were run for each parameter, one to examine the effect of exposure versus control, and a second model to test for differences between the exposure treatments. Periphyton parameters were transformed [$\log_{10}(x+1)$] to correct for non-normality. Least-squares regression was used to determine the rate of change in parameters over time.

Algal Colonization

Grids of artificial substrates were installed at mile -10.5 mile bar and at -13.5 mile bar (both sites were on river left) on February 22, 1991. Substrates were 15 x 15 x 2 cm tiles sawn from Navajo sandstone slabs collected at the canyon rim. Substrates were placed in grids of 15 tiles at five levels: <5,000, 5,000, 11,000, 13,000, and 22,000 cfs, and were collected after 10, 20, 40, 57, and 63 days in situ. On days 57-60 (April 19-21, 1991) flows were constant at 5,000 cfs. On each collection date three tiles were randomly collected from each grid. All material (not necessarily attached) on the top surface (excluding the sides) of each tile was brushed and flushed into a jar for transport to the lab.

Periphyton on natural cobbles was sampled monthly from August 1991 through December 1991 at -13.5 mile bar (river left) and at -14 mile bar (river right). Cobbles were sampled at four levels: <5,000; 8,000; 15,000; and 20,000 cfs. For cobbles from below the 5,000 cfs level (i.e., those with a dense filamentous algal coverage), a circular 4.15-cm² area was isolated with a neoprene rubber-gasketed template and the periphyton within sheared off and scraped loose using an X-acto #17 knife blade. The dislodged material was removed with forceps and the scraped area backflushed with a dropper of river water. The same method was used for cobbles at higher levels, except that a small brush was used instead of a knife. Fifteen to twenty random samples were collected at each level and site on each date.

Material accumulated (periphyton, sand, debris) on sandstone tiles was extracted in acetone as described above for seston. Following chlorophyll determination the material was transferred to crucibles and the acetone allowed to evaporate. Ash-free biomass was determined as for seston. Periphyton samples from natural cobbles were dried and ashed as for seston samples.

Analysis of covariance was used to test for effects of site, level, and time in situ on periphyton biomass and chlorophyll *a*. Biomass and chlorophyll were transformed [$\log_{10}(x+1)$]. Least-squares regression through the origin was used to determine the rate of biomass and chlorophyll accretion for each level at each site in the spring experiment. Least-squares regression was used to determine the rate of biomass accretion on natural cobbles after the first monthly sample (August) in the autumn 1991 experiment.

Diel Feeding Chronology of Rainbow Trout

Twenty-four-hour studies of trout diet were conducted on April 10-11, 1991 at -4.0 mile bar during regular spring flows, and on May 28-29 and July 12-13 at -13.5 mile bar

during 15,000 cfs and 5,000 cfs constant flows respectively. An unsuccessful attempt was made to collect fish on July 19, 1991 during fluctuating flow. In the April sample, trout were collected from a side channel; on the other dates, trout were collected in the main channel. Trout were collected at approximately 4 h intervals (6 samples total) using a trammel net. An attempt was made to collect 10 trout > 250 mm TL at each sample interval. Trout were weighed (± 2 g), and measured, and the viscera were removed and preserved in 10% formalin.

Invertebrate drift was collected by towing a high-speed Miller tube as for CPOM at the upstream end of the fish collection site. Two drift samples were collected just prior to each fish collection interval, and preserved in 10% formalin.

In the laboratory, the cardiac stomach was removed from the viscera anterior to the pyloric caeca. The total volume of stomach contents and volume of individual food item categories were measured volumetrically.

Drift samples were sorted into eight categories: *Gammarus lacustris*, chironomid adults, pupae, and larvae, oligochaetes, cladocerans, *Cladophora*, and debris. *Cladophora* and debris were dried and ashed as described above for CPOM.

Analysis of covariance was used to examine the effect of time of day on the volume of gut contents (Jenkins and Green 1977, Trippel and Hubert 1990). Fish length was the covariate. Volume of stomach contents and fish length were transformed [$\log_{10}(x+1)$] to correct for non-normality. One-way ANOVA was used to compare mean volume of stomach contents among sample dates.

Results

Lake Powell Forebay Limnology

Concentration of FPOM in the forebay varied with season (Figure 2.1). Mean concentration (all depths combined) was highest in August, 1991 (2.0 mg AFDM/l) and lowest in December, 1990 (0.45 mg AFDM/l). Spring and autumn FPOM concentrations were near 1 mg AFDM/l. There was only limited vertical variation in concentration except in August, 1991, when there was a strong epilimnial peak (> 3 mg AFDM/l at 10 m), and in November, 1991, when there was a slight increase in FPOM concentration in the metalimnion.

The small number of sampling depths make interpretation of vertical patterns in FPOM chlorophyll *a* concentration difficult. On all dates there was a peak at 12 m, and a

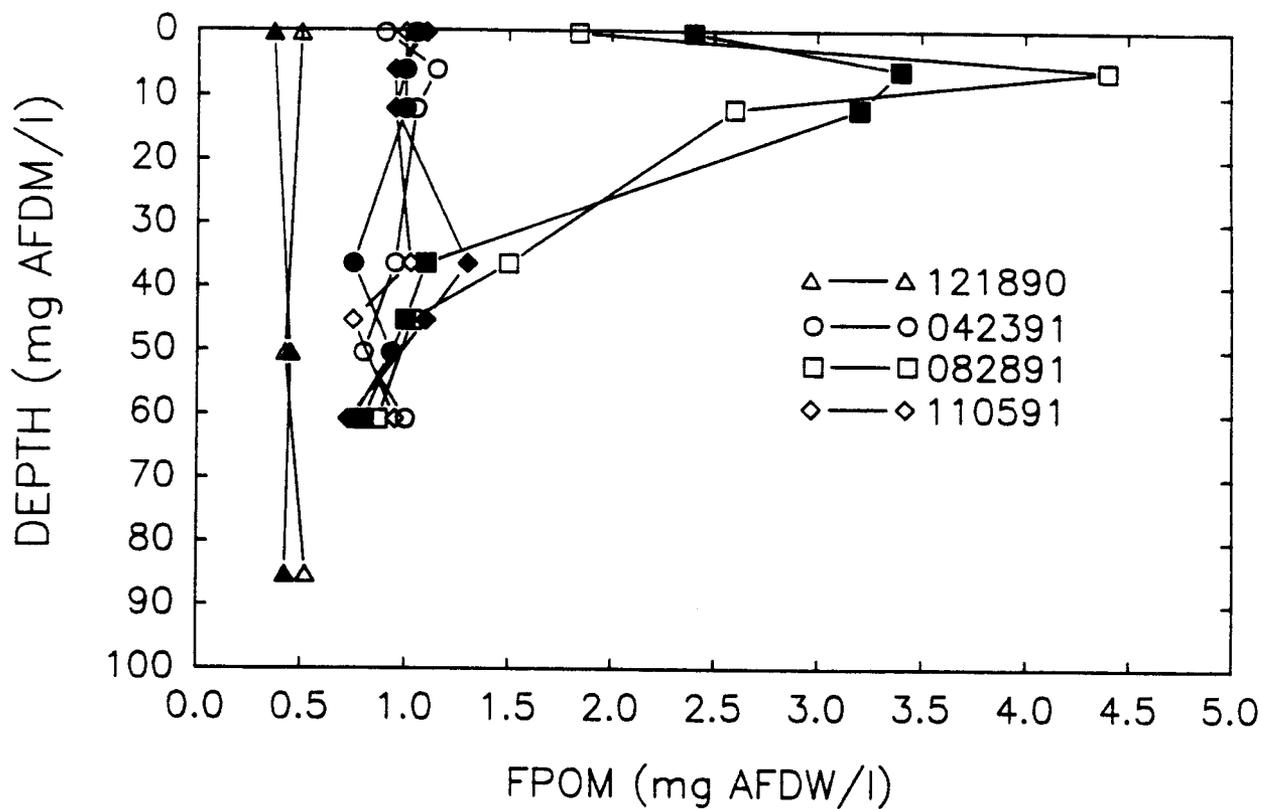


FIGURE 2.1--FPOM concentration with depth at the Lake Powell forebay station. Open symbols are daytime samples; closed symbols are nighttime samples.

hypolimnetic minimum near penstock depth (~50 m, Figure 2.2). Pheophytin *a* concentration was generally less than chlorophyll *a*, and increased with depth.

Temperature profiles indicated that the forebay was at least weakly stratified on all sample dates, but no data are available for the coldest months (Figure 2.3). The lake was still stratified in December 1990 and November 1991, when the metalimnion probably reached penstock depth, was weakly stratified in March 1990 and April 1991, and was well stratified by June 1991. Daytime surface water temperatures ranged from 12 °C in December to 26 °C in August. Water temperature at penstock depth (~50 m) ranged from ~7 °C in winter and early spring to ~9 °C in autumn. Metalimnion depth was ~10 m in summer and ~40 m prior to complete mixing.

Dissolved oxygen profiles were clinograde or negative heterograde (Wetzel 1983) on all sampling dates (Figure 2.4). Summer profiles had metalimnetic oxygen maxima at 10-20 m, and hypolimnetic minima. Metalimnetic oxygen minima in late autumn were likely caused by the concentration of organic matter in the metalimnion at the chemocline (Johnson and Page 1981). This interpretation is partially supported by the vertical distribution of chlorophyll *a* in the forebay. Metalimnetic oxygen minima in spring were likely caused by advective replacement of the hypolimnion by cold, oxygen-rich underflows.

The shapes of specific conductance profiles were similar on all dates (Figure 2.5). Conductance was generally constant in the epilimnion and metalimnion, and decreased rapidly through the hypolimnion. There was no clear seasonal trend in conductance at penstock depth; large (100 μ mhos/cm) between-year differences were noted, e.g., March 1990 versus April 1991.

Organic Matter Transport

CPOM concentration varied over the diel period (Figure 2.6; $F_{3,40}=3.66$, $P<0.02$) and among seasons ($F_{3,40}=8.02$, $P<0.01$). CPOM concentrations differed only between 1600 h (0.03 mg AFDM/l) and 0400 h (0.01 mg AFDM/l) (*t*-test, $t=-2.26$, $P<0.05$). For all Lee's Ferry seston samples, coarse and fine, mean concentration at 1000 h on the first day was not different from the concentration at 1000 h on the second day. CPOM concentration varied among sample dates (Figure 2.7: $F_{13,42}=2.76$, $P<0.01$), and was higher in April 1991 (0.06 mg AFDM/l) than in October through February 1990-1991 (<0.01 mg AFDM/l). There were apparent peaks in mean daily CPOM concentration in autumn and spring.

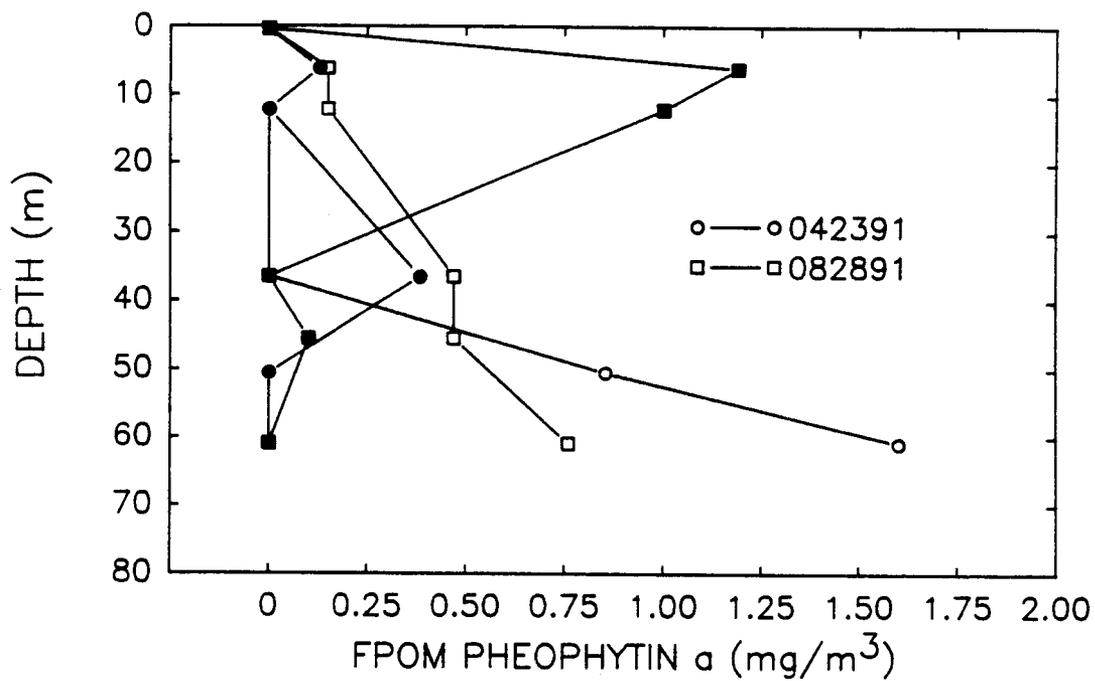
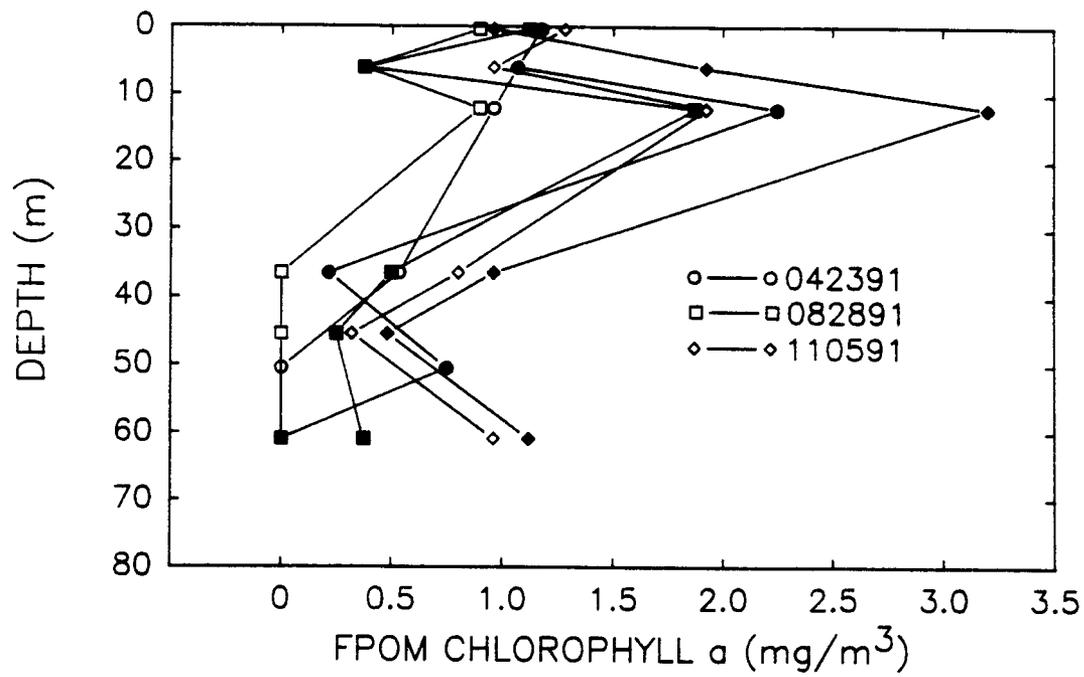


FIGURE 2.2--FPOM chlorophyll *a* and pheophytin *a* concentration with depth at the Lake Powell forebay station. Open symbols are daytime samples; closed symbols are nighttime samples.

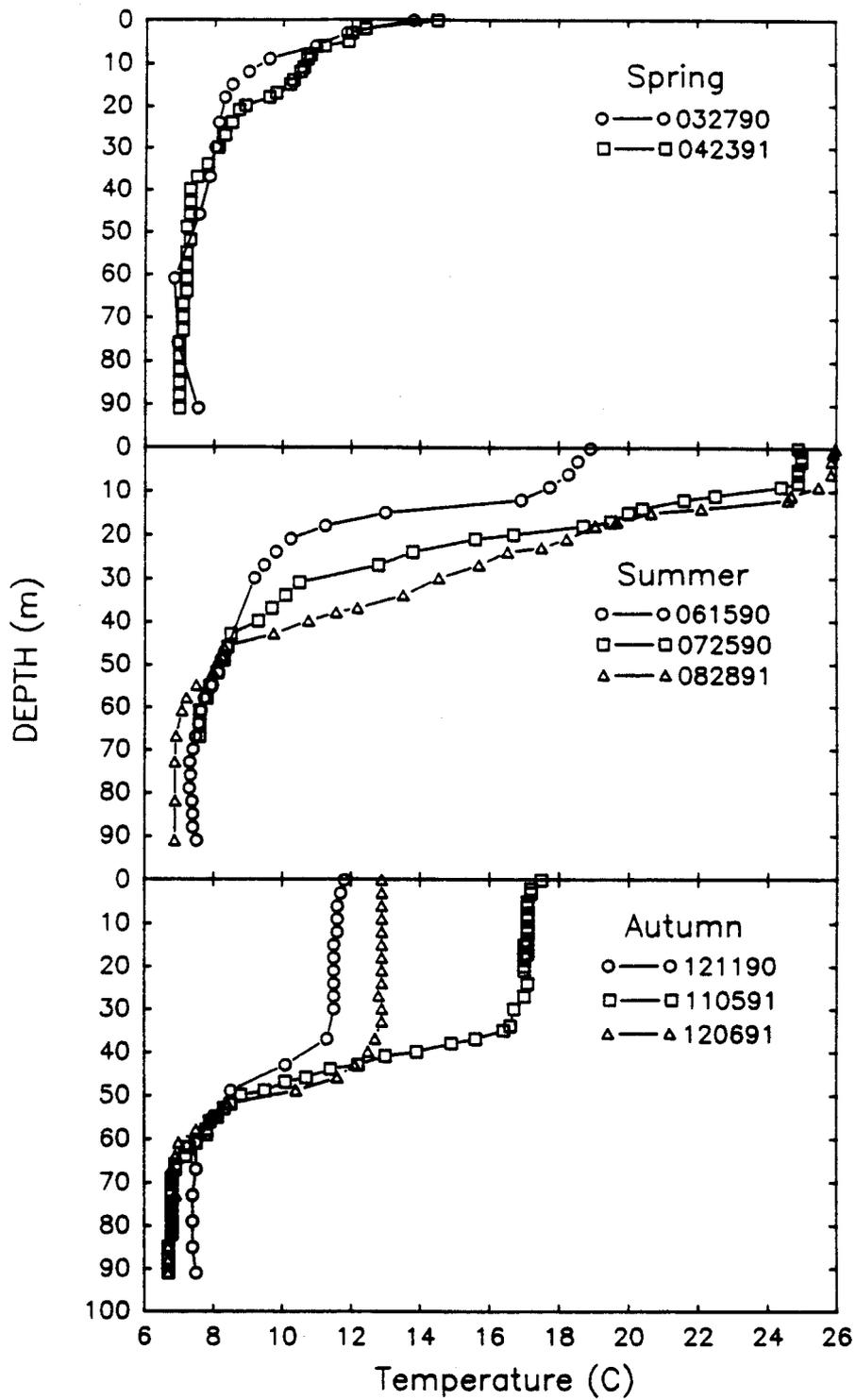


FIGURE 2.3--Temperature profiles at the Lake Powell forebay station.

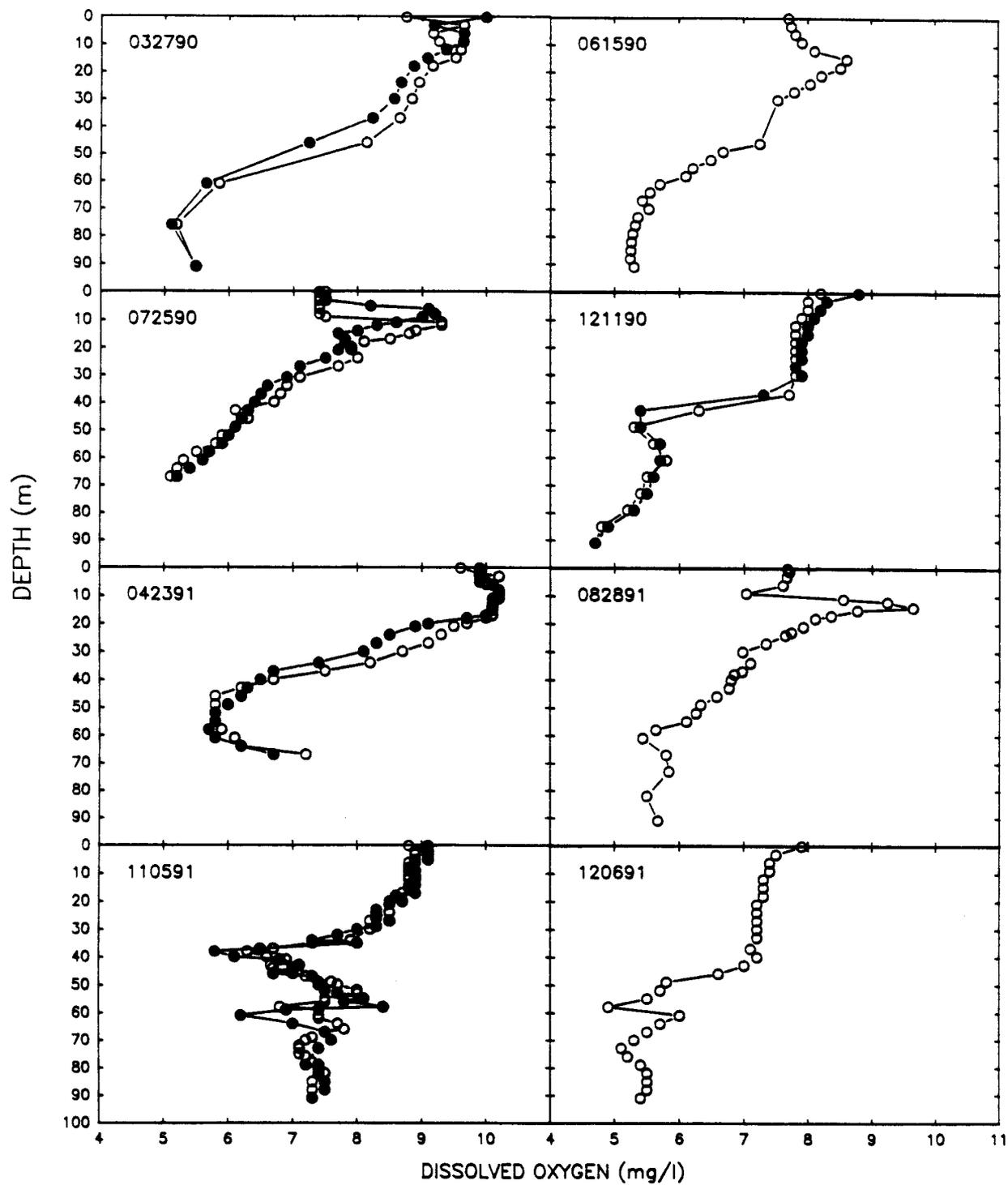


FIGURE 2.4--Dissolved oxygen profiles at the Lake Powell forebay station. Open symbols are daytime profiles; closed symbols are nighttime profiles.

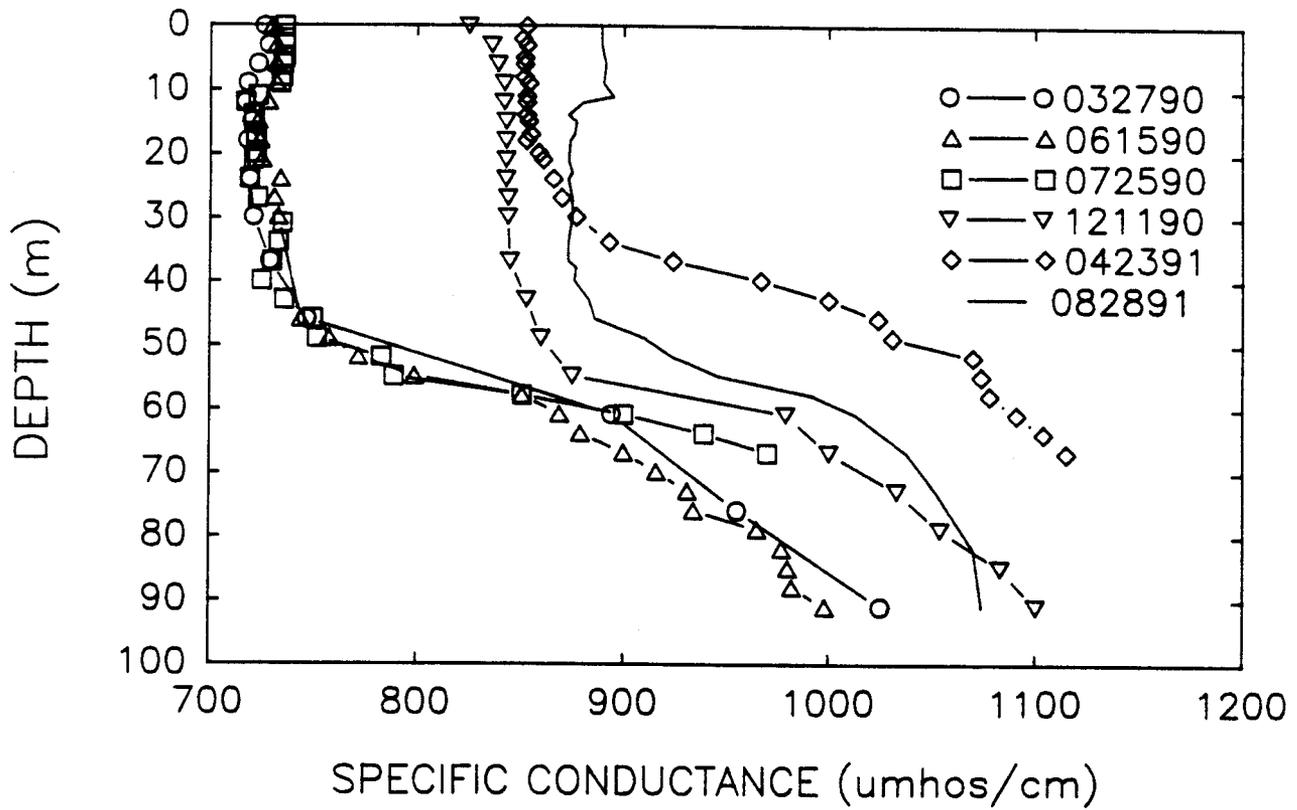


FIGURE 2.5--Specific conductance profiles at the Lake Powell forebay station.

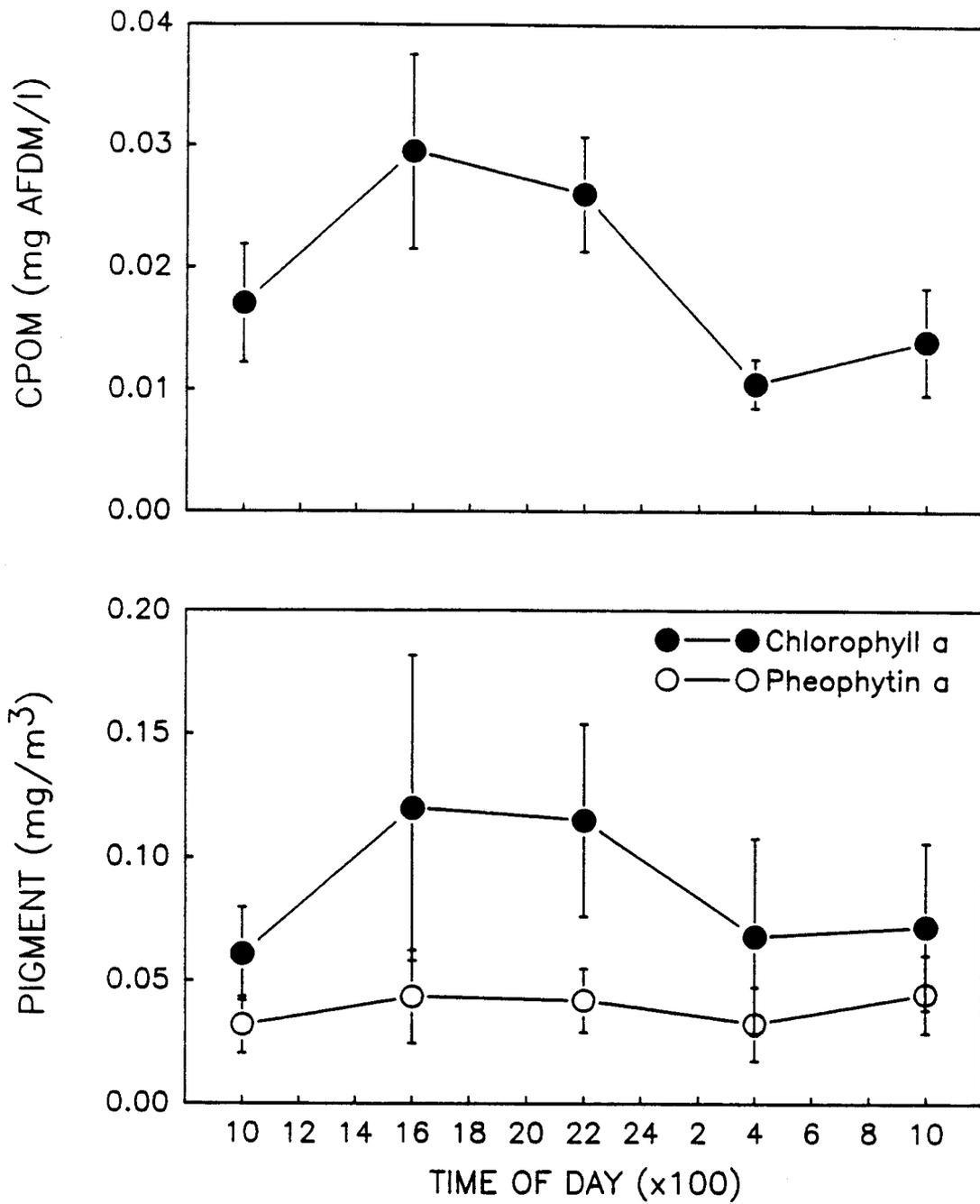


FIGURE 2.6--Diel variation in CPOM and CPOM chlorophyll *a* and pheophytin *a* concentration at Lee's Ferry. Means (\pm SE) are pooled across sample dates.

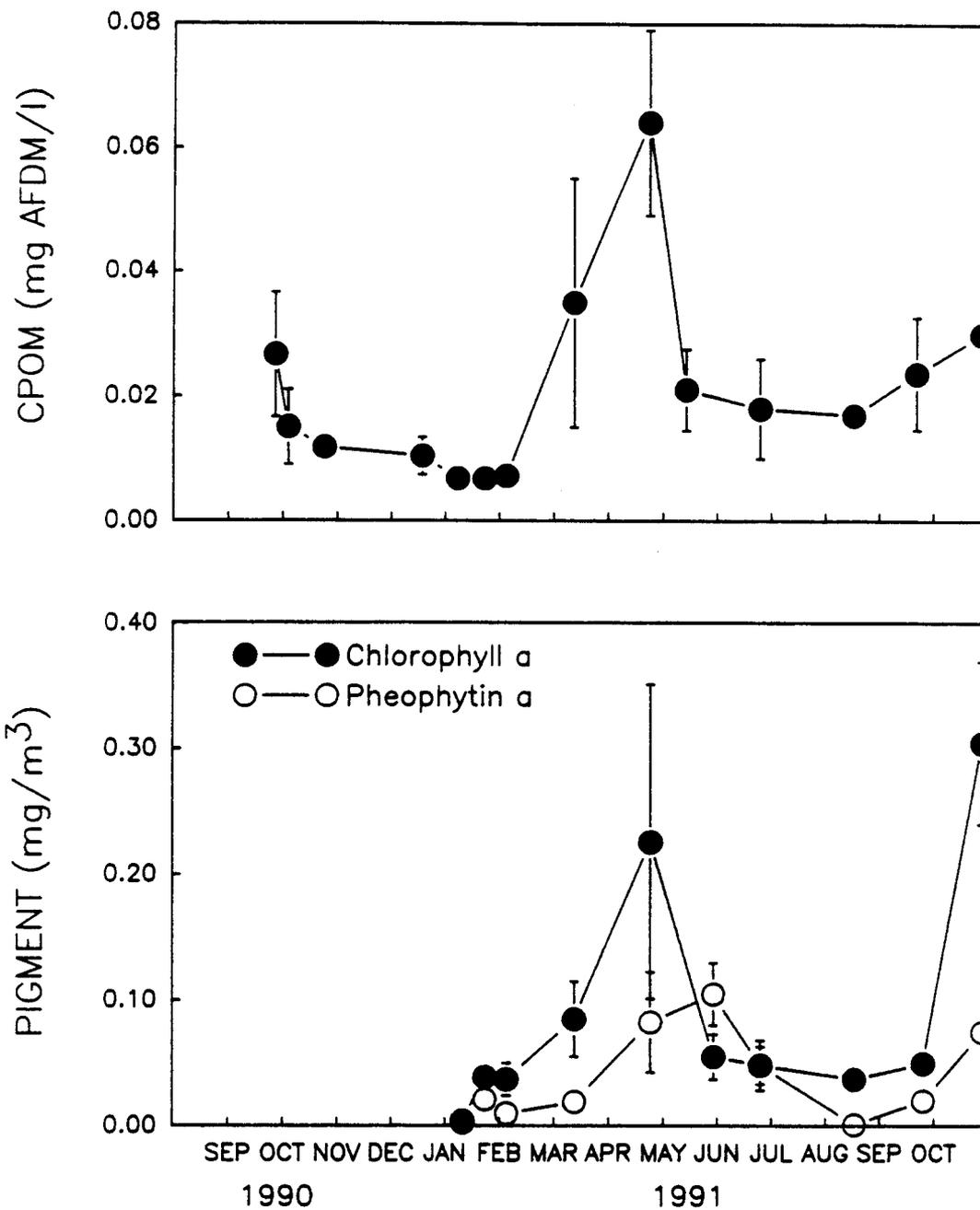


FIGURE 2.7--Variation among sample dates in CPOM and CPOM chlorophyll *a* and pheophytin *a* concentration. Means (\pm SE) are pooled across time of day. Plant pigments were not determined for CPOM collected before January 1991.

CPOM chlorophyll *a* and pheophytin *a* concentrations did not vary significantly over the diel period (Figure 2.6; chlorophyll *a*: $F_{3,34}=0.59$, $P=0.62$; pheophytin *a*: $F_{3,34}=0.16$, $P=0.92$), but the trend was similar to CPOM with concentration maxima and minima at 1600 and 0400 h, respectively. CPOM pigment concentrations varied among sample dates (Figure 2.7; chlorophyll *a*: $F_{9,28}=4.31$, $P<0.01$; pheophytin *a*: $F_{9,28}=4.76$, $P<0.01$). Mean daily CPOM and CPOM chlorophyll *a* were rank correlated ($r_s = 0.90$, $P<0.01$). As with CPOM, there were spring and autumn peaks in mean daily concentration of CPOM plant pigment: chlorophyll *a* concentration was higher in October 1991 than all other samples except March and April 1991; pheophytin *a* concentration was higher in May 1991 than in winter 1991 or late summer 1991.

The mean (\pm SE) percentage of carbon in CPOM was slightly higher in CPOM collected at 0400 (36 ± 1.23) than in CPOM collected at 1600 (33 ± 1.24 ; paired- $t=1.77$, $P=0.10$, $n=13$). There was no effect of time day on C:N ratio (Figure 2.8; 13.4 ± 2.83 , paired- $t=0.63$, $P=0.54$, $n=12$), on the mean percentage of nitrogen (2.6 ± 0.7 , paired- $t=0.16$, $P=0.88$, $n=12$), or on the mean percentage of phosphorus (0.07 ± 0.01 , paired- $t=0.93$, $P=0.37$, $n=12$) in CPOM. Sample size is small, but CPOM quality was higher (lower C:N, higher percentage nitrogen and phosphorus) at 0400 h than at 1600 h on most sample dates.

Mean concentration of FPOM did not vary significantly over the diel period at Lee's Ferry ($F_{3,39}=0.60$, $P=0.62$) or at Glen Canyon Dam ($F_{3,39}=0.23$, $P=0.88$). At Lee's Ferry, there was a trend toward maxima and minima at 1600 and 0400 h, respectively (Figure 2.9), as seen for CPOM. Mean concentration of FPOM at Lee's Ferry (0.58 mg AFDM/l) was not different from the mean concentration in Glen Canyon Dam (0.55 mg AFDM/l; $F_{1,102}=0.25$, $P=0.62$). The interaction of site and season was significant ($F_{3,102}=5.97$; $P<0.01$): the mean concentration of FPOM was higher at Lee's Ferry only in spring.

FPOM concentration varied among sample dates at Lee's Ferry (Figure 2.10, $F_{13,42}=2.76$, $P<0.01$) and at Glen Canyon Dam ($F_{13,41}=4.97$, $P<0.01$). At Lee's Ferry, mean daily FPOM concentration was higher in March (0.84 mg AFDM/l) and April (0.91 mg AFDM/l) 1991 than in October 1990 (<0.45 mg AFDM/l) and August and September 1991 samples (<0.4 mg AFDM/l). At Glen Canyon Dam, there was no spring 1991 maximum in FPOM concentration.

Chlorophyll *a* was not detected in FPOM samples collected after April 1991 (Figure 2.11). For previous dates (Figure 2.9), the effect of time of day was not significant at Lee's Ferry ($F_{3,13}=0.94$, $P=0.45$) or at Glen Canyon Dam ($F_{3,12}=0.07$, $P=0.49$). The diel pattern

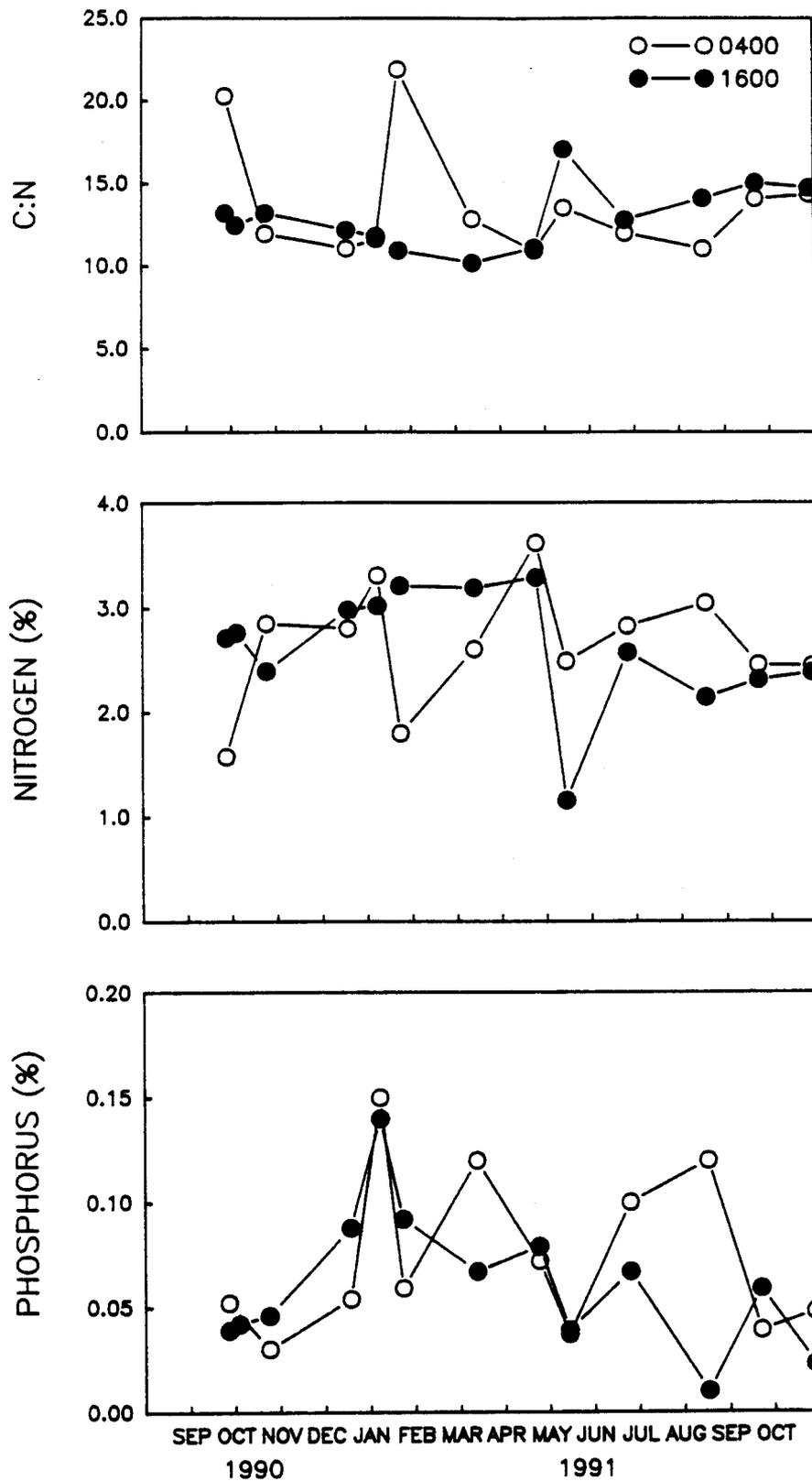


FIGURE 2.8--Variation among sample dates in nutrient content of CPOM collected at 0400 and 1600 h.

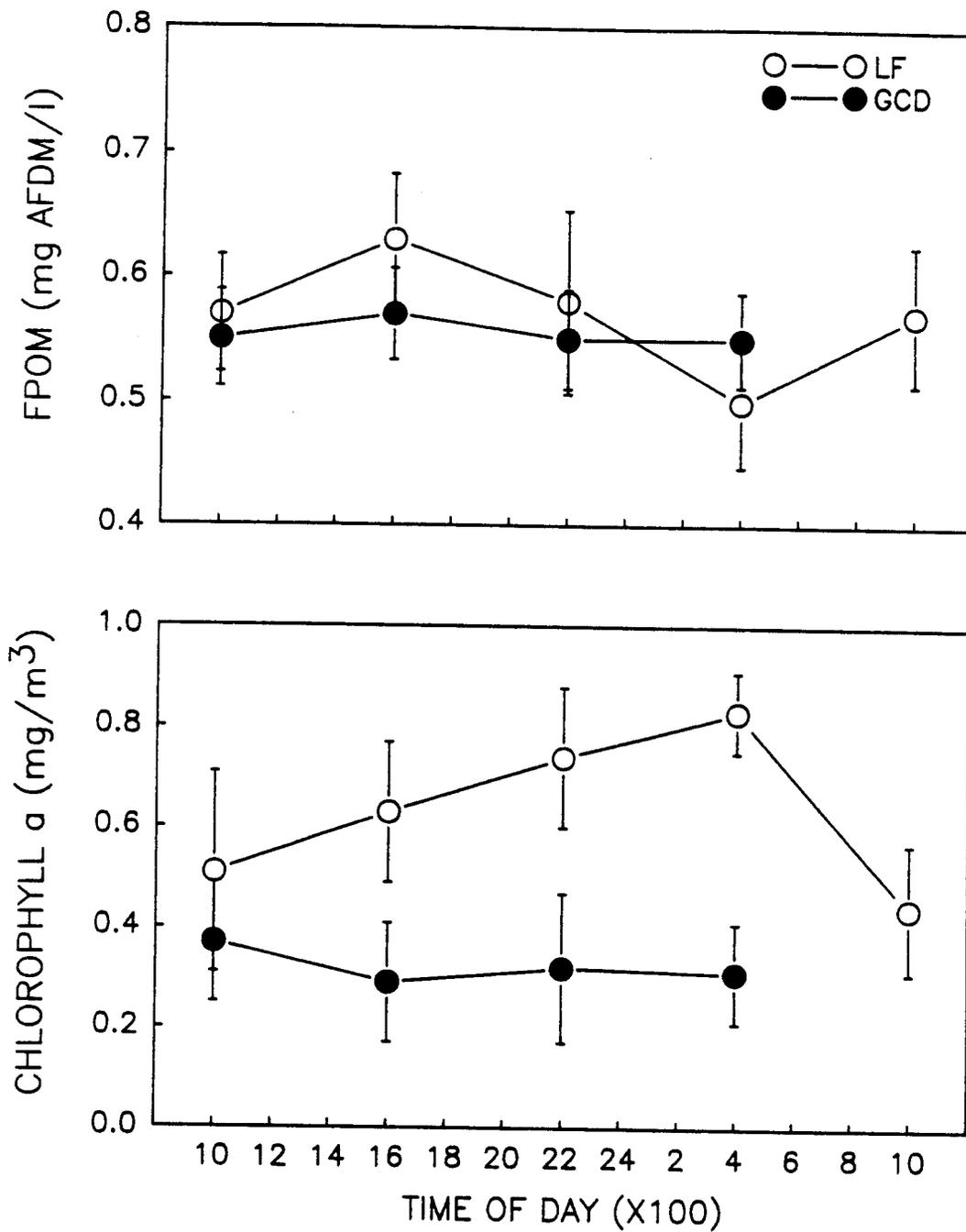


FIGURE 2.9--Diel variation in FPOM and FPOM chlorophyll *a* concentration at Lee's Ferry (LF) and Glen Canyon Dam (GCD). Means (\pm SE) are pooled across sample dates. Chlorophyll *a* values are means for dates on which FPOM chlorophyll *a* was detected.

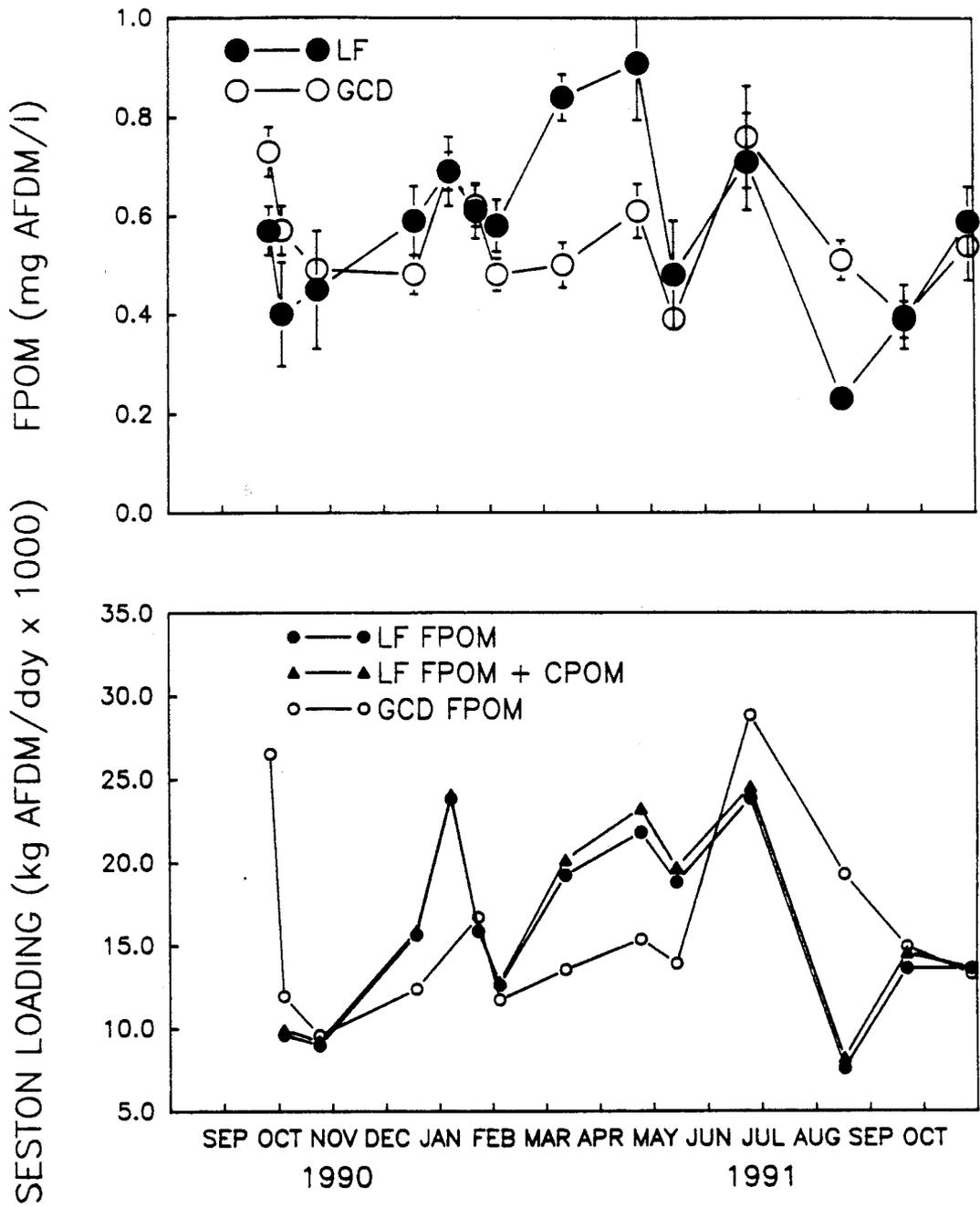


FIGURE 2.10--Variation in FPOM concentration and seston loading at Lee's Ferry (LF) and Glen Canyon Dam (GCD). Means (\pm SE) are pooled across time of day. Loading is based on flow-weighted mean seston concentration.

in FPOM Chlorophyll *a* concentration at Lee's Ferry was unlike that of FPOM concentration; chlorophyll *a* concentration increased to a maximum at 0400 h. Mean chlorophyll *a* concentration was higher at Lee's Ferry (0.70 mg/m³, January-April 1991) than at Glen Canyon Dam (0.32 mg/m³; $F_{1,31}=17.4$, $P<0.01$). Pheophytin *a* was detected on all dates, and did not vary with time of day at Lee's Ferry ($F_{3,33}=0.1$, $P=0.96$) or at Glen Canyon Dam ($F_{3,33}=0.1$, $P=0.96$). There was no effect of site on mean concentration of pheophytin *a* concentration ($F_{1,75}=0.61$, $P=0.44$).

FPOM chlorophyll *a* concentration at Lee's Ferry varied among dates ($F_{9,27}=48.7$, $P<0.01$). For dates when chlorophyll was detected in FPOM from Lee's Ferry, the concentration was lower in (late) January and February 1991 than at other times (Figure 2.11). The effect of date on FPOM chlorophyll *a* at Glen Canyon Dam was also significant ($F_{9,30}=28.27$, $P<0.01$); the chlorophyll *a* concentration was higher in winter than in spring. FPOM pheophytin concentration varied among dates at Lee's Ferry ($F_{3,27}=12.74$, $P<0.01$) and at Glen Canyon Dam ($F_{9,30}=26.73$, $P<0.01$). At both sites there were maxima in late spring-summer and in autumn; concentration was lowest in winter at both sites. Overall, chlorophyll *a* and pheophytin *a* were inversely rank correlated at Lee's Ferry ($r_s=-0.84$) and at Glen Canyon Dam ($r_s=-0.76$).

The pattern of seston loading was similar to concentration (Figure 2.10). There was no difference between Lee's Ferry and Glen Canyon Dam in mean flow-weighted seston concentration (LF: 0.59 ± 0.06 mg AFDM/l; GCD: 0.53 ± 0.3 mg AFDM/l; paired- $t=-1.18$, $P=0.26$, $n=12$) or in daily seston load (LF: $15,700\pm 1548$ kg AFDM/day; GCD: $15,100\pm 1450$ kg AFDM/day; paired- $t=0.4$, $P=0.7$, $n=12$). Loading was generally higher at Lee's Ferry in winter and spring and was higher at Glen Canyon Dam in summer and autumn. The effect of CPOM on total loading at Lee's Ferry was small.

Nutrient concentrations were not significantly different between Lee's Ferry and Glen Canyon Dam for any of the parameters (paired- t test, $P>0.05$; Table 2.1). Mean total inorganic nitrogen (TIN) values (0.33 mg/l) were similar to those reported previously for Glen Canyon (Maddux et al. 1987). Mean total PO₄ (0.006 mg/l) was less than reported by (Maddux et al. 1987), but our estimate is biased by a large number of samples with concentrations below detection limits. The ratio of TIN:orthophosphate was high (>80) suggesting that phosphorus is more likely to be potentially limiting to algal growth than nitrogen (Skulberg 1982, Grimm and Fisher 1986). Our observations (Angradi et al., unpublished m.s), and those of others (e.g., Pinney 1991) indicate that standing biomass of

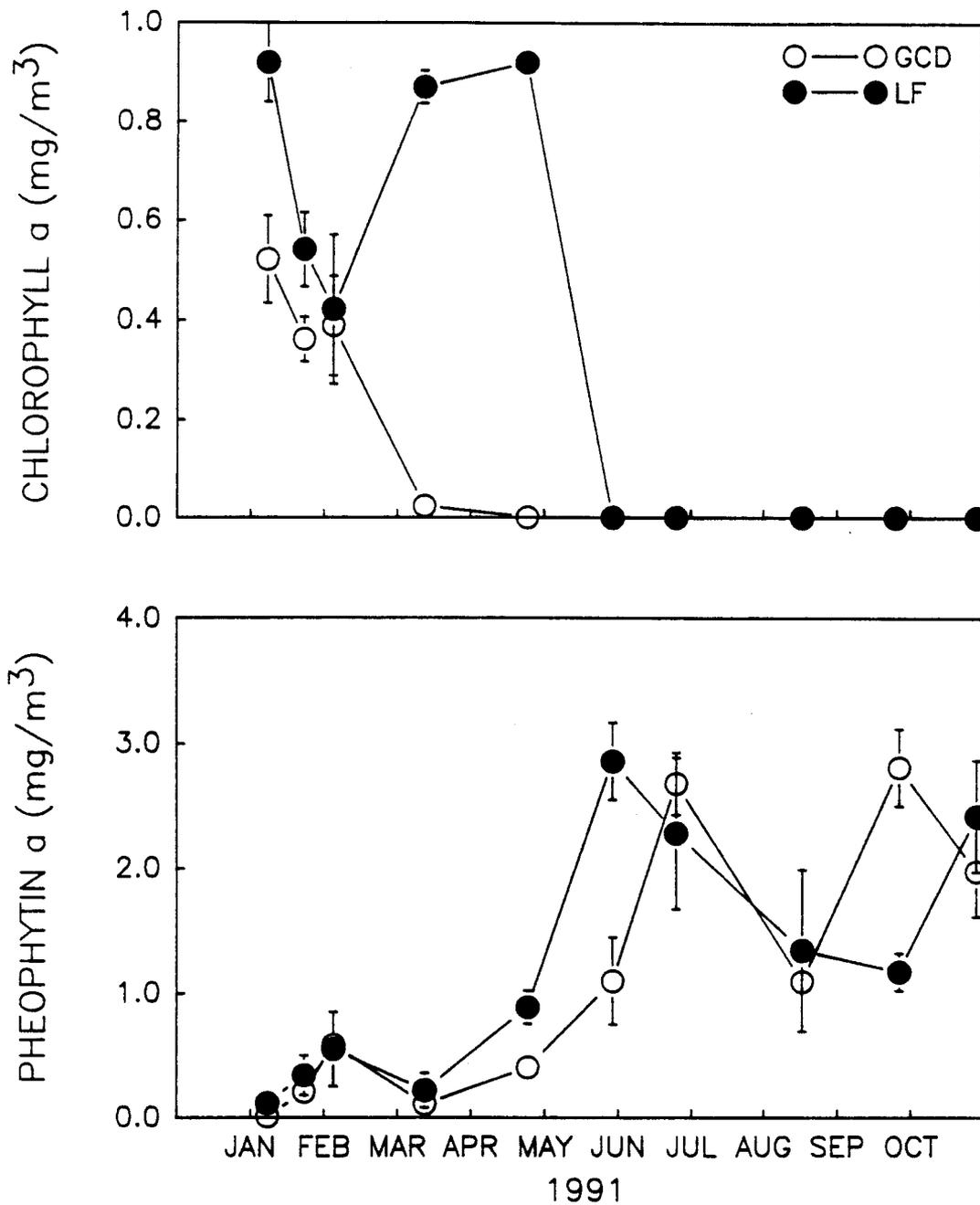


FIGURE 2.11--FPOM chlorophyll *a* and pheophytin *a* concentration at Glen Canyon Dam (GCD) and Lee's Ferry (LF). Means (\pm SE) are pooled across time of day.

TABLE 2.1.--Concentration (mg/l) of nutrients at Lee's Ferry (LF) and Glen Canyon Dam (GCD). Means are pooled across samples on each date (n = 4). Values in original data set that were below detectable limits (DL) were replaced with DL/2. Detection limits for phosphorus were reduced from 0.01 to 0.001 in 1991. COD, chemical oxygen demand; DON, dissolved organic nitrogen; TON, total organic nitrogen; TIN, total inorganic nitrogen; DOC, dissolved organic carbon; nd, no data.

Date	DON (0.2)		TON (0.2)		TIN (0.2)		NH ₄ (0.01)		NO ₂ + NO ₃ (0.01)	
	GCD	LF	GCD	LF	GCD	LF	GCD	LF	GCD	LF
072590	nd	nd	nd	nd	nd	nd	nd	nd	0.30	0.30
092790	nd	nd	nd	nd	nd	nd	nd	nd	0.31	0.29
092790	nd	nd	0.43	0.26	0.39	0.33	0.03	0.005	0.36	0.32
100390	nd	nd	0.47	0.26	0.31	0.36	0.005	0.063	0.30	0.30
102390	nd	nd	0.33	0.34	0.33	0.31	0.018	0.01	0.31	0.30
121790	0.12	0.08	0.32	0.26	0.31	0.32	0.098	0.017	0.30	0.30
100791	0.12	0.17	0.39	0.29	0.17	0.18	0.009	0.01	0.16	0.17
012291	0.20	0.22	0.27	0.42	0.16	0.16	0.004	0.001	0.16	0.16
022491	0.47	0.42	0.42	0.42	0.26	0.24	0.051	0.028	0.21	0.21
031191	0.14	0.11	0.19	0.11	0.43	0.41	0.013	0.019	0.42	0.39
042391	0.21	0.16	0.28	0.36	0.46	0.42	0.016	0.015	0.45	0.41
052891	0.29	0.26	0.44	0.51	0.40	0.39	0.014	0.018	0.38	0.37
062491	0.14	0.14	0.24	0.21	0.37	0.38	0.013	0.013	0.36	0.27
Mean	0.21	0.19	0.34	0.31	0.33	0.32	0.016	0.018	0.31	0.30

TABLE 2.1---Continued

Date	Total PO ₄ (0.01,0.001)		Ortho PO ₄ (0.01,0.001)		DOC		TOC		COD		Silica	
	GCD	LF	GCD	LF	GCD	LF	GCD	LF	GCD	LF	GCD	LF
072590	0.008	0.004	0.005	0.005	nd	nd	nd	nd	14.4	10.7	8.4	8.3
092790	0.005	0.005	0.005	0.005	nd	nd	nd	nd	9.6	11.4	8.5	8.2
092790	0.023	0.014	0.005	0.015	nd	nd	nd	nd	13.0	14.0	8.6	8.1
100390	0.005	0.009	0.006	0.005	nd	nd	nd	nd	9.5	13.0	8.3	8.1
102390	0.006	0.005	0.008	0.005	nd	nd	nd	nd	14.8	13.5	8.4	8.1
121790	0.005	0.003	0.001	0.001	nd	nd	nd	nd	8.5	5.0	8.5	8.4
100791	0.009	0.012	0.0005	0.0006	nd	nd	nd	nd	5.0	5.0	7.8	7.8
012291	0.005	0.003	0.002	0.001	nd	nd	nd	nd	5.0	5.0	7.7	7.7
020491	0.005	0.004	0.001	0.001	nd	nd	nd	nd	10.8	12.0	7.8	7.7
031191	0.002	0.002	0.003	0.01	3.03	3.03	3.13	2.88	5.0	5.0	8.2	7.7
042391	0.003	0.001	0.004	0.003	3.00	2.95	2.93	3.43	nd	nd	7.8	7.7
052891	0.003	0.005	0.0005	0.0006	2.70	3.05	2.70	2.95	nd	nd	7.7	7.8
062491	0.003	0.009	0.0006	0.002	nd	nd	nd	nd	nd	nd	7.5	7.5
Mean	0.006	0.006	0.003	0.004	2.91	3.01	2.92	3.08	9.6	9.5	8.1	7.9

periphyton is much greater immediately below Glen Canyon Dam than at Lee's Ferry. Algal uptake of phosphorus in Glen Canyon may be limit downstream productivity.

Water temperature at Glen Canyon Dam was nearly constant at 8 °C during much of the study (Figure 2.12). There is some evidence that water temperature at the dam rises rather sharply in autumn as thermal convection warms the lake to increasing depths prior to maximum mixing. Daily temperature variation at Lee's Ferry was greatest in the June sample (3 °C).

Periphyton Exposure

Fresh periphyton from the two zones (6,500-5,000 cfs = >5,000 cfs, and <5,000 cfs) differed dramatically in appearance. Periphyton from the shallower (>5,000 cfs) zone was bright green. Filaments were long, coarse to the touch, and free of visible epiphytes. Periphyton from the deeper zone (<5,000 cfs) was dark brownish-green. Filaments were shorter, slimy to the touch, and much of the outermost biomass was not filamentous, indicating heavy epiphyte colonization. Chlorophyll *a*:biomass ratio was higher (≥ 3 mg/g AFDM) in periphyton from the deeper zone than in periphyton from the shallower zone (≤ 2.0 mg/g AFDM).

Exposed periphyton was quickly bleached in experiment I. Bleached periphyton from the two zones differed in appearance. Periphyton from <5,000 cfs turned nearly white following exposure. Periphyton from >5,000 cfs turned brown, but many underlying filaments remained green. The ratio of chlorophyll *a*:*b* before the experiment was higher in periphyton from <5,000 cfs confirming a higher epiphyte load on algae from the deeper zone ($F_{1,8}=6.02$, $P<0.05$; Figure 2.13). The interaction of depth and time exposed was significant ($F_{5,40}=4.34$, $P<0.01$) indicating that the effect of depth decreased with time during the experiment, which suggests that chlorophyll *a* in epiphytes decomposed faster than chlorophyll *a* in the host *Cladophora*.

The mean percentage of the original chlorophyll remaining after exposure in experiment I was higher for periphyton from the >5,000 cfs zone ($F_{1,8}=6.54$, $P<0.05$), but the effect of depth did not interact with time exposed ($F_{5,40}=1.26$, $P=3.01$; Figure 2.13). This indicates that the resistance to chlorophyll decomposition (the coefficient *k*, Table 2.2) of periphyton from >5,000 cfs was equal to periphyton from <5,000 cfs, and that the amount of chlorophyll *a* remaining at the end of the experiment depended on the initial amount. Chlorophyll *a* in periphyton from >5,000 cfs decreased less immediately following

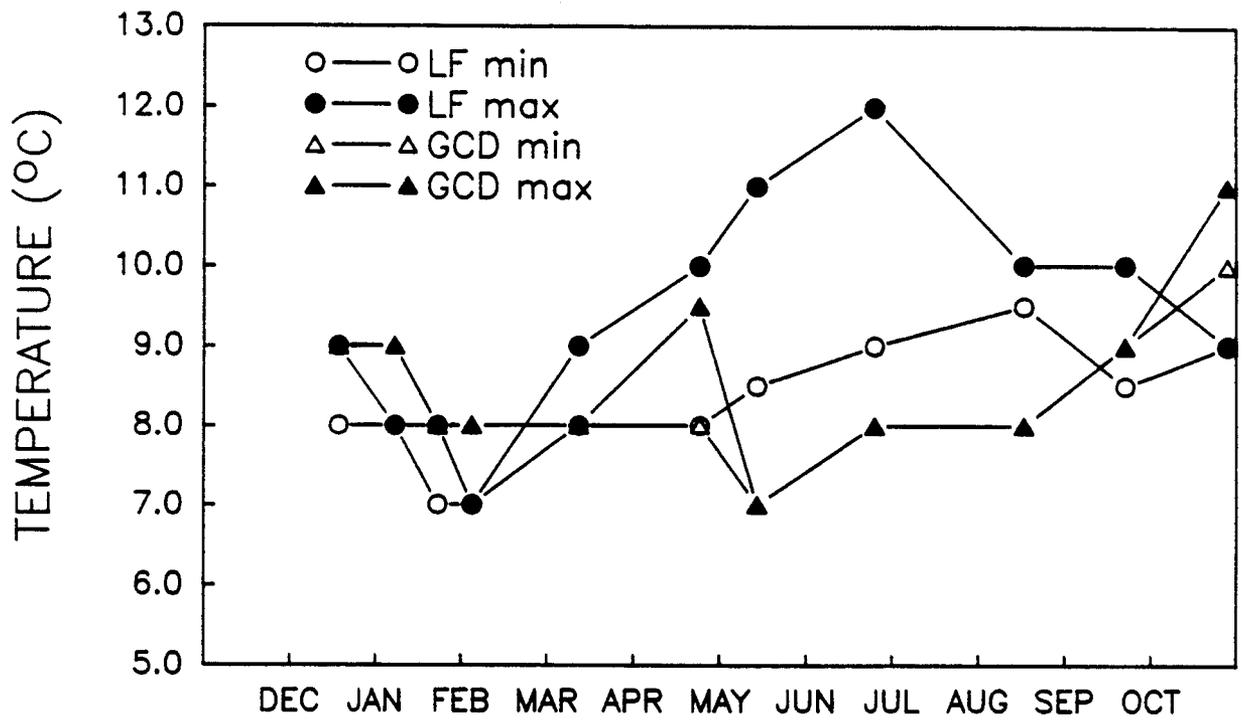


FIGURE 2.12--Water temperature on 1990-1991 sample dates at Lee's Ferry (LF) and Glen Canyon Dam (GCD).

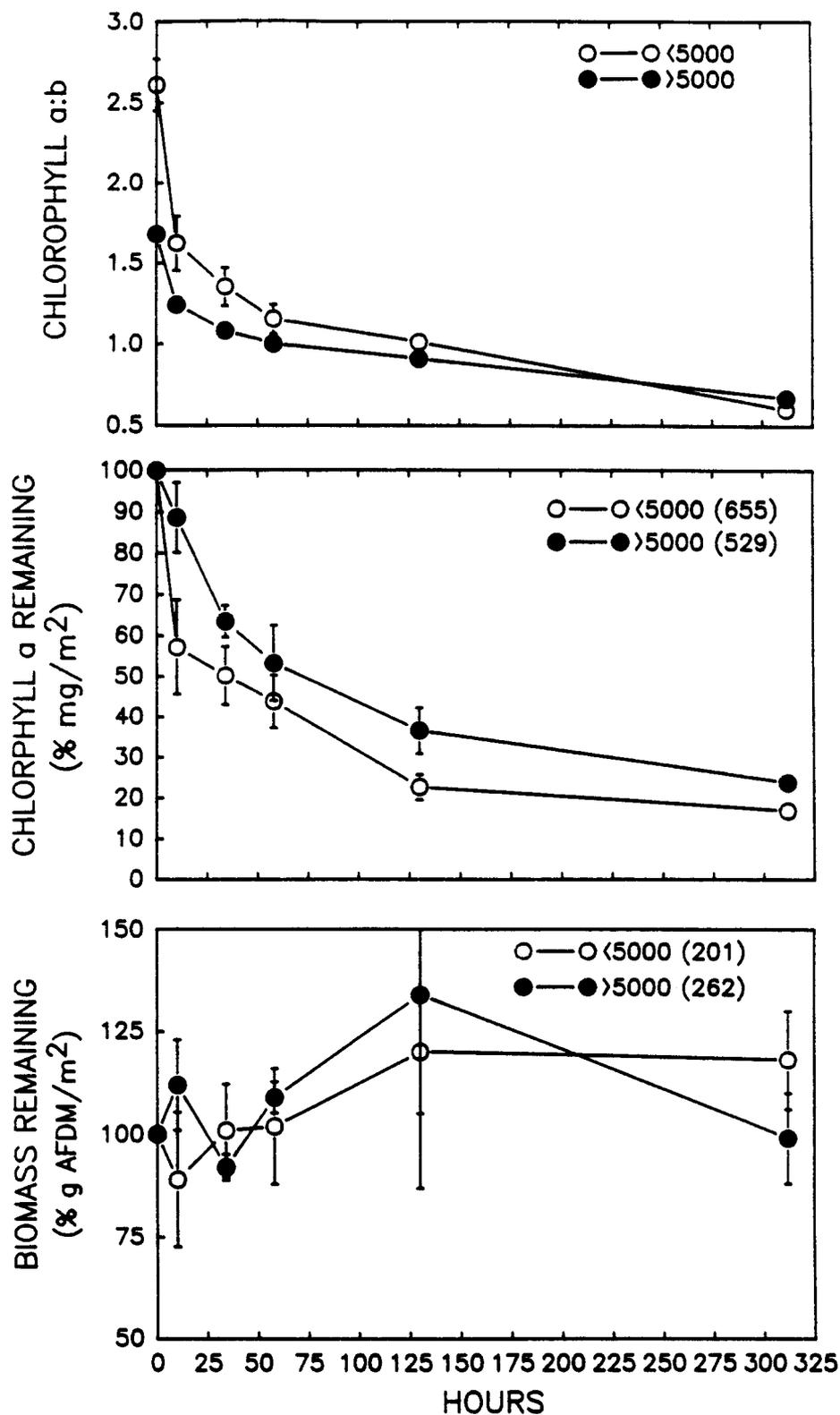


FIGURE 2.13--Effect of exposure time on periphyton parameters in exposure experiment I. Error bars are 1 SE of the mean (n=5). Open and closed symbols denote periphyton collected from above and below the 5000 cfs at -14 mile bar, respectively. Initial chlorophyll *a* and biomass values are in parentheses.

TABLE 2.2.--Rate of chlorophyll *a* decay in periphyton following exposure. The dependent variable is \log_{10} -transformed percent of original chlorophyll *a* (mg/m^2) remaining. Unit of time is hours; unit of PAR is moles/m^2 . The rate coefficient is k . In experiment II, only measurements through 168 h are included in the models, and data are pooled across exposure treatments, excluding controls.

	Level (cfs)	Independent Variable	Constant	k	SE	r^2	n
Experiment I	< 5000	Time	1.79	-0.002	0.0003	0.63	30
		PAR	1.79	-0.001	0.0002	0.61	30
	> 5000	Time	1.90	-0.002	0.0002	0.61	30
Experiment II		PAR	1.89	-0.001	0.0001	0.61	30
	< 5000	Time	1.86	-0.003	0.0005	0.64	24
	> 5000	Time	1.90	-0.002	0.0004	0.61	24

exposure, but then caught up with the other depth treatment suggesting that effects of periphyton structure on exposure tolerance may only be detected for moderate disturbances.

As expected (because there was no physical removal agent), periphyton biomass did not change during the experiment ($F_{5,40}=0.95$, $P=0.46$, Figure 2.13). Mean biomass of periphyton from $>5,000$ cfs (275 g AFDM/m²) was higher than from $<5,000$ cfs (205 g AFDM/m²; $F_{1,8}=7.09$, $P<0.05$).

Mean Chlorophyll *a* of periphyton attached to cobbles decreased with time and cumulative PAR throughout experiment I (Table 2.2). The decrease in parameters was negative exponential (Figure 2.13); chlorophyll *a* and the ratio chlorophyll *a*:*b* decreased most rapidly immediately following exposure. Models were similar for both time exposed and cumulative PAR.

In experiment II, all exposed periphyton turned brown within two days of reinundation. Exposed periphyton had a lower chlorophyll *a*:*b* ratio ($F_{2,18}=43.80$, $P<0.01$) than controls indicating that in exposed periphyton chlorophyll *a* decreased faster than chlorophyll *b* (Figure 2.14). The ratio following exposure was lower for periphyton exposed for 48 h than for periphyton exposed for 24 h ($F_{1,12}=5.22$, $P<0.05$), and the effect was independent of depth ($F_{1,12}=1.11$, $P=0.31$). The ratio following exposure differed between depths for the exposed periphyton ($F_{1,12}=52.97$, $P<0.01$), and the interaction of depth and time was significant ($F_{3,36}=7.09$, $P<0.01$): the *a*:*b* ratio of periphyton from $<5,000$ cfs decreased faster, but only initially, than periphyton from $>5,000$ cfs (Figure 2.14).

Between 168 and 336 h the chlorophyll *a*:*b* ratio of periphyton on cobbles increased to controls levels (Figure 2.14). Colonization of the sandstone tiles by the chlorophyte *Ulothrix tenkissima* (D. Blinn, personal communication) was extremely rapid in the experiment (Figure 2.15). Accretion of chlorophyll *a* on tiles was fastest late in experiment II, which corresponds to the increase in the chlorophyll *a*:*b* ratio in the exposed periphyton. *Ulothrix* also was observed colonizing the periphyton in the exposed treatments (which appeared completely nonviable at this point). Fresh *Ulothrix* and *Cladophora* from the Colorado River have similar ratios of chlorophyll *a*:*b* (T. Angradi, unpublished data), and we conclude that the increase in this parameter late in the experiment resulted from *Ulothrix* colonization rather than from recovery of the original assemblage.

The percent of original periphyton chlorophyll *a* remaining (Figure 2.16) following exposure was lower in the exposed treatments than in the controls ($F_{2,18}=42.34$, $P<0.01$). There was a slight effect of depth on percent chlorophyll *a* remaining for the exposed treatments ($F_{1,12}=4.26$, $P=0.06$); the percent remaining was higher in periphyton from the

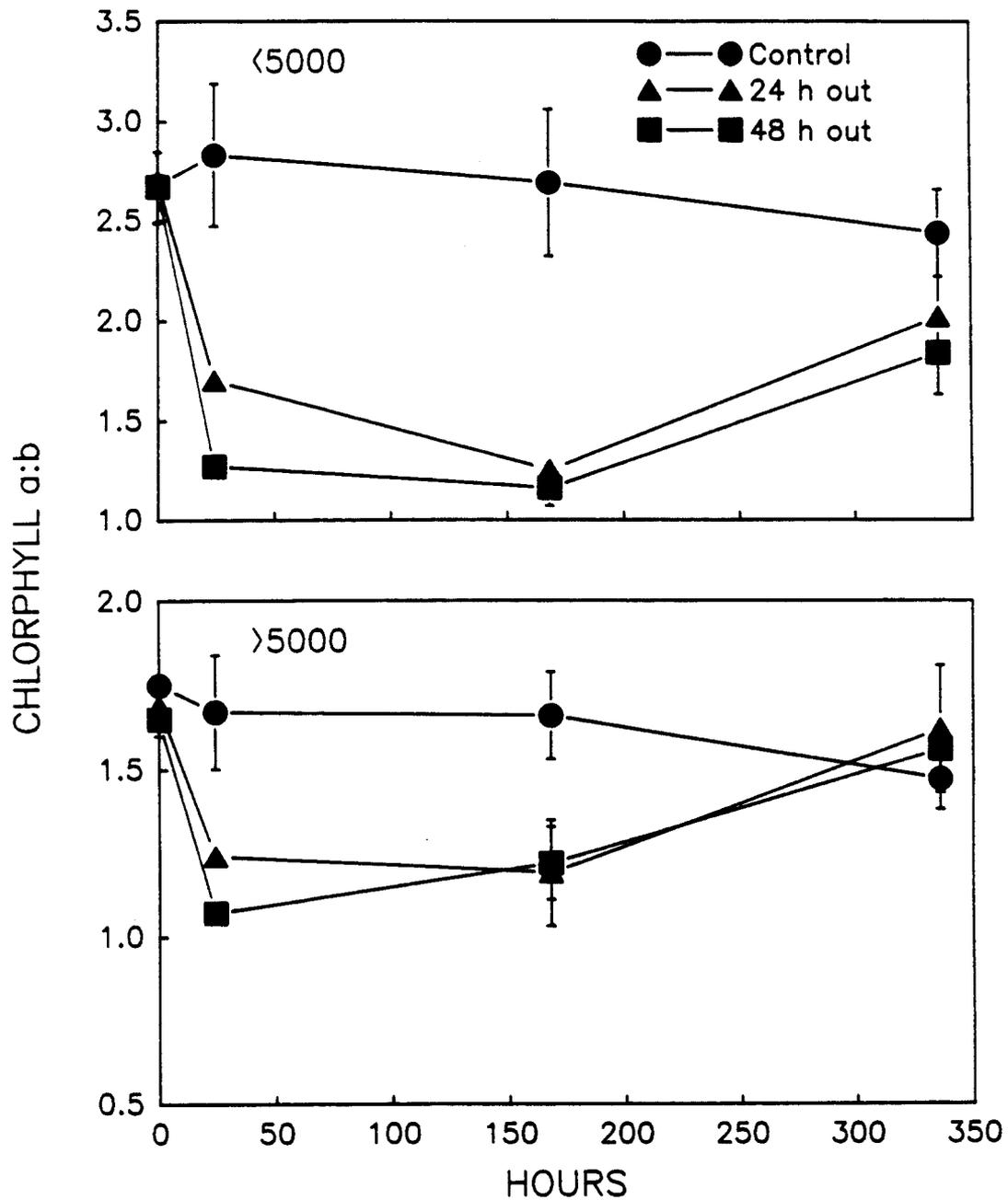


FIGURE 2.14--Effect of exposure time (symbols) and level (graphs) on the chlorophyll *a:b* ratio of periphyton with time reinundated in exposure experiment II. Error bars are 1 SE of the mean (n=4).

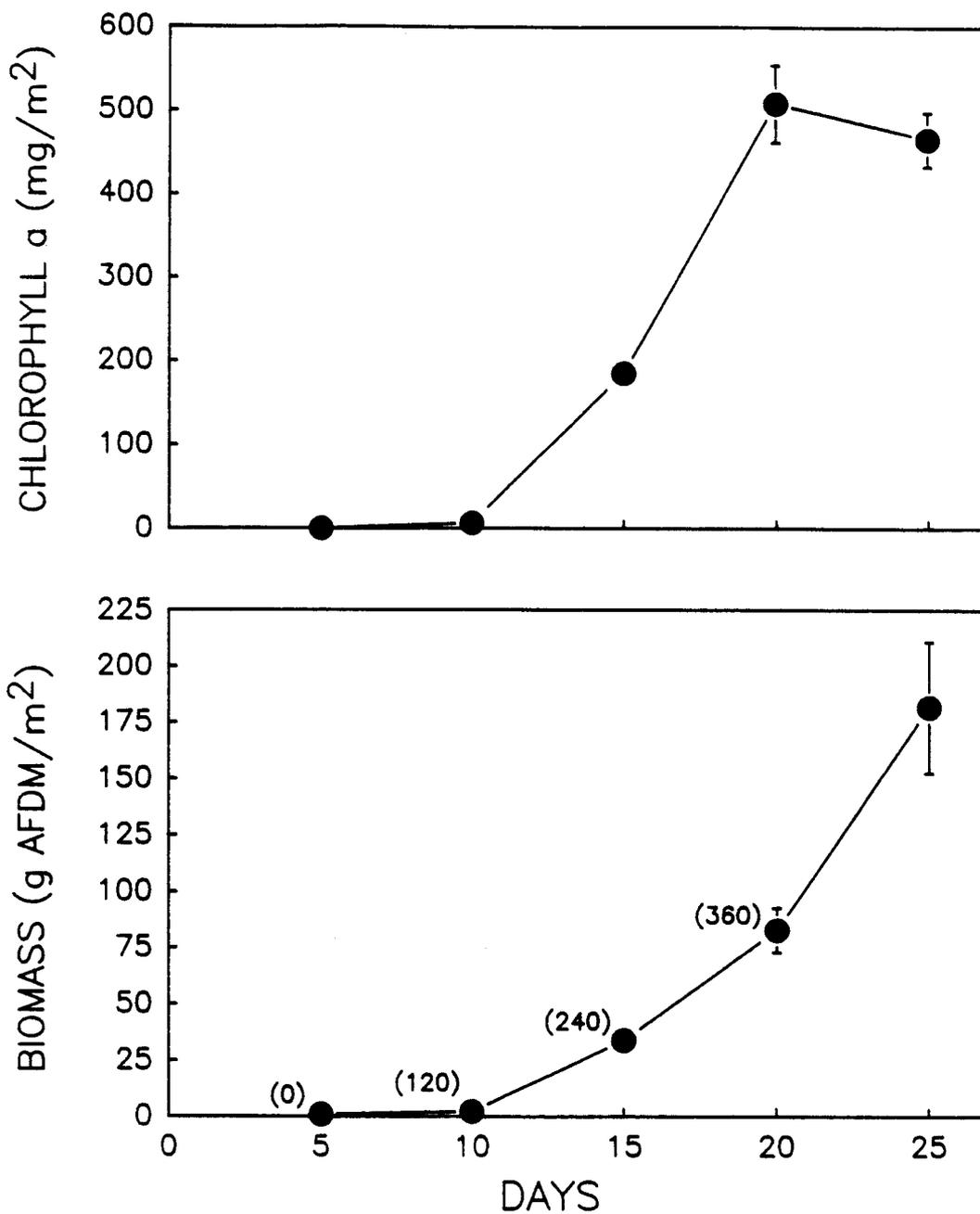


FIGURE 2.15—Accretion of chlorophyll *a* and biomass on sandstone tiles in the sluiceway. Error bars are 1 SE of the mean ($n > 5$). Values in parentheses correspond to time (h) reinundated in exposure experiment II. Least-squares regression through-the-origin models are, Log_{10} Chlorophyll $a = 0.12$ (days), $r^2 = 0.94$, $n = 39$, Log_{10} Biomass = 0.09 (days), $r^2 = 0.96$, $n = 39$.

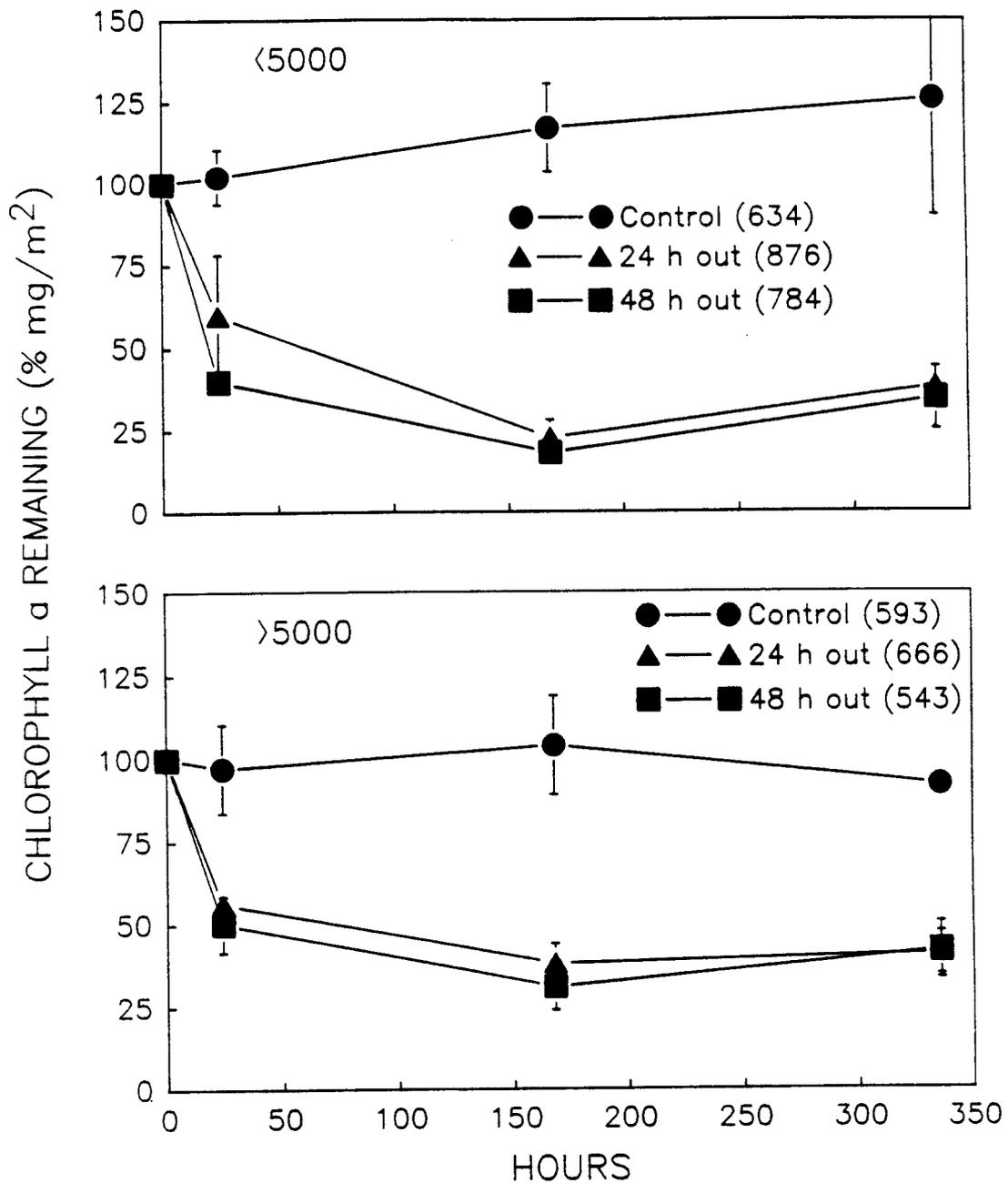


FIGURE 2.16--Effect of exposure time (symbols) and level (graphs) on percent of initial periphyton chlorophyll *a* remaining in exposure experiment II. Error bars are 1 SE of the mean (n=4). Values in parentheses are initial chlorophyll *a* values.

>5,000 cfs. The effect of exposure treatment was not significant ($F_{1,12}=2.15$, $P=0.17$). The slight increase in chlorophyll *a* late in the experiment in the exposed treatments was not detected in controls; we attribute this increase to *Ulothrix* colonization of dead *Cladophora* filaments.

Rate of chlorophyll decomposition (*k*) was higher in periphyton from <5,000 cfs (Table 2.2). Decomposition models derived from experiments I and II were very similar, suggesting that reinundation had little effect on the short-term (<2 weeks) trajectory of decomposition following exposure.

The percent of original periphyton biomass remaining following exposure (Figure 2.17) was lower in the exposed treatments than in the controls ($F_{2,18}=42.34$, $P<0.01$). There was no effect of depth ($F_{1,12}=0.53$, $P=0.48$) or time exposed ($F_{1,12}=0.24$, $P=0.63$) on percent biomass remaining in exposed periphyton. The interaction of depth and exposure was significant, however ($F_{1,12}=6.61$, $P<0.05$); the effect of time exposed was significant only for periphyton from >5,000 cfs, in which periphyton exposed for 48 h retained less biomass than periphyton exposed for 24 h (Figure 2.17).

Algal Colonization

Periphyton biomass and chlorophyll *a* on sandstone tiles at -10.5 and -13.5 mile bars increased with time *in situ* in spring 1991 (Figure 2.18 and 2.19; biomass: $F_{1,116}=41.03$; chlorophyll *a*: $F_{1,126}=61.68$, $P<0.01$). The effect of site was not significant for biomass ($F_{1,116}=3.09$, $P=0.08$) or for chlorophyll *a* ($F_{1,126}=1.02$, $P=0.32$). Periphyton biomass ($F_{4,116}=42.38$) and chlorophyll *a* ($F_{1,126}=109.80$) were higher at lower levels ($P<0.01$). Rates of biomass and chlorophyll *a* accretion at the <5,000 cfs (0.03-0.04/d) and 5,000 cfs levels (0.02/d) were similar at both sites (Table 2.3). Accretion was slight at the 11,000 and 13,000 cfs levels and was not significant at the 22,000 cfs level. There was a decrease in periphyton parameters between day 57 and 63 (before and after a two day, 5,000 cfs, controlled flow period).

Mean periphyton biomass on natural cobbles (autumn 1991) varied among dates at -13.5 mile bar ($F_{3,161}=2.59$, $P=0.05$), but not at -14 mile bar (Figure 2.20; $F_{3,192}=0.47$, $P=0.7$). Mean biomass in August at mile -14 (94 g AFDM/m²) was higher than in November (47 g AFDM/m²) (Tukey test, $P<0.05$). Mean biomass was higher at -14 mile bar (95 g AFDM/m₂) than at mile -13.5 (74 g AFDM/m₂) during the study ($F_{1,329}=17.87$, $P<0.01$). Periphyton biomass was significantly higher at lower levels at both sites (Figure 2.20). Biomass decreased after the August sample at all levels except 8000 cfs at -14 mile

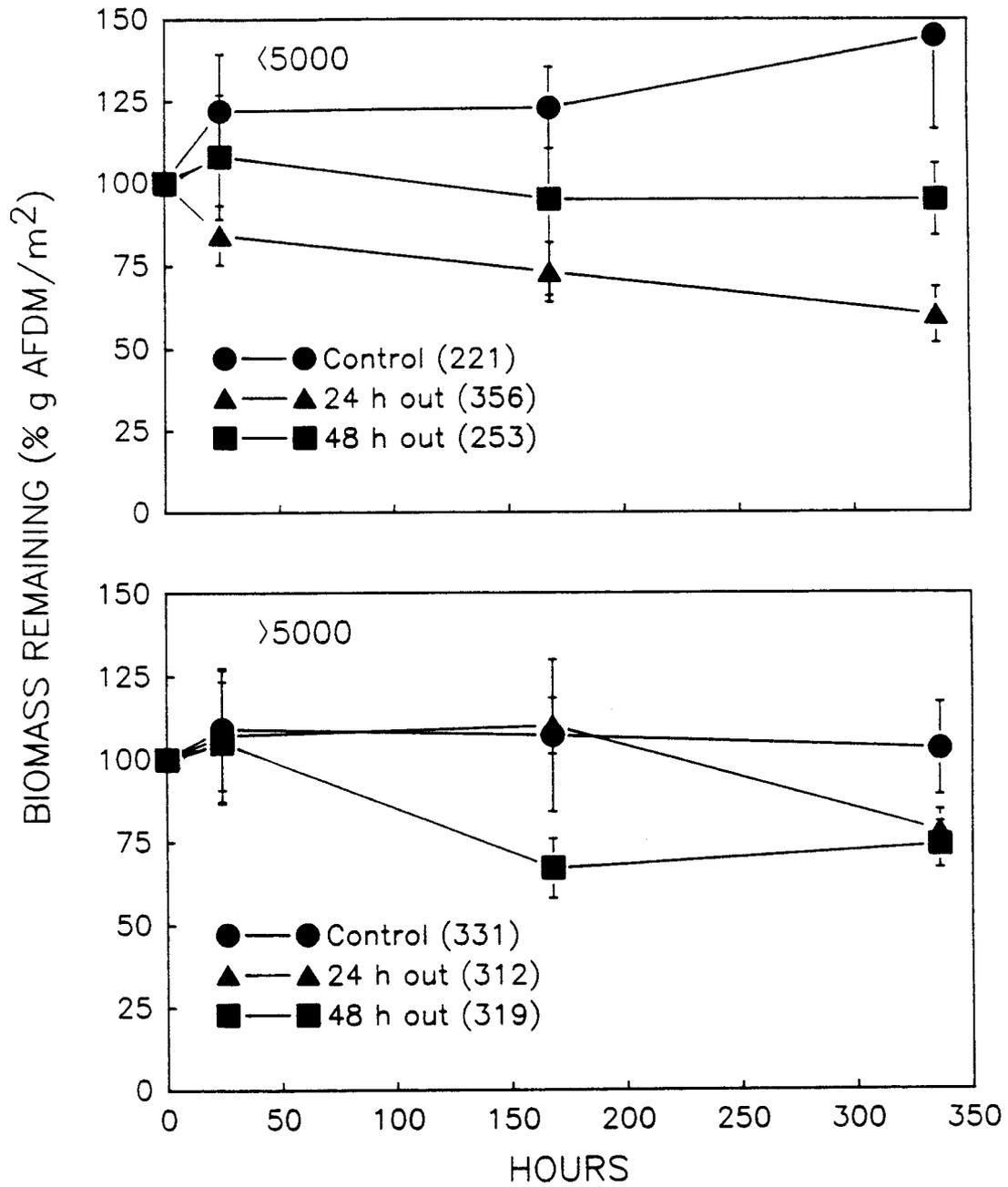


FIGURE 2.17--Effect of exposure time (symbols) and level (graphs) on percent of initial periphyton biomass remaining in exposure experiment II. Error bars are 1 SE of the mean (n=4). Values in parentheses are initial biomass values.

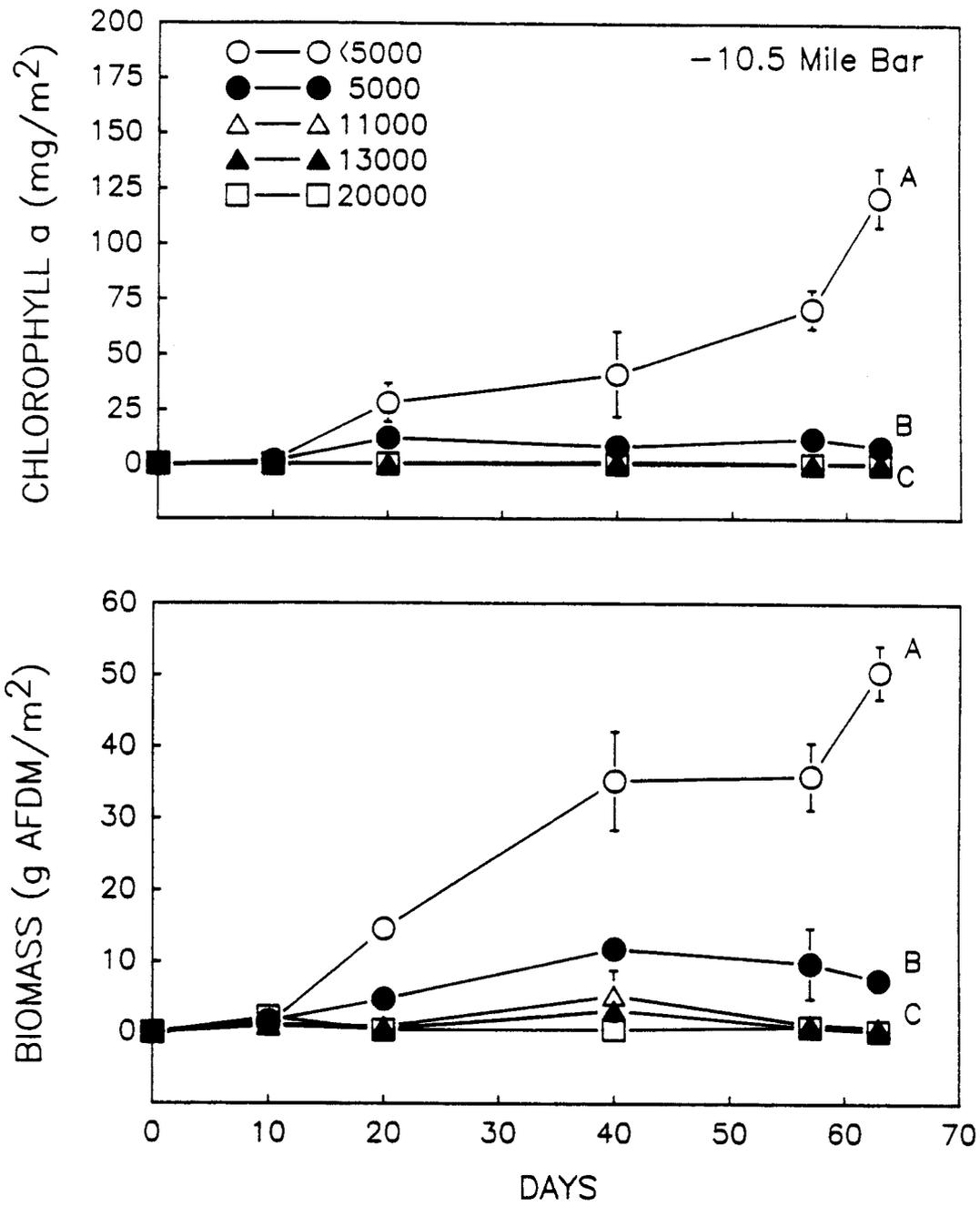


FIGURE 2.18--Accretion of chlorophyll *a* and biomass on sandstone tiles at five levels (symbols) in spring 1991 at -10.5 mile bar. Error bars are 1 SE of the mean ($n=3$). Letters to the right of lines indicate Tukey groups for means pooled across sample date.

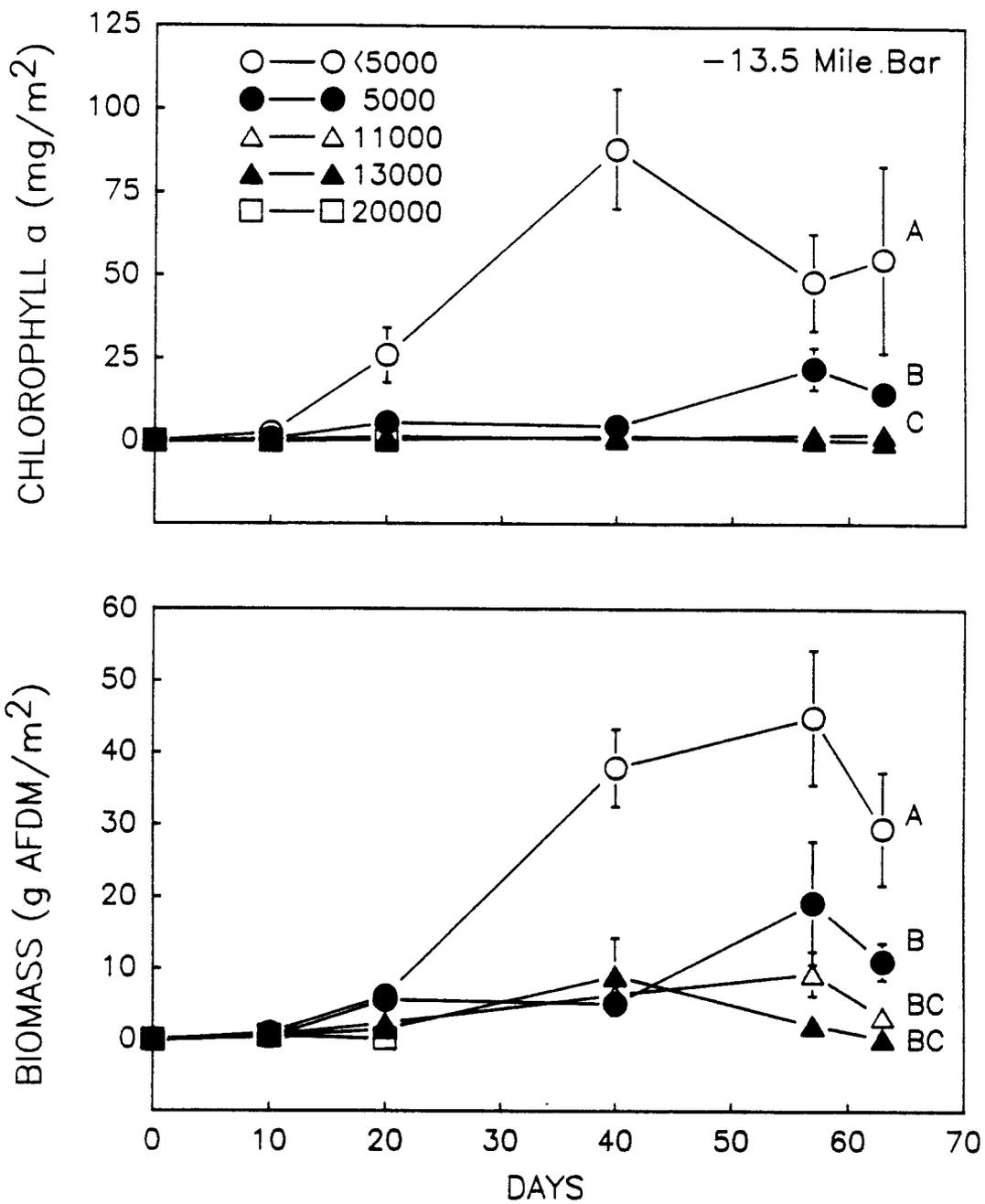


FIGURE 2.19--Accretion of chlorophyll *a* and biomass on sandstone tiles at five levels (symbols) in spring 1991 at -13.5 mile bar. Error bars are 1 SE of the mean (n=3). Letters to the right of lines indicate Tukey groups for means pooled across sample date.

TABLE 2.3.--Biomass and chlorophyll *a* accretion rates on sandstone tiles placed at five levels at two sites in Glen Canyon in spring 1991. Rates (*k*) are regression slopes (through the origin) of log₁₀-transformed biomass (g AFDM/m²) or chlorophyll (mg/m²) against time (days); ns, not significant.

Site (mile)		Level (cfs)				
		< 5,000	5,000	11,000	13,000	22,000
<i>Biomass</i>						
10.5	n	15	15	13	14	13
	<i>k</i>	0.030	0.018	0.007	0.006	0.003
	SE	0.002	0.002	0.002	0.002	0.001
	<i>r</i> ²	0.97	0.79	0.57	0.45	0.35
13.5	n	13	13	14	13	4
	<i>k</i>	0.029	0.02	0.015	0.010	0.005
	SE	0.002	0.002	0.002	0.003	0.003
	<i>r</i> ²	0.05	0.92	0.86	0.52	ns
<i>Chlorophyll a</i>						
10.5	n	15	14	14	14	15
	<i>k</i>	0.035	0.020	0.003	0.001	0.0004
	SE	0.002	0.003	0.001	0.0005	0.0004
	<i>r</i> ²	0.94	0.81	0.64	ns	ns
13.5	n	15	15	15	14	6
	<i>k</i>	0.033	0.021	0.007	0.003	0.002
	SE	0.003	0.002	0.002	0.001	0.001
	<i>r</i> ²	0.88	0.91	0.84	0.40	ns

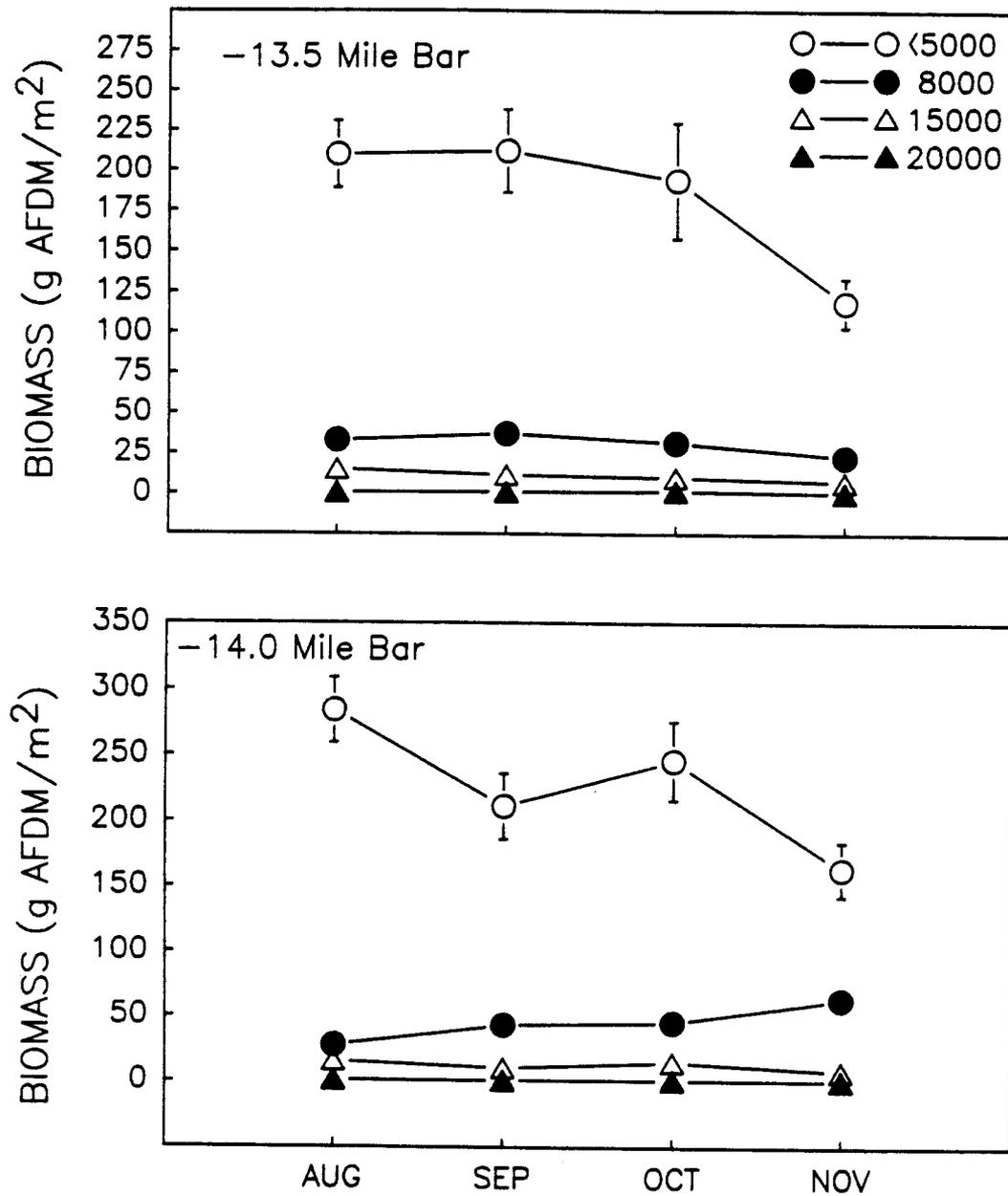


FIGURE 2.20--Accretion of biomass on natural cobbles at four levels (symbols) at -14 mile bar and -13.5 mile bar in autumn 1991. Error bars are 1 SE of the mean ($n > 10$). Letters to the right of lines indicate Tukey groups for means pooled across sample date.

bar (Table 2.4). Changes were slight in all cases ($<0.005/\text{day}$); accretion rate on natural cobbles at the 8,000 cfs level at -14 mile bar ($0.003/\text{day}$) was ca. four times lower than on sandstone tiles the previous spring (interpolated from Table 2.3).

TABLE 2.4.--Biomass accretion rates on natural cobbles at four levels at two sites in Glen Canyon in fall 1991. Rates (k) are regression slopes of log-transformed biomass (g AFDM/ m^2) against time (days since the first sample in August); ns, not significant.

Site (mile)		Level (cfs)			
		< 5,000	8,000	15,000	20,000
13.5	n	54	49	49	9
	k	-0.003	-0.001	-0.004	-0.0003
	SE	0.001	0.001	0.001	0.001
	r^2	0.160	0.05ns	0.340	0.01ns
14.0	n	64	63	52	13
	k	-0.002	0.003	-0.003	-0.0008
	SE	0.001	0.001	0.001	0.001
	r^2	0.150	0.260	0.210	0.150

Diel Feeding Chronology of Rainbow Trout

There was no effect of time of day on volume of trout stomach contents on any date (Figure 2.21; April 10-11: $F_{5,51}=1.72$, $P=0.15$; May 29-30: $F_{5,49}=0.32$, $P=0.90$; July 12-13: $F_{5,50}=0.072$, $P=0.99$). The covariate, fish length, was significant on all dates (April 10-11: $F_{5,51}=8.85$, $P<0.01$; May 29-30: $F_{5,49}=5.85$, $P<0.05$; July 12-13: $F_{5,50}=8.93$, $P=0.01$). Two trout with high stomach content volumes (>15 ml), one at 1930 and one at 2330 h on April 10, 1991, account for the apparent pattern on that date.

Mean stomach content volume varied among dates ($F_{2,168}=40.96$, $P<0.01$), with May 29-30 $>$ July 12-13 $>$ April 10-11 (Table 2.5). When everything except individual

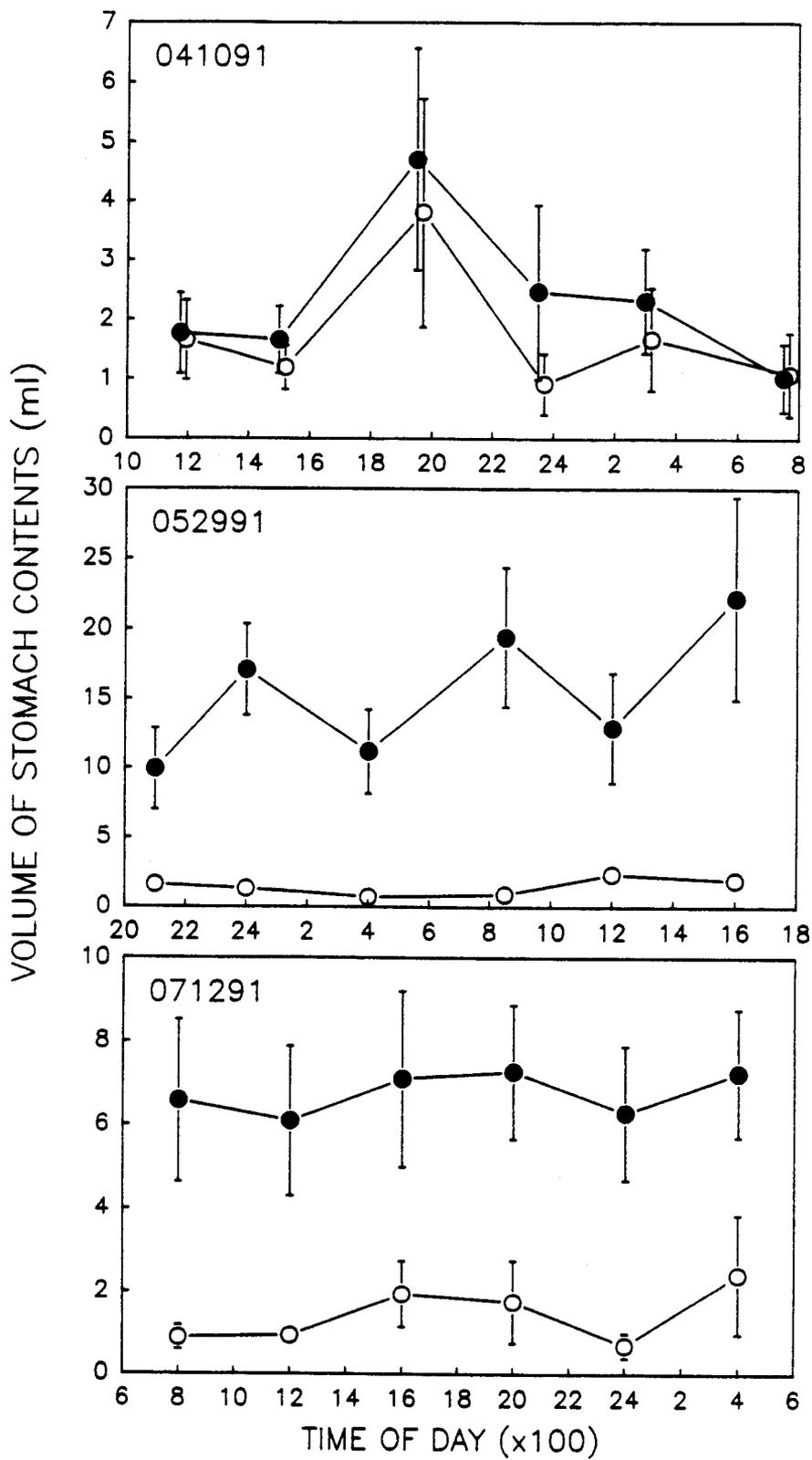


FIGURE 2.21--Diel variation in mean (\pm SE) volume of stomach contents of rainbow trout on three dates. Closed symbols indicate total volume of stomach contents; open symbols indicate volume of identifiable animals. Points for April 10-11, 1991 are offset for clarity.

TABLE 2.5.--Length, weight, and volume of stomach contents of rainbow trout collected in Glen Canyon diel feeding studies. Values are means \pm SE.

Date	Time	n	Length (mm)	Weight (g)	Gut contents
041091	1145	10	402 \pm 18	544 \pm 63	1.76 \pm 0.68
041091	1500	10	411 \pm 12	626 \pm 75	1.65 \pm 0.56
041091	1930	8	426 \pm 23	581 \pm 67	4.70 \pm 1.88
041091	2330	10	393 \pm 15	538 \pm 68	2.46 \pm 1.47
041191	0300	10	429 \pm 17	656 \pm 90	2.31 \pm 0.88
041191	0730	10	423 \pm 11	612 \pm 58	1.03 \pm 0.57
Mean		58	414 \pm 7	593 \pm 24	2.24 \pm 0.44
052991	2100	10	396 \pm 16	534 \pm 62	9.89 \pm 2.95
053091	0000	9	464 \pm 14	869 \pm 79	17.07 \pm 3.28
053091	0400	10	441 \pm 19	767 \pm 88	11.15 \pm 3.05
053091	0830	10	448 \pm 7	836 \pm 57	19.39 \pm 5.00
053091	1200	10	437 \pm 15	715 \pm 83	12.87 \pm 3.98
053091	1600	7	447 \pm 16	730 \pm 59	22.19 \pm 7.27
Mean		56	438 \pm 6	740 \pm 32	15.03 \pm 1.74
071291	0800	7	427 \pm 16	667 \pm 79	6.58 \pm 1.95
071291	1200	9	411 \pm 19	579 \pm 72	6.09 \pm 1.80
071291	1600	10	427 \pm 9	672 \pm 49	7.10 \pm 2.12
071291	2000	10	445 \pm 14	755 \pm 79	7.27 \pm 1.62
071391	0000	11	424 \pm 13	648 \pm 71	6.28 \pm 1.61
071391	0400	10	450 \pm 7	734 \pm 27	7.24 \pm 1.54
Mean		57	431 \pm 5	677 \pm 27	6.77 \pm 0.69

identifiable animal food items was omitted from the analysis, the effect of time of day was still not significant (Figure 2.22; April 10-11: $F_{5,47}=1.34$, $P=0.27$; May 29-30: $F_{5,47}=1.46$, $P=0.22$; July 12-13: $F_{5,49}=0.76$, $P=0.59$), nor did the mean volume vary among dates ($F_{2,161}=0.34$, $P=0.72$).

The composition of stomach contents varied dramatically between the April sample and the two later collections (Table 2.6). In April, chironomids were the most important item (59% of the total volume) in trout stomachs. On the other dates, *Cladophora* occupied the most volume (>75%) in the stomachs. On all dates, three taxa, Chironomidae, *Gammarus lacustris*, and Mollusca (snails) comprised 90-98% of the volume of identifiable animals. Fish eggs (mostly trout) were present in stomachs only in the April sample. There was no apparent diel pattern in the composition of stomach contents except perhaps that fewer chironomids were in the stomachs at 1145 h of the April sample than at other times on that date.

Density of drifting invertebrates was low ($<4/m^3$) and did not vary appreciably except in the April (regular spring flows) sample when a large number of chironomids were collected in the afternoon sample (Figure 2.22). On that date, 99% of the organisms captured were chironomids. In the May (15,000 cfs constant flows) and July (5,000 cfs constant flows) sample dates, only chironomids were collected. More *Cladophora* drifted during the day than at night (Figure 2.22), and the pattern was most pronounced in April.

Discussion

Lake Powell Forebay

In general, the circulation pattern in the forebay during our study agrees with what others have reported for the lower part of the reservoir (e.g., Gloss et al. 1980, Johnson and Merritt 1979, Merritt and Johnson 1977, Johnson and Page 1981, Stanford and Ward 1991), and will not be reviewed here.

Comparison of temperature at penstock depth (Figure 2.3, 2.23) and as sampled within the dam (Figure 2.12) indicate a rather close correlation. However, comparison of FPOM and FPOM chlorophyll at the two sites (Figures 2.1, 2.2, 2.10, 2.11) reveals an apparent anomaly. In December 1990, the FPOM concentration at the two sites was similar (0.5 mg AFDM/l), but on all subsequent dates, concentration at penstock depth (ca. 1.0 mg AFDM/l) was higher than in water withdrawn from the penstocks (0.5-0.6 mg AFDM/l). Chlorophyll *a* was detected in samples from the dam only in winter and early spring.

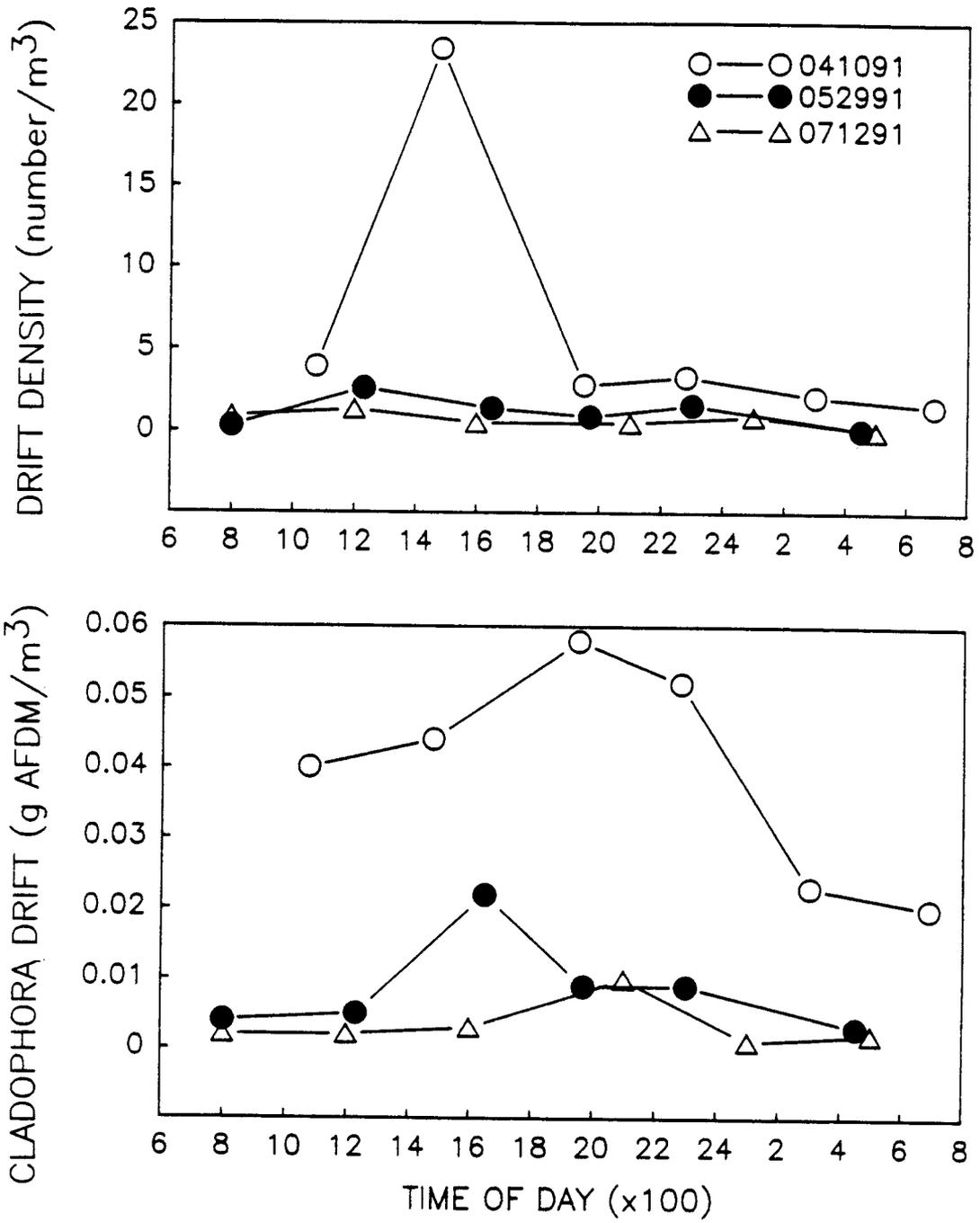


FIGURE 2.22--Mean (n=2) drift of invertebrates and *Cladophora glomerata* debris on three dates.

TABLE 2.6.--Percentage composition (by volume) of stomach contents of rainbow trout collected in Glen Canyon diel feeding studies.

Taxon	Time of Day						Mean
	1145	1500	1930	2330	0300	0730	
<i>April 10-11, 1991</i>							
Chironomidae	19.4	70.4	77.5	31.9	68.1	88.5	59.3
<i>Cladophora</i>	0.0	2.1	16.0	0.2	19.7	9.2	7.9
<i>Gammarus lacustris</i>	31.6	6.9	0.0	0.0	0.4	1.3	6.7
Mollusca	31.0	0.0	0.0	0.0	0.0	0.0	5.2
Fish eggs	15.5	3.8	3.4	1.7	3.6	0.1	4.7
Coleoptera	0.0	0.0	0.1	0.0	0.0	0.0	<0.1
Diptera	0.6	0.1	0.5	0.0	0.9	0.3	0.4
Terrestrial insects	0.0	0.0	0.3	0.0	0.0	0.0	<0.1
Nematoda	1.2	1.4	0.0	0.0	0.4	0.1	0.5
Unidentified animal	0.0	0.7	0.0	62.3	0.0	0.0	10.5
Organic detritus	0.0	11.1	1.1	2.6	4.4	0.2	3.2
Sand, Gravel	0.6	3.5	1.3	1.2	2.4	0.1	1.5
Taxon	2100	0000	0400	0830	1200	1600	Mean
<i>May 29-30, 1991</i>							
Chironomidae	7.5	5.0	1.9	4.0	16.3	6.2	6.8
<i>Cladophora</i>	74.9	88.9	92.9	93.9	80.2	91.2	87.0
<i>Gammarus lacustris</i>	8.5	2.6	3.9	0.3	2.2	2.1	3.3
Mollusca	0.5	0.2	0.1	0.0	0.0	0.4	0.2
Unidentified animal	0.9	0.0	1.2	1.8	1.2	0.0	0.9
Diptera	5.8	0.7	0.0	0.0	0.0	0.0	1.1
Sand, gravel	1.8	2.7	0.1	0.0	0.0	0.1	0.8
Taxon	0800	1200	1600	2000	0000	0400	Mean
<i>July 12-13, 1991</i>							
Chironomidae	5.6	13.8	18.0	20.6	1.15	4.1	10.6
<i>Cladophora</i>	82.5	80.3	69.7	71.3	87.6	64.3	76.0
<i>Gammarus lacustris</i>	0.7	0.7	3.8	1.3	6.7	22.8	6.0
Mollusca	6.4	3.7	7.3	3.8	2.9	6.1	5.0
Oligochaeta	0.8	0.0	0.0	0.0	0.0	0.1	0.1
Terrestrial insects	0.0	0.2	0.2	0.0	0.0	0.0	<0.1
Nematoda	0.0	0.0	0.0	0.1	0.0	0.0	<0.1
Unidentified animal	0.7	0.0	1.0	0.0	0.0	2.3	0.7
Sand, gravel	3.2	1.3	0.0	2.8	1.2	0.3	1.5

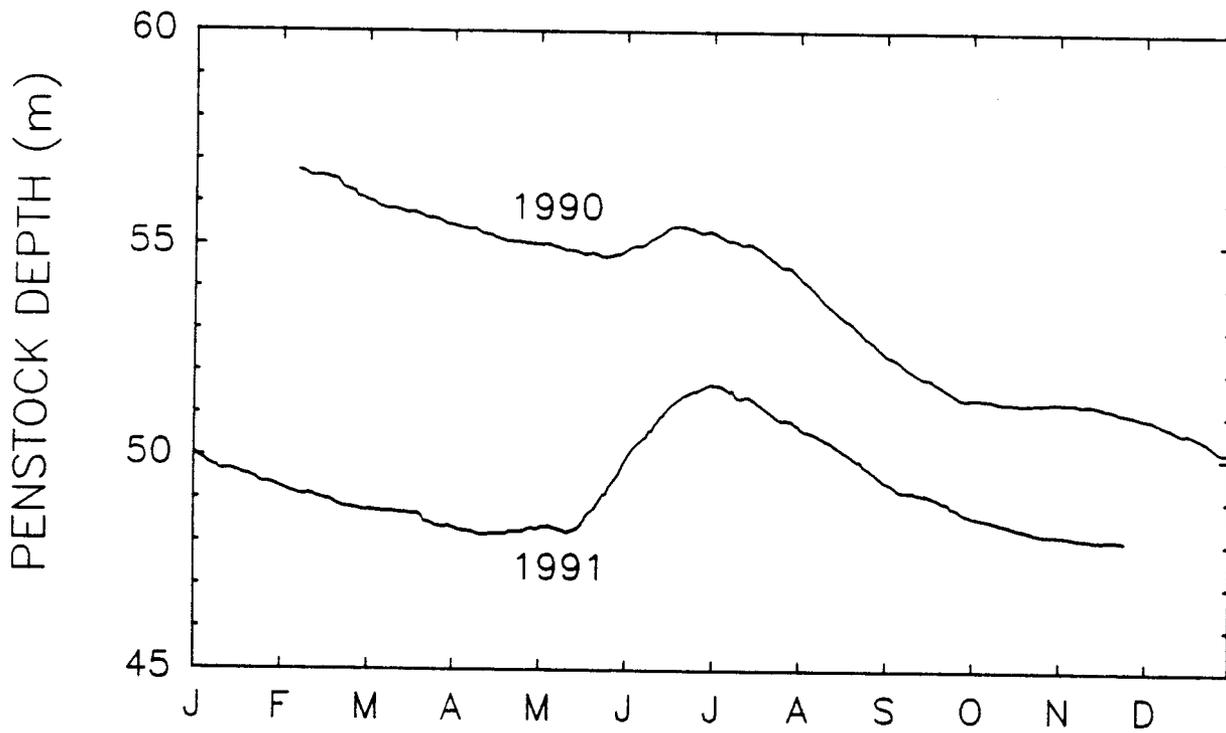


FIGURE 2.23--Penstock depth during the study. Lake Powell surface elevation = penstock depth + 1057.

Following stratification (Figure 2.3), only pheophytin *a*, a breakdown product, was present. Chlorophyll *a* was depressed at penstock depth on all dates, but was usually present in detectable concentrations. Obviously, more study is needed to determine how water releases from the dam influence the depth from which particulate and dissolved material is withdrawn from the forebay in each season.

Longer term changes in lake surface elevation will also influence the actual penstock withdrawal depth. The surface elevation of Lake Powell has decreased in recent years (from Figure 2.23). If this trend continues, an increasing volume of warm surface water may enter the penstocks in some seasons which would have downstream effects at several trophic levels (e.g, Blinn et. al. 1989).

Organic Matter Transport

Diel patterns of seston concentration in most unregulated non-tidal streams reflect biological processes (e.g., photosynthesis, animal migration, feeding, and excretion) and are often subtle and difficult to detect (Burney 1990). Seasonal and storm related patterns generally account for most of the temporal variation seston concentration in streams (Cummins et al. 1983, Burney 1990).

Daily flow fluctuations caused significant diel variation in seston concentration in Glen Canyon. CPOM concentration at Lee's Ferry exhibited a hysteresis pattern in which the relationship between discharge and concentration varied over the diel period (Figure 2.24). CPOM concentration increased fastest during the initial ascent of the hydrograph and decreased more slowly during the descending limb. FPOM concentration at Lee's Ferry responded to the daily hydrograph in some months (October 1990, Figure 2.2) and not in others (March 1991). The reason for the variable and generally small effect of flow on FPOM is not clear. We speculate that FPOM (phytoplankton) is exported from the reservoir in proportion to the volume of water released, which dampens diel variation in FPOM concentration.

There were peaks in CPOM concentration in spring and autumn. CPOM was overwhelmingly comprised of *Cladophora* debris, and we speculate that seasonal variation in CPOM concentration reflects the phenology of this algae. The autumn increase in CPOM concentration corresponded to a decrease in periphyton standing stock (Figure 2.20) caused by decreasing day length. The reasons for the spring peak are not clear. Most likely, renewal of rapid growth with increasing day length caused the sloughing of senescent, overwintered filaments. A research flow just prior to the April 1991 sample may have

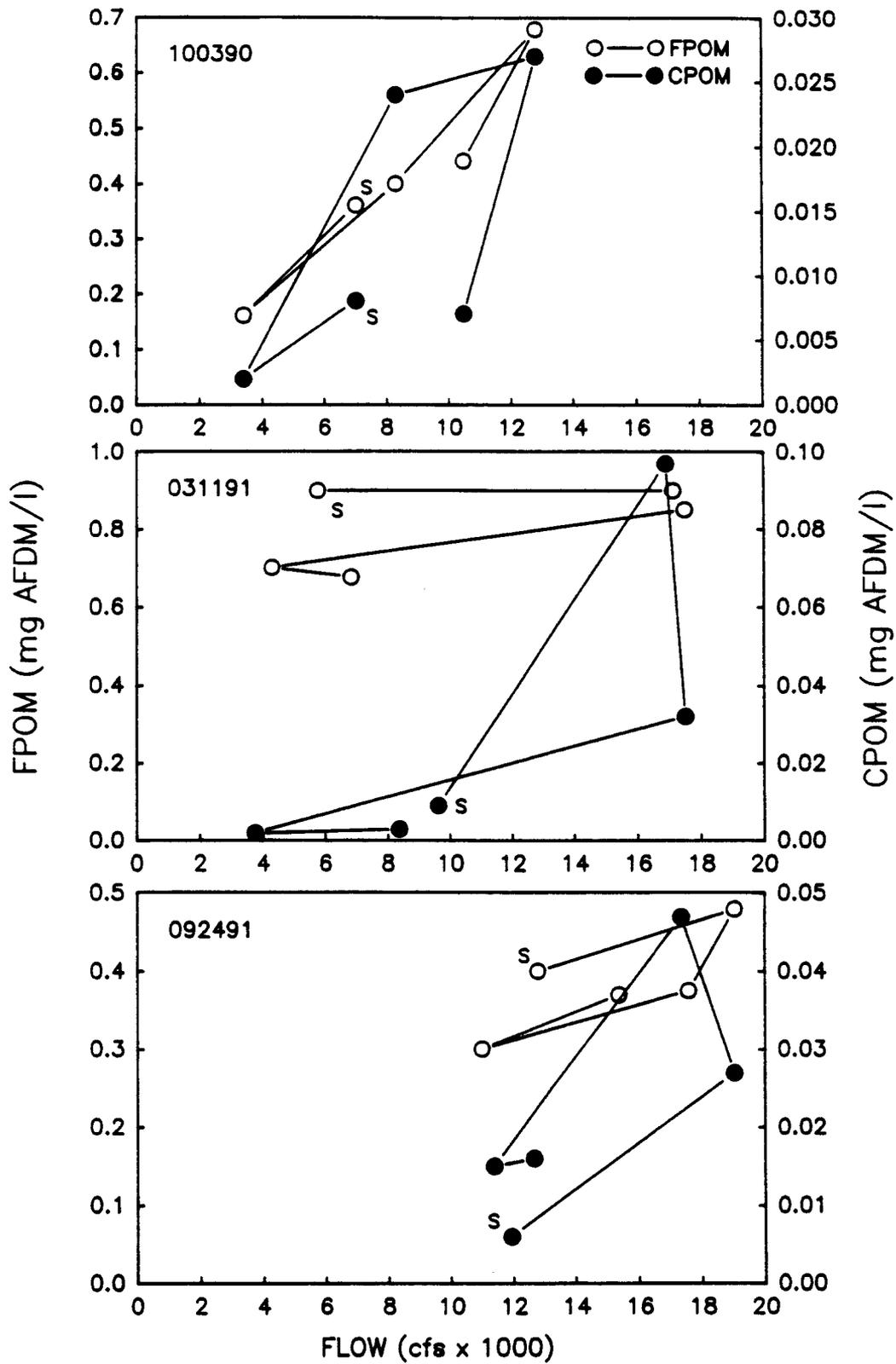


FIGURE 2.24--Hysteresis in discharge-sediment relationships for selected dates. Trajectories indicate change in sediment concentration associated with the daily hydrograph. S indicates the starting sample.

increased CPOM (and FPOM) concentration somewhat, but the trend was apparent in March, during normal winter flows.

In most cases, nutritional quality (e.g., C:N) of CPOM collected at 0400 h was higher than CPOM collected at 1600 h during the ascent of the daily hydrograph (Figure 2.8), probably because material entrained with rising water levels increased the relative proportion of lower quality terrestrial debris and nutrient-depleted aquatic debris in transport. Additional research, possibly with stable isotopes, is needed to determine the origin and fate of organic particles in Glen and Grand Canyons.

There was no difference in mean annual FPOM concentration or seston loading between the dam and Lee's Ferry (Figure 2.10). A general seasonal pattern was that exports from Glen Canyon exceeded imports from Lake Powell in winter and spring, and imports exceeded exports in summer and autumn. More CPOM was exported from the reach than was imported, but CPOM only comprises a small percentage of the total seston (3% by mass; Table 2.7). Limited data suggest that the concentration of dissolved organic matter was similar at both sites (Table 2.1). The pattern of FPOM chlorophyll concentration was generally similar at the two sites (except in spring) suggesting either that the phytoplankton was all reservoir-derived or that river-derived phytoplankton replaced downstream losses in reservoir-derived phytoplankton.

Dams retain organic matter (Ward and Stanford 1983) and reduce the seston concentration immediately downstream. However, most other studies of seston concentration in tailwaters have demonstrated an increase in the mean annual concentration of total particulate organic matter within a relatively short distance downstream from the dam (Table 2.7) resulting from tributary and allochthonous inputs and from high autotrophic production in the clear, nutrient enriched tailwater.

We did not observe a longitudinal increase in seston concentration in Glen Canyon. We hypothesize that several interacting features of the system account for this unexpected result. There are no tributaries and fine terrestrial inputs are probably minimal. There are several deep pools upstream of Lee's Ferry which may trap a portion of the seston that would otherwise exit the reach. Autotrophy below the dam appears to be very intense, however, and these explanations are unsatisfactory.

The periphyton community is well developed below the dam which may produce a very short organic matter spiraling (downstream cycling) distance (Webster 1975, Newbold et al. 1982, Elwood et al. 1983) and hence very efficient processing (reduction to finer size fractions) of organic matter such that autochthonous production is processed a short distance

TABLE 2.7.--Comparison of mean total annual seston concentration (mg AFDM/l) among western tailwaters. Lee's Ferry is 25 km downstream from Glen Canyon Dam.

River	Range	Mean	Reference
<u>Colorado River</u>			
Glen Canyon Dam	0.38-0.76	0.55	This study
Lee's Ferry			
CPOM	0.01-0.06	0.02	This study
FPOM	0.23-0.91	0.58	
Below Davis Dam	0.43-1.05	0.75	Lieberman and Burke 1991
Below Parker Dam	0.48-1.38	0.91	Lieberman and Burke 1991
<u>South Platte River, CO</u>			
0.3 km Below Cheesman Dam		0.8	Ward 1976
5.0 km Below Cheesman Dam		1.8	Ward 1976
<u>North Fork, Snake River, ID</u>			
0.3 km Below Island Park Dam	0.35-0.59	0.43	T. Angradi, Unpublished data
5.5 km Below Island Park Dam	0.45-2.20	1.47	T. Angradi, Unpublished data
9.0 km Below Island Park Dam	0.37-2.42	1.23	T. Angradi, Unpublished data

downstream from its point of origin during most of the year. At the extremes, organic matter originating in Glen Canyon may be respired (=oxidized) by animals, bacteria, fungi, and algae within the periphyton matrix itself (e.g., Paul et al. 1991), or it may be exported and ultimately respired in the Grand Canyon or Lake Mead. If spiraling distance in Glen Canyon is indeed short, the effect of high autotrophic production just below the dam may be obscured at 25 km (Lee's Ferry). Preliminary evidence (Figure 2.25) suggests that the downstream change in seston concentration within the reach is not a simple function of cumulative upstream area, and probably depends on the interaction of hydrology (e.g., stream power) and geomorphology (e.g., distribution of cobble bars where benthic autotrophy is concentrated).

This is relevant because stream reaches are linked. Downstream reaches depend on inefficiency of processing--"leakage"-- from upstream reaches (Cummins 1979, Vannote et al. 1980, Minshall et al. 1983). Processing efficiency may be related to dam operations. Daily flow fluctuations, as an energetic physical process, may increase or decrease (more likely) the efficiency of organic matter processing by entraining unprocessed organic matter. Flow regulation and resulting high autotrophy tends to dampen seasonal fluctuations in organic matter transport (Angradi 1991, unpublished manuscript). If the flow fluctuations are below the disturbance threshold for periphyton, they may further decrease between-season variance in seston concentration by preventing the accumulation of a high standing biomass of periphyton and nonviable organic matter. If so, daily flow fluctuations may reduce the magnitude of seasonal export pulses linked to the phenology of important algal taxa. Unfortunately, nearly all of the periphyton in the zone of fluctuation was destroyed by research flows before the studies and experiments reported herein were begun. The degree to which conditions existing during this study reflect normal seston dynamics is uncertain.

Periphyton Exposure

Our experiments confirm the finding of Usher and Blinn (1990) that a relatively brief (12 h) daytime exposure results in a significant reduction in periphyton chlorophyll *a* and biomass. Chlorophyll *a* and the ratio of chlorophyll *a*:*b* decreased faster initially in periphyton on cobbles from <5,000 cfs, suggesting that the lack of epiphytes on *Cladophora* from >5,000 cfs may result from the low tolerance of diatoms to desiccation (but see Pinney 1991). There was some evidence from experiment I (Figure 2.13) that the periphyton from >5,000 cfs might tolerate a brief (< 12 h) exposure better than periphyton

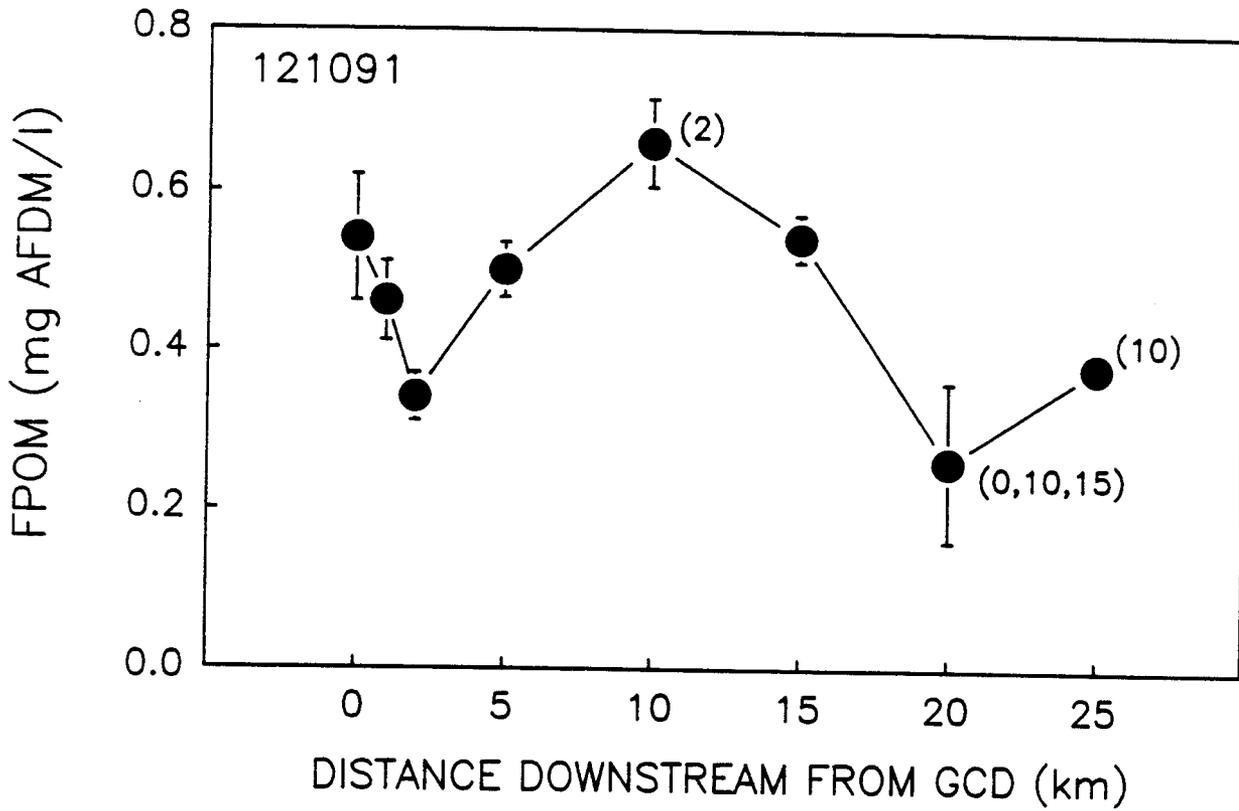


FIGURE 2.25--Mean (± 1 SE, $n=4$) concentration of FPOM with distance downstream from Glen Canyon Dam on December 10, 1991 between 1200 and 1400 h. Samples at 0 km were collected from draft tubes within Glen Canyon Dam (GCD). Numbers in parentheses indicate upstream sites with significantly different concentrations. Flows from Glen Canyon Dam were nearly constant at $\sim 14,100$ cfs from 1000-2000 h.

from < 5,000 cfs. The initial rapid loss in chlorophyll *a* was followed by a loss of biomass. Biomass decreased less in our experiments than was reported by Usher and Blinn (1990), but the initial biomass of periphyton in their study was ten times less than in ours. A general finding of our study is that exposure to summer daytime environmental conditions caused changes that were mostly independent of level and duration of exposure. Possible "adaptations" of the partially exposed periphyton (> 5,000 cfs), such as low chlorophyll *a*:biomass ratio, and the absence of epiphytes, were overwhelmed by the exposure treatments. The ability of periphyton to recover from even brief exposures is unknown.

Pinney (1991), reported that periphyton at Lee's Ferry was able to persist through weeks of exposure during autumn months. Usher et al. (1986) reported that freezing caused significant losses of periphyton. Obviously, the resistance to disturbance depends strongly on the ambient climatic conditions. More study is needed to determine how resistance changes with season and community development.

Algal Colonization

Spring and autumn colonization studies indicated that accretion of biomass and chlorophyll *a* was very slow in the zone of daily water level fluctuations. In the spring study there was measurable accretion, but assuming that maximum periphyton biomass in the zone of fluctuation generally approaches that in the permanently inundated channel (Pinney 1991, Usher et al. 1987), periphyton in the fluctuating zone did exhibit much recovery in two months. A research flow (5,000 cfs) at the end of the colonization experiment reduced the amount of chlorophyll *a* and biomass on tiles in the zone of fluctuation--further evidence that disturbance alters periphyton communities, in this case by setting back periphyton development two weeks or more.

In the autumn colonization study there was a slight increase in periphyton biomass at the 8,000 cfs level at one site. Interpretation is confounded by a seasonal effect, but the rate of increase (0.003/day) was very low; at this rate it would take > 700 days for 200 mg AFDM/m² of periphyton to accumulate (estimates for the 11,000 cfs level from the spring study are similar).

Analysis of flows that occurred during each colonization study (Figure 2.26) indicates that relatively small differences (<25%) in the amount of time that levels were inundated resulted in large differences in colonization rates. For example, during March and April in the spring study, tiles at the 5,000 cfs level were dewatered only about 20-30% of the time, but much less periphyton accumulated on them than on tiles inundated 100% of the time.

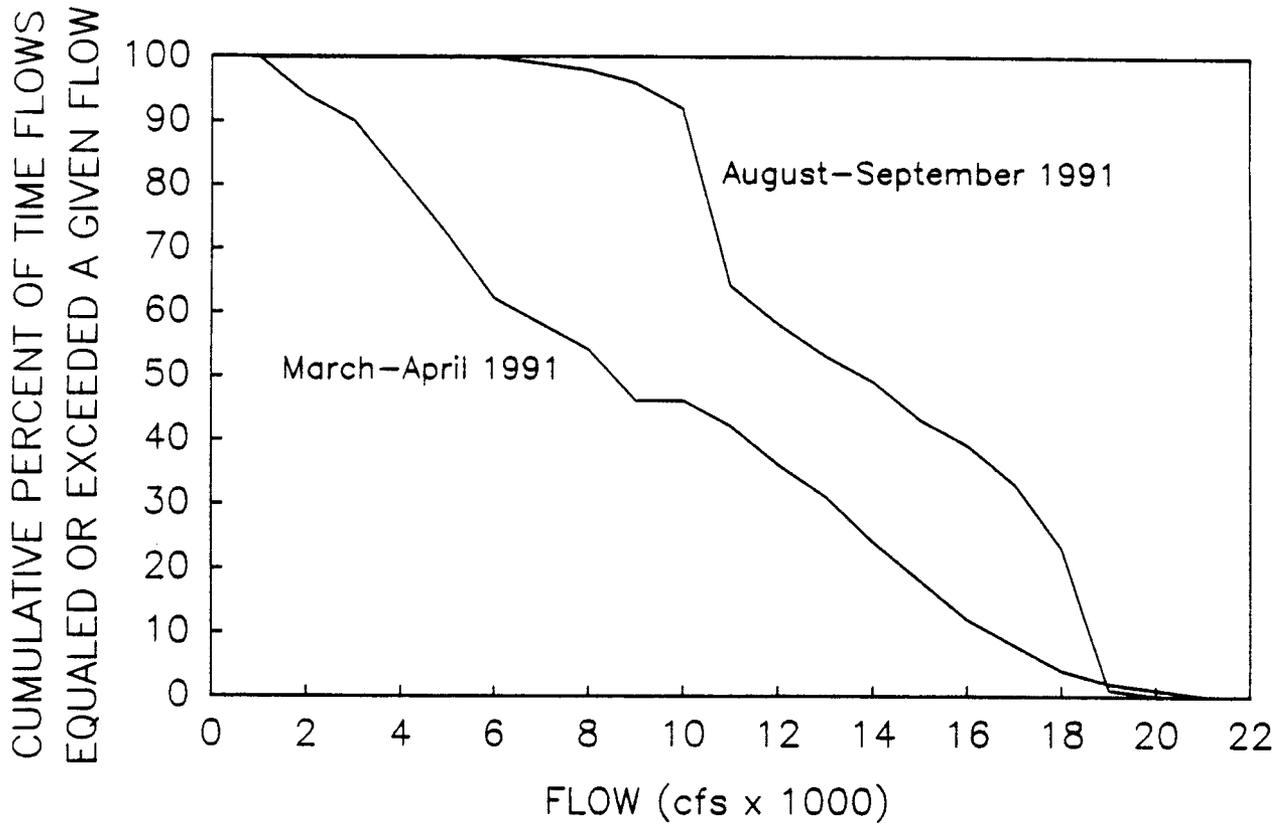


FIGURE 2.26--Cumulative percent of time flows equaled or exceeded a given flow in Glen Canyon for two intervals. The March-April 1991 interval corresponds to the spring colonization study. The August-September interval corresponds to part of the autumn colonization study (1992 water year data were unavailable). Data are from USGS gaging station near Glen Canyon Dam.

The comparability of accretion rates for different substrates in different season is arguable (e.g., Blinn et al. 1980, Lamberti and Resh 1985), but if our estimates are in the range of the true rate, then periphyton in the zone of fluctuation in Glen Canyon has low resilience compared with other published studies (Steinman and McIntire 1990; Niemi et al. 1990 reported that the minimum, maximum, and median recovery times of lotic periphyton were about 7, 150, and 40 days, respectively). This suggests that daily flow fluctuations have a strong negative effect on some aspect of periphyton recovery, and that disturbances severe enough to destroy the periphyton will have protracted (probably > 1 year) ecosystem-level effects under fluctuating flows.

Diel Feeding Chronology of Rainbow Trout

The effect of diel changes in flow on trout behavior could not be evaluated in this study because no non-spawning trout were collected during fluctuating flows. Most studies of adult rainbow trout in rivers have demonstrated diel variation in the amount of food in the stomach (e.g., Angradi and Griffith 1990). In our study the stomach content volume was greater (albeit not significantly so) in afternoon and evening samples than in early morning, suggesting that feeding was reduced at night (Eggers 1977). Our findings for the composition of stomach contents agrees closely with previous studies (Persons et al. 1985, Maddux et al 1987). Three categories, *Cladophora*, Chironomidae, and *Gammarus* accounted for most (70-95%) of the volume of material present. This lack of diet diversity in adult trout and the correlation between periphyton biomass and invertebrate density (Liebfried and Blinn 1986) results in a tight trophic coupling of trout and *Cladophora* (and its epiphytes) in Glen Canyon.

The lack of a distinct diel pattern of drift may partially explain the lack of diel variation in stomach content volume. *Gammarus*, which drifts in response to changes in flow (Liebfried and Blinn 1986), was absent from the drift in the May and July samples, and chironomids, which are less responsive to variation in flow, numerically dominated the drift.

195 1000 1000 1000

3. Trout

Sue A. Morgensen

The flow regime below Glen Canyon Dam affects rainbow trout (*Oncorhynchus mykiss*) populations in the Glen Canyon tailwater both indirectly and directly. Indirect effects involve ecosystem processes and lower trophic levels discussed in the previous chapter. Direct effects include stranding and dewatering of all life stages and displacement of individuals from preferred habitats during such activities as feeding and reproduction. Stranding is a source of mortality for adult trout and their progeny in the tailwater, and displacement may cause increased energy expenditure, reduced food intake, and disruption of reproductive activities.

The findings presented here deal with three aspects of the trout fishery in Glen Canyon relative to the flow regime: spawning, stranding, and movement (as measured by radio telemetry). Other studies which are being conducted but are not presented here relate to trout diet, growth, and population structure.

Successful natural reproduction of trout in the Glen Canyon tailwater has several prerequisites related to flow. Flows must inundate spawning areas long enough to allow trout to build redds and fertilize eggs; redds must remain moist and oxygenated for eggs to hatch, and; suitable fry-rearing habitat must be available. Armoring caused by sediment-depleted water releases from the dam (Pemberton 1976) limits the availability of suitable spawning substrates downstream from the dam. Fluctuating flows may render conditions within redds unsuitable for egg survival, strand alevins at emergence, and limit the availability of fry rearing habitat.

Kondolf et al. (1989) found suitable spawning gravels in Glen Canyon. Instream flow analysis in the tailwater showed that spawning bars are first exposed at flows of 8,000-10,000 cfs (Persons et al. 1985). In this study we have attempted to estimate the proportional loss of spawning habitat at specified flows at four spawning bars in Glen Canyon, as well as to further define suitable substrate size and acceptable amounts of fine sediment.

Stranding and mortality of trout in dewatered pools is a conspicuous direct effect of fluctuating flows. The magnitude of stranding may depend on time of year, magnitude of the fluctuations, ramping rates, and the length of time discharge remains low. The spawning season may be a particularly critical time of year (November-April), because many of the areas where fish become stranded provide otherwise suitable spawning habitat.

We used radio telemetry to quantify fish movements relative to flow conditions. Changes in river stage, current velocity, and wetted area that accompany fluctuating flows may affect the behavior of adult trout during foraging and spawning. Male trout typically occupy and defend defined areas of spawning bars (Hunter 1991). If flows decline, individuals may be forced from these areas interrupting spawning. In like manner, trout feed at the most energetically favorable positions in the channel, areas of limited current velocity, such as "eddy fences", where low velocity areas are adjacent to faster currents with a high density of drifting food organisms (Li and Brocksen 1977). As discharge from Glen Canyon Dam rises and falls, the preferred sites may become less energetically favorable or dewatered causing fish to move.

Methods

Trout Spawning

Bars at river miles -4.0, -6.1, -8.9 and -14.0 were chosen for spawning surveys (Figure 2.1). The four bars were selected because spawning has occurred at these locations in the past, and because they appeared to represent a continuum in substrate size distribution from the dam downstream. The bar at -6.1 mile is somewhat unique in that it is not continuous with the shoreline at most flows, and may be subjected to higher current velocities.

Twenty stakes were placed along the high water mark on each bar to facilitate mapping. The x,y,z coordinates of each stake were surveyed by USGS personnel using a Nikon electronic distance meter and a hand held prism. Coordinates were also measured around the perimeter of the bars at 3,000, 5,000 and 11,000 cfs discharges and indexed to known bench marks.

Measurements of the wetted perimeter of each spawning bar at 3,000, 5,000, 8,000 and 11,000 cfs constant discharge were made from the stakes. Cloth tapes and hip chains were used to measure the distance from each stake to the waters edge along a compass bearing perpendicular to the shoreline. These measurements, combined with USGS surveys, were used to create contour maps of the bars. Where USGS survey data were not available (8,000 cfs), interpolations were made from curves fitted for each bar to the best stage discharge relationship available (T. Randle, personal communication). Contour maps were adjusted by comparing them to aerial photographs.

Bars were sampled during 5,000 cfs controlled flows in June and July, 1991 for sediment particle size and embeddedness. Embeddedness refers to the degree to which coarser particles are buried in fine sediments. On each bar, 7-19 transects were run perpendicular to the river bank at 15 m intervals. The size of the surficial substrate and an embeddedness code were recorded at one meter intervals along each transect. Substrate size was calculated as the geometric mean diameter of the particle intersected by the upstream edge of the tape at each meter mark. A nonparametric median test was used to compare median substrate size among spawning bars and transects. Codes used for embeddedness were, 0 = not embedded, 1 = 1-25% embedded, 2 = 26-50% embedded, 3 = 51-75% embedded and 4 = >75% embedded.

Three equally spaced samples of spawning gravels were taken from each of five equally spaced transects on each bar by forcing a 30-cm diameter cylinder into the substrate and excavating the material within to a depth of 10 cm. Coarse substrate was sieved in the field (76.2 mm, 50.8 mm, and 25.4 mm), and weighed (± 1 g). Fine (< 25.4 mm) substrate was returned to the lab, sun-dried, sieved (12.7 mm, 6.4 mm, 3.2 mm, 2 mm, 1 mm, 0.5 mm, 0.25 mm, and 0.045 mm), and weighed.

Cumulative percentages (by weight) of size fractions were calculated for the excavated materials. Percentile values for 16% (D16) and 84% (D84) were used to calculate the geometric mean substrate diameter for each bar [$D_g = (D16 \times D84)^{0.5}$]. Differences among spawning bars and among transects at each bar were evaluated with a multiple ANOVA and Tukey's honestly significant difference multiple range test at the 0.05 significance level.

Beginning in November, 1990, the four spawning bars were checked every two weeks for redd development. Spawning bars were surveyed at least once a month to locate, mark and map active redds. The bearing of each redd was taken from two stakes and the locations were plotted on the maps by triangulation. A nonparametric Kruskal-Wallis test was used to compare redd density among transects. A subsample (378) of the redds at -4.0 mile bar was mapped and used in the calculations of percentage of redds at selected elevations.

Trout Stranding

A study of trout stranding was begun in November 1989. During that month, the river from Glen Canyon Dam to Lee's Ferry was surveyed several times at low flows to identify stranding pools and to determine at what flows they become isolated from the main channel. Approximate flows at each site were estimated from discharge records from Glen

Canyon Dam. Subsequent surveys were conducted at night in order to sample the low flows and to avoid interference from predators and anglers which remove stranded fish from pools.

Stranding areas were surveyed four times each month from February 1990 through April 1990. From May, 1990 through March, 1991, stranding pools were examined during each controlled flow and twice a month during other flows.

Maximum length, width, and depth of each stranding pool was measured to the nearest cm. During surveys, the number of fish stranded, dead or alive, was recorded. Water temperature, dissolved oxygen (DO), pH, and conductivity were measured with a Hydrolab. Dead fish were collected, weighed to the nearest gram, and measured to the nearest mm (TL). Stranding pools were resurveyed periodically to determine how long it took for stranded trout to die (if they did). Trout which survived stranding were tagged with numbered Floy tags and released into the main channel.

Trout Movement

Radio telemetry was used to evaluate the response of trout to constant and fluctuating flow regimes. Five adult trout (42-52 cm TL) from -13.5 mile were implanted with radio transmitters in November 1990. Five additional trout from -6.1 mile were implanted in December 1990. Transmitters (Custom Telemetry & Consulting, Inc.) were approximately 7 cm long by 2 cm wide, resin coated, and had internal antennae. They emitted signals in the 40 Mhz range at a pulse rate of approximately 40 cycles/min and had an expected life span of 9-12 months. Surgical procedures used to implant transmitters were described by Winter (1983). Fish were anesthetized with tricaine methanesulfonate (MS-222). After implantation trout were held in river water until they recovered, and released near the point of capture.

Implanted trout were located using a Model 2000 Advanced Telemetry programmable receiver with a whip antennae mounted on a boat. Portable hoop antennas were used for directional triangulation. Once the general vicinity of a trout was determined, two biologists were deployed to the nearest shore, one upstream from the fish and one downstream. Two-way radios (ca. 47 Mhz) were used to communicate and coordinate readings. An azimuth was established by sweeping the area with a hoop antennae to establish signal direction, and simultaneous triangulation bearings were taken from known locations using hand-held compasses.

To avoid disturbing the fish, triangulations on all implanted trout in a given area were made prior to measuring habitat parameters. In most cases it was possible to wade to the triangulated position. In deeper water a boat was used.

Each fish location was classified as run, riffle, pool, eddy or backwater. Macrohabitat measurements of depth, distance to shore, substrate size, cover and velocity were made for each site. Substrate size was classified as silt, sand, gravel, cobble, rubble, or boulder. At wadeable locations, a Marsh-McBirney flow meter was used to measure velocity at the bottom, midwater, and surface.

Triangulations and habitat measurements were made on implanted trout located three times per day for two consecutive days during four controlled flows and two normal flows. Sample days during constant and fluctuating flow periods were sequential to avoid seasonal variation. Fluctuating flow observations were timed to catch the low, peak and declining flows. The same time periods were used during constant flows.

Hourly triangulations over a 24 h period were also made for four implanted trout, two during constant flows, and two during fluctuating flows. Distance traveled per hour and per day were calculated by mapping successive trout locations and measuring distances. Nonparametric Kruskal-Wallis or Mann-Whitney U tests were used to compare distance traveled per day and per hour, and habitat characteristics.

Results

Trout Spawning

Geometric mean substrate diameter based on transect-intersect data ranged from 46 mm (SD=34, n=1577) at -4 mile bar to 94 mm (SD=72, n=517) at -14 mile bar. The bar at -6.1 mile had a mean substrate diameter of 74 mm (SD=55, n=177), and the mean for -8.9 mile bar was 60 mm (SD=40, n=1017). The overall mean gravel diameter for all study bars was 59 mm (SD=48, n=3288); overall median gravel diameter was 46 mm.

A nonparametric median test indicated that median spawning gravel size differed among the four spawning bars (Table 3.1; $X^2=185.21$, $df=3$, $P<0.01$). The bars at -6.1 and -14.0 mile had higher proportions of the largest and finest fractions (Figure 3.1). For all spawning bars, there was a significant difference (K-W test, $X^2=344.44$, $df=18$, $P<0.01$) in substrate size among transects (Table 3.2). At all bars except -6.1 mile, substrates were larger at the upstream end than at the downstream end.

TABLE 3.1.--Percent of surficial substrate samples > and < median substrate particle size (46 mm) at four spawning bars in Glen Canyon.

	River Mile			
	-4.0	-6.1	-8.9	-14.0
> 46 mm	38	63	58	67
< 46 mm	62	37	42	33
Total Number	1577	177	1017	517

TABLE 3.2.--Percent of surficial substrate of samples > and < median substrate particle size (46 mm) by transect ordered downstream to upstream (all spawning bars combined).

	Transect									
	1	2	3	4	5	6	7	8	9	10
> 46 mm	21	21	22	45	36	39	48	56	53	57
< 46 mm	79	79	78	55	64	61	52	44	47	45
Total number	164	158	152	187	283	159	197	176	191	189
	11	12	13	14	15	16	17	18	19	
> 46 mm	60	56	64	54	66	62	69	73	68	
< 46 mm	40	44	36	46	34	38	31	27	32	
Total number	187	194	179	171	137	143	151	146	111	

Size descriptors (drawn from cumulative size distributions in Appendix 3.1) of gravel samples excavated from the four spawning bars are presented in Table 3.3. Percentile values D16, D50 and D84 refer to the sizes for which 16%, 50% and 84% of the sample is finer. The tendency of D50 to exceed D_g in spawning gravels indicates that the distribution of sediment sizes is skewed towards finer materials (Kondolf et al 1989).

Gravel samples were collected in June and July, 1991, after spawning was over and high flows had partially redistributed sediments. No effort was made to excavate from within redds. Thus, these results may be compared to unspawned gravels from other studies, but should not be directly compared to gravels from within active redds.

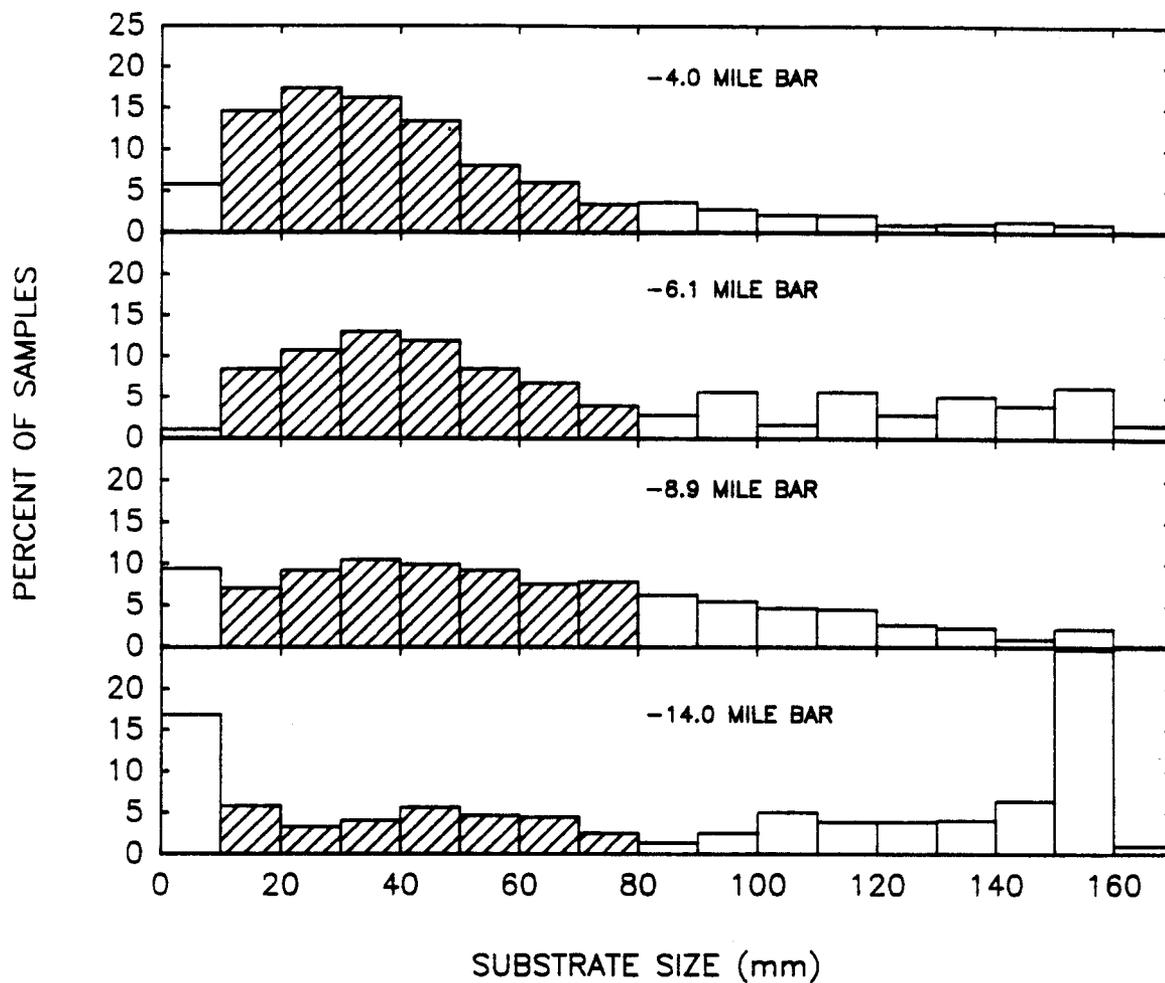


Figure 3.1.--Substrate particle size distribution for four Glen Canyon spawning bars. Shaded area includes suitable spawning gravel sizes (Raleigh et al. 1984).

TABLE 3.3.--Size descriptors for potential spawning gravel samples. (D16 = 16% finer, D50 = 50% finer, D84 = 84% finer, D_g = geometric mean (D16 x D84)^{0.5}).

River Mile	Transect	n	D16	D50	D84	D_g (mm)	Percent <	
							0.85	3.35
-4.0	1	3	1.3	13.9	34.8	6.7	12.6	24.7
-4.0	5	3	2.4	20.3	46.6	10.6	8.9	20.2
-4.0	9	3	2.8	24.4	57.1	12.6	9.0	19.5
-4.0	13	3	3.4	32.9	90.5	17.5	8.4	17.0
-4.0	17	3	5.0	47.4	106.1	23.0	7.3	13.6
Mean		15	3.0	27.8	67.0	14.1	9.2	19.0
-6.1	5	3	3.6	26.8	111.1	20.0	10.2	15.3
-6.1	7	3	11.7	80.3	129.6	38.9	6.8	9.9
-6.1	9	3	10.5	73.1	126.8	36.5	6.7	10.0
-6.1	11	3	3.9	40.0	93.2	19.1	10.6	15.9
-6.1	12	3	6.8	55.2	114.0	27.8	8.2	12.1
Mean		15	7.3	58.7	114.9	28.5	8.5	12.6
-8.9	1	3	0.5	10.4	31.1	3.9	44.9	50.6
-8.9	5	3	1.8	28.0	66.1	10.9	13.2	19.8
-8.9	9	3	2.5	43.0	94.1	15.3	12.7	19.0
-8.9	13	3	3.4	40.0	102.3	18.7	10.6	16.1
-8.9	18	3	10.5	56.9	109.7	33.9	7.2	10.9
Mean		15	3.7	35.6	80.7	16.5	17.7	23.3
-14.0	1	3	5.3	35.3	79.6	20.5	47.0	49.4
-14.0	4	3	4.7	49.3	128.3	24.6	11.9	16.5
-14.0	7	3	12.7	56.9	127.6	40.3	6.5	9.8
-14.0	10	3	22.4	74.9	130.4	54.1	7.1	10.0
-14.0	13	3	9.0	67.8	123.7	33.4	8.9	11.5
Mean		15	10.8	56.9	117.9	34.6	16.3	19.4

There were significant differences in D50 among the spawning bars and among transects (Table 3.4). A Tukey's multiple range test indicated that the bars at -4.0 and -8.9 mile were different from those at -6.1 and -14.0, and the three downstream transects were different from the two upstream transects. The same relationship held true for D_g (Table 3.4). There were no significant differences between inshore and deeper samples across any bar (ANOVA, $F=0.5$, $n=60$, $P=0.61$).

TABLE 3.4.--Summary of MANOVA tests of effects of spawning bar and transect on median (D50) and geometric mean (D_g) diameter of substrate using UNIQUE sums of squares.

Source of Variation	Sum of Squares	df	Mean Squares	F	P
D50					
WITHIN CELLS	9944.51	40	248.61		
Spawning Bar	10653.49	3	3551.16	14.28	<0.01
Transect	7520.57	4	1880.14	7.56	<0.01
Bar x Transect	4756.91	12	396.41	1.59	0.13
D_g					
WITHIN CELLS	6302.81	40	157.57		
Spawning Bar	3433.86	3	1144.62	7.26	<0.01
Transect	2662.11	4	665.53	4.22	<0.01
Bar x Transect	2156.35	12	179.70	1.14	0.30

The percent of fine material less than 0.85 mm and 3.35 mm was also calculated (Table 3.3). Kondolf et al. (1989) stated that the percentage of fines < 0.85 mm should be under 14, and the percentage < 3.35 mm should be under 30. All samples from Glen Canyon fell within these criteria except for two samples from the downstream edge of -14.0 mile bar and one sample from the downstream edge of -8.9 mile bar (Appendix 3.1). These samples are for unspawned gravels; active redds would presumably contain fewer fines.

The mean embeddedness rating for all bars was 1.45. Embeddedness generally decreased with distance from the dam. The bar at -14.0 mile had the highest embeddedness rating (1.8) and -4.0 mile bar had the lowest (1.3). The mean embeddedness at -6.1 had a higher than expected (1.7).

Because trout dig new redds through old ones (Hunter 1991) it was impossible to tell if subsequent redds at the same location were duplicate counts or new redds. No attempt

was made to eliminate duplicate counts of the same redd. No redds were located on -14.0 mile bar in 1991; 30 redds were found at -6.1 mile bar; 430 redds at -4.0 mile bar, and 178 redds at -8.9 mile bar. Our observations suggest that most spawning occurred in March and April in 1991.

Only 10% of the total redds located were below the 3,000 cfs discharge level (Figures 3.2-3.4). At discharge levels of 11,000 cfs, 29% of the redds were exposed; 59% were exposed at 8,000 cfs, and; 83% were exposed at 5,000 cfs.

Density of redds was negatively correlated (Pearson's $r=-0.27$) with substrate size. Substrate size was significantly different (K-W test, $X^2=275.40$, $n=3288$, $P<0.01$) between density groups. Density of redds generally increased as substrate size decreased. The highest density of redds was found in substrates with a mean diameter of 37 mm. Spawning activity was greatest at -4.0 and -8.9 mile bars, the two bars with the smallest surficial substrate size and the lowest D50 and D_g values.

Trout Stranding

Eleven major stranding pools were identified (Table 3.5). Large numbers of spawning adult trout became stranded in winter and spring, especially at -4.0, -8.9, -9.7 and -13.0 mile bars. Trout displayed a strong affinity for specific spawning areas. For example, we rescued 13 adult trout from -13.0 mile bar on February 24, 1991; the fish were tagged with numbered Floy tags and released. On March 4, 1990, five of the 13 trout returned to the same location and died when the pools dewatered.

In summer, high temperatures (up to 29 °C) and high dissolved oxygen (up to 24 mg/l) in the stranding pools were the major cause of trout mortality at 0.5, -4.0, -11.9 and -14.8 miles. On one day in May, 1990, 86 adult trout died at -11.9 mile and 94 died at -14.8 miles, presumably due to high temperatures. Smaller pools (e.g., -11.0 mile) trap relatively few adult trout, but sometimes trap and kill large numbers of trout fry.

A total of 1924 adult trout and 1048 fry were found in stranding pools during this study. Fifty-one percent of the adult trout, and 47% of the fry were dead or dying when we arrived at stranding pools.

Number of fish stranded varied considerably among stranding pools due to their size, location and proximity to spawning areas (Table 3.6). The mean number of stranded adult trout ranged from 2 at -14.82 to 51 at -14.83 miles (Table 3.6). Stranded juvenile to adult trout ranged from 180 to 608 mm TL, but most were mature adults (Figure 3.5). Mean length was 437 mm (SD=53, $n=496$) and mean weight was 735 g (SD=225, $n=448$).

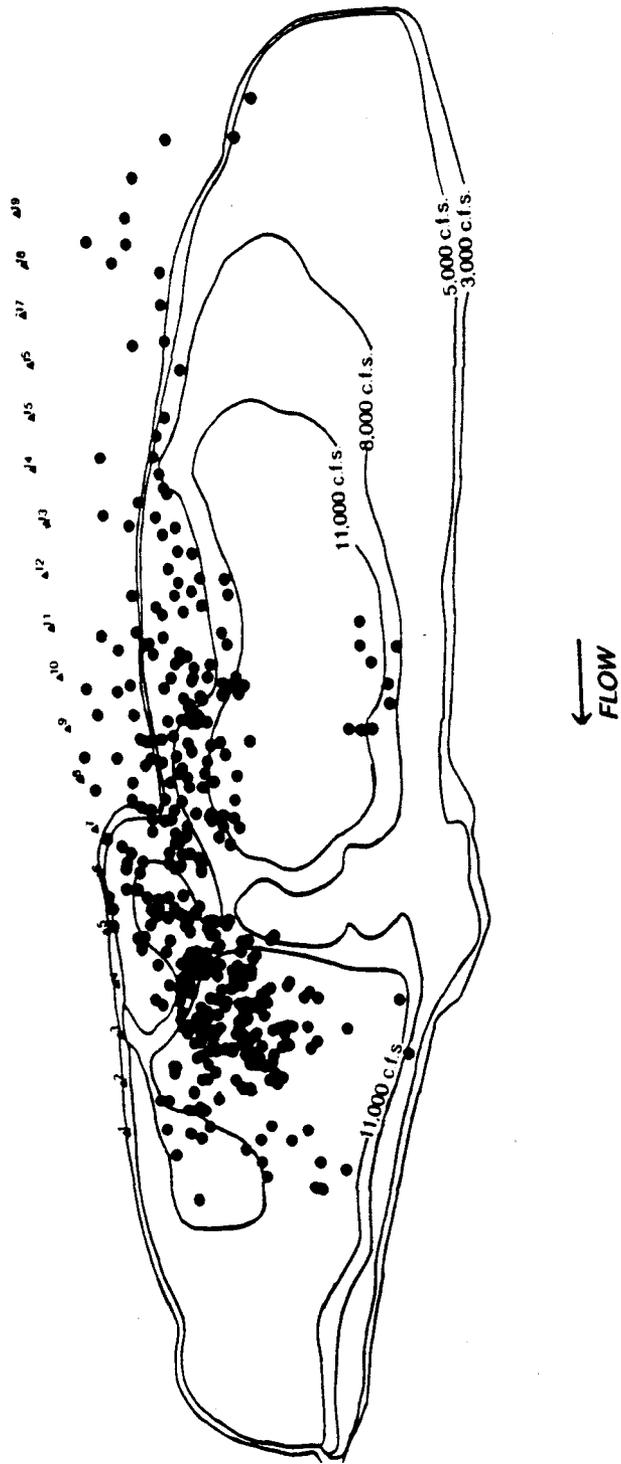


FIGURE 3.2.--Discharge contour map of -4.0 bar showing redd (closed circles) and survey stake (closed triangles) locations.

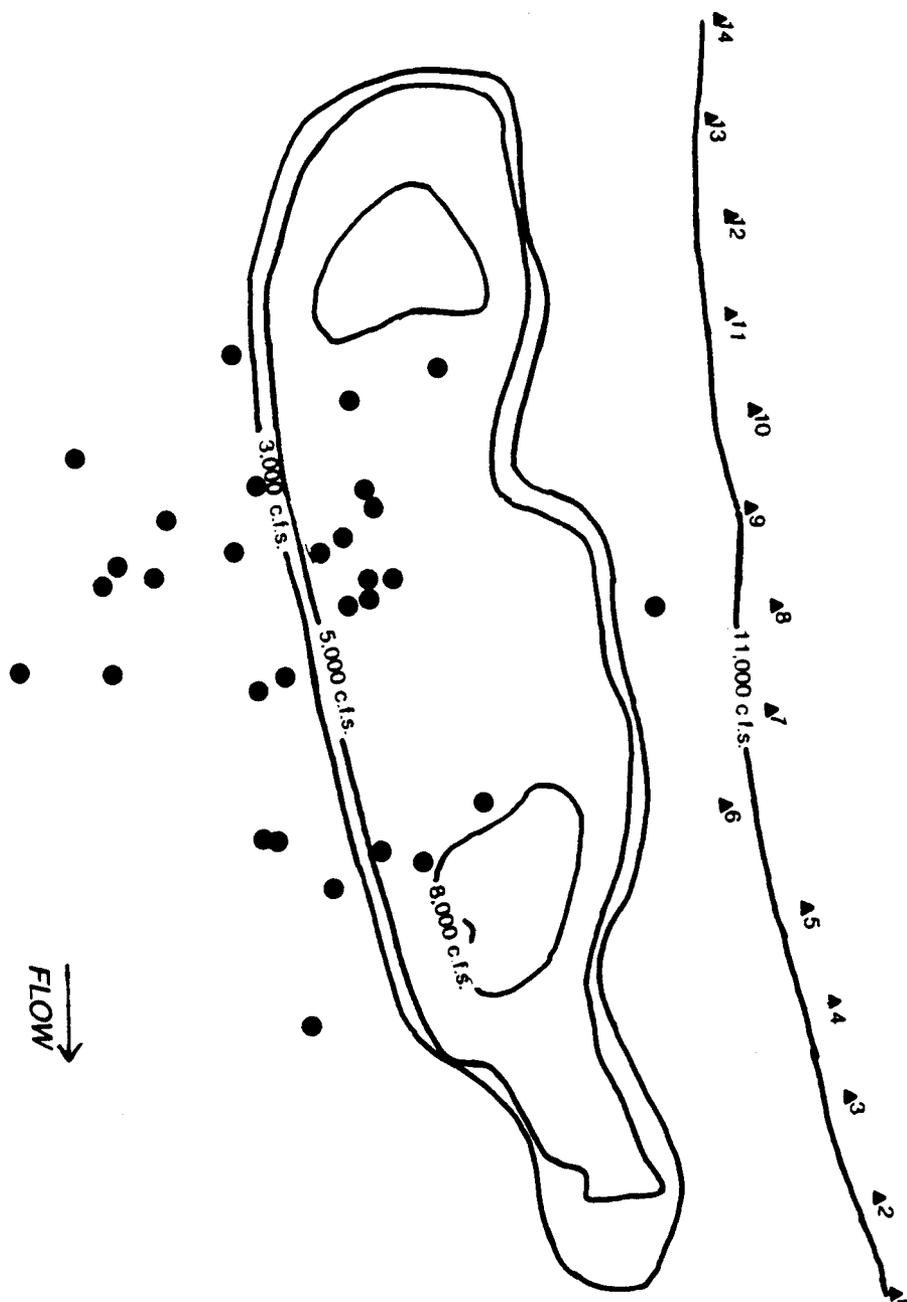


FIGURE 3.3.—Discharge contour map of -6.1 mile bar showing redd (closed circles) and survey stake locations (closed triangles).

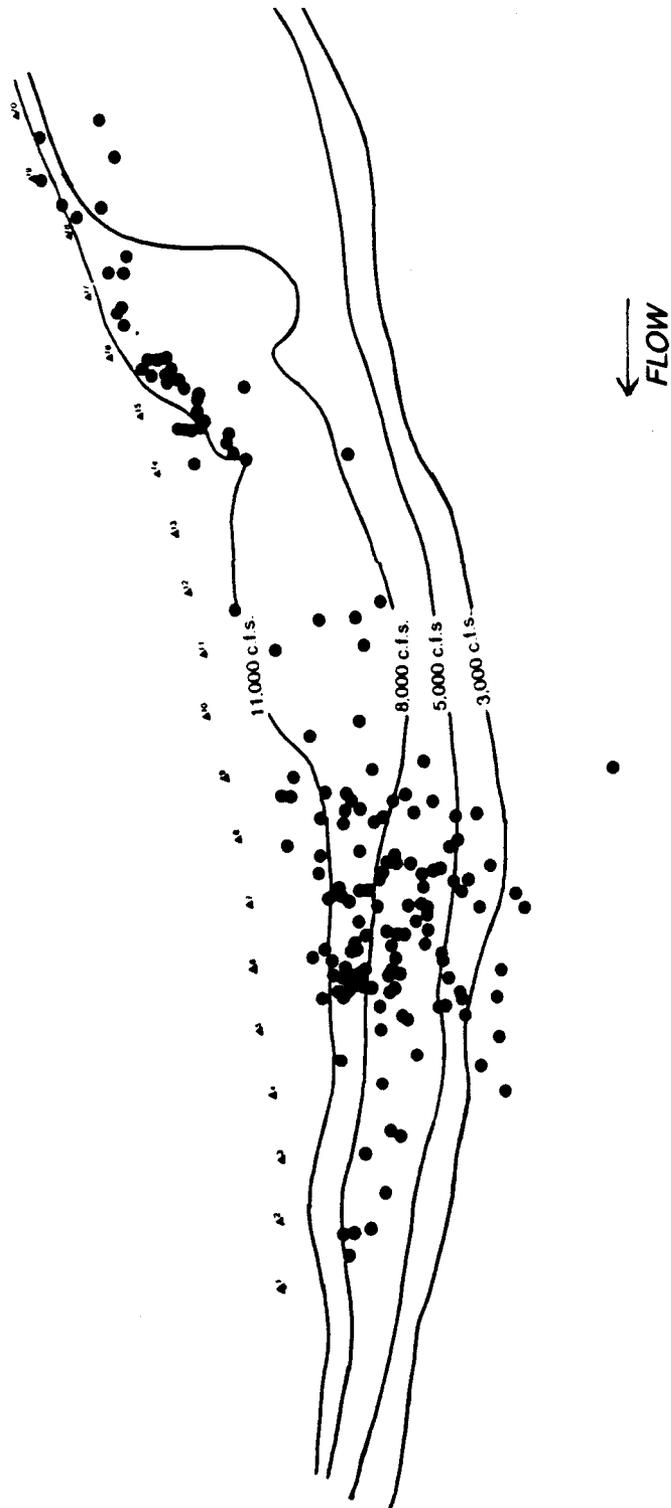


FIGURE 3.4.--Discharge contour map of -8.9 mile bar showing redd (closed circles) and survey stake (closed triangles) locations.

TABLE 3.5.--Maximum dimensions, discharge at isolation and causes of trout mortality for major stranding pools between Glen Canyon Dam and Lee's Ferry

Location RM Side	Max. Length (m)	Max. Width (m)	Max. Depth (m)	Isolates at (cfs)	Major Causes of Mortality
0.5 R	100	20	0.6	8,000	Winter: none Summer: water quality
-4.01 R	100	10	0.5	7,000	Dewatering, predation
-4.02 R	60	12	0.3	5,000	Dewatering, predation
-8.2 L	50	5	0.2	6,000	Winter: dewatering Summer: water quality
-8.9 R	23	7	0.6	8,000	Dewatering, water quality
	30	3	<0.1	7,000	Dewatering
	35	2	0.2	7,000	Dewatering
-9.7 R	20	2	0.2	6,000	Dewatering, water quality
-11.0 R	5	1	0.2	5,000	Dewatering (affects mostly fry)
-11.7 R	15	3	0.4	8,000	Dewatering
-11.9 R	50	10	0.2	4,000	Summer: water quality
-13.0 R	4.5	2.2	0.07	all at	Dewatering (affects
	1.3	1.0	0.3	9,000	all pools)
	1.0	1.4	0.05		
	9.6	5.8	0.2		
	4.6	2.0	0.1		
-14.0 R	15	5	0.4	5,000	Dewatering
-14.81 R	4	7	0.3	11,000	Dewatering
-14.82 R	4	7	0.3	10,000	Dewatering
-14.83 R	29	14	0.2	4,000	Dewatering, water quality

TABLE 3.6.--Descriptive statistics [mean, standard deviation (SD), range and total count] of stranded adult rainbow trout by location.

River Mile	Mean	SD	Range	n	Count
<i>Adults</i>					
0.50	17.3	17.55	0-42	9	156
-4.01	4.0	4.57	0-14	26	105
-4.02	13.3	17.29	0-50	9	120
-8.20	3.5	4.57	0-13	21	73
-8.90	6.0	9.02	0-36	27	161
-9.70	2.2	4.31	0-18	21	47
-11.00	2.5	0.71	2-3	2	5
-11.70	7.2	19.01	0-82	18	130
-11.90	35.3	32.97	0-86	6	212
-13.00	8.6	18.80	0-100	32	274
-14.00	4.9	5.70	0-20	14	68
-14.81	3.7	5.60	0-27	36	134
-14.83	1.9	3.03	0-10	28	54
-14.83	51.0	46.03	0-98	3	153
<i>Fry</i>					
-4.01	29.2	60.07	0-256	27	788
-8.20	1.9	5.57	0-25	21	39
-8.90	0.6	1.96	0-9	27	17
-9.70	1.0	2.89	0-10	21	22
-10.40	122.0			1	122
-11.70	0.6	1.34	0-4	18	10
-13.00	0.4	1.18	0-6	32	12
-14.00	2.3	2.58	0-8	14	32
-14.81	0.0	0.17	0-1	36	1
-14.82	0.2	0.67	0-3	28	5

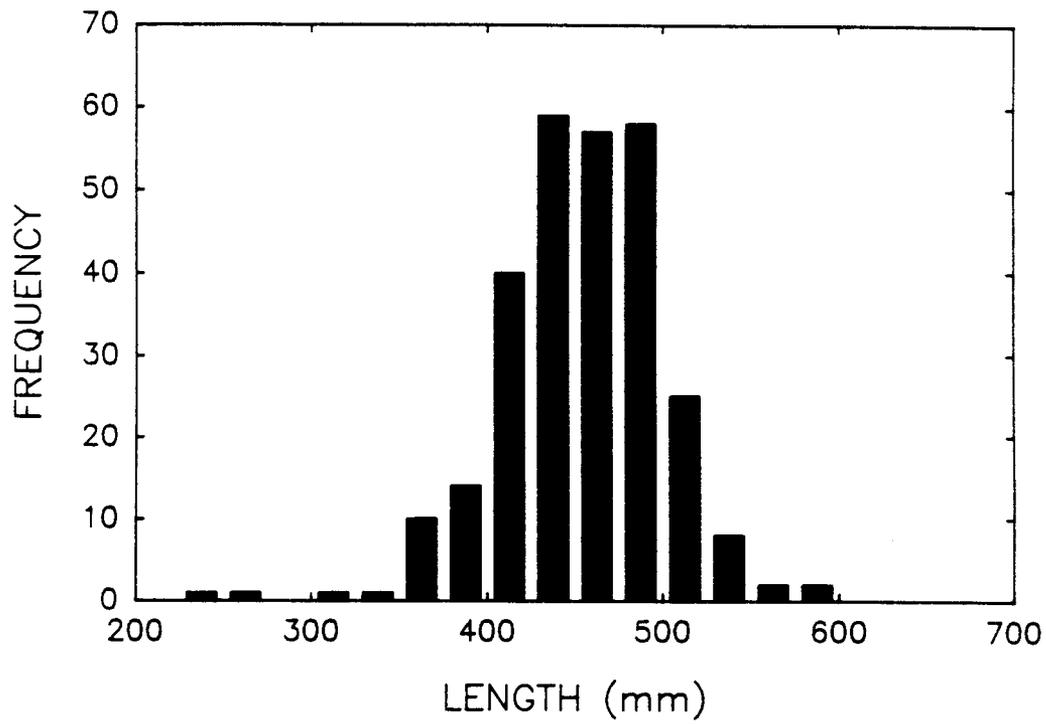


FIGURE 3.5.--Length frequency distribution of rainbow trout stranded by decreasing flows in the Lee's Ferry reach (December 1989-March 1991).

On June 30, 1990, 232 dead adult trout were found at -9.6 mile in a large connected pool > 1 m deep. Although the pool was not isolated from the river, the fish would have had to traverse approximately 100 m of shallow (10-20 cm) gravel bar to reach the mainchannel. The temperature in the pool reached 25° C. This event occurred during a controlled flow (5000 cfs) while air temperatures were extremely high.

The pool at -4.01 mile stranded the most fry. We found a total of 788 stranded fry over 27 sampling days (Table 3.6). The maximum number of stranded trout fry observed was 256 at -4.01 mile. On one occasion 122 fry were stranded and died at -10.4 mile (Table 3.6), an area which did not otherwise strand fish. The mean number of stranded fry ranged from 0 at several locations, to 29 at -4.02 mile.

In the spring of 1990, each of the above locations was surveyed to determine the length of time between when the pool became isolated and when trout died (Table 3.7). Seasonal differences in mortality were observed. Mortality in November through February probably resulted from dewatering, while poor water quality also contributed to mortality in March through October. Our observations suggest that time from pool isolation to mortality ranged from 4 to 64 h.

Movement

Between November 1990 and November 1991, 337 observations were made on implanted trout. Two of the ten implanted trout were lost immediately and were never relocated. Three trout travelled considerable distances following implantation. The first stayed at -13.5 mile for a month then moved to -9.5 mile, -8.0 mile, -11.0 mile, -11.5 mile, -11.7 mile and back to -11.5 mile during a three month period. The second left -6.0 mile bar on December 12, 1990 and was relocated at -4.0 mile bar on December 16, 1990 and at +2.0 mile on March 27, 1991. The third trout stayed at -6.0 mile bar for a week, moved to -2.5 mile from January 10 to February 28, 1991, and was not relocated again until October 8 1991 at -12 mile.

The five trout which remained near the location where they were originally captured were tracked three times a day during the following flows: 5,000 cfs constant, 11,000 cfs constant, "B" (5,000-15,000 cfs), "C" (8,000-20,000 cfs), normal winter, and normal spring. There was no significant difference in distance traveled between fish (K-W test, $X^2=3.685$, $n=41$, $P=0.45$).

Mean distance travelled per day ranged from 32 m during the "B" study flow to 130 m during the normal winter flow (Table 3.8; K-W test, $X^2=15.5982$, $n=41$, $P<0.01$). The

TABLE 3.7.--Time to kill and percent mortality of rainbow trout for stranding pools in Glen Canyon.

Months	Location	Isolating Flow	Time to kill (h)	% Mortality
Mar-Oct	0.5	< 8,000	16	50
Mar-Oct	-4.01	< 7,000	10	30
Mar-Oct	-4.01	< 7,000	20	100
Mar-Oct	-4.02	< 5,000	6	20
Mar-Oct	-4.02	< 5,000	20	100
All	-8.2	< 6,000	10	100
Mar-Oct	-8.9	< 8,000	8	100
Nov-Feb	-8.9	< 8,000	10	100
All	-9.7	< 6,000	7	80
All	-9.7	< 6,000	10	100
All	-11.0	< 5,000	8	100
All	-11.7	< 8,000	10	100
Mar-Oct	-11.9	< 4,000	15	100
All	-13.0	< 9,000	7	40
All	-13.0	< 9,000	9	80
All	-13.0	< 9,000	10	100
Mar-Oct	-14.0	< 5,000	64	100
Mar-Oct	-14.81	< 11,000	7	100
Nov-Feb	-14.81	< 11,000	4	100
All	-14.82	< 10,000	7	100
Mar-Oct	-14.83	< 4,000	18	90
Mar-Oct	-14.83	< 4,000	19	100

Mean distance travelled per day ranged from 32 m during the "B" study flow to 130 m during the normal winter flow (Table 3.8; K-W test, $X^2=15.5982$, $n=41$, $P<0.01$). The mean distance traveled per hour for fish followed for 24 hours was not different among flows (Mann-Whitney U test, $Z=-1.67$, $P=0.09$, $n=92$).

TABLE 3.8.--Mean distance traveled per day, distance from shore, and maximum depth of implanted rainbow trout.

Study Flow (cfs)	Mean	SD	Cases
<i>Mean distance traveled per day (m)</i>			
5,000 constant	107.4	85.02	17
11,000 constant	32.0	12.17	3
Study B (5,000-15,000)	31.5	17.31	4
Study C (10,000-20,000)	66.7	25.70	3
Normal fall	91.5	86.97	2
Normal winter	130.0	85.38	12
<i>Mean distance from shore (m)</i>			
5,000 constant	23.3	17.33	67
11,000 constant	12.1	7.14	15
Study B	22.5	16.65	22
Study C	16.9	11.25	16
Normal fall	16.8	11.56	28
Normal winter	15.3	8.08	48
<i>Mean depth (m)</i>			
5,000 constant	1.0	0.90	68
11,000 constant	0.8	0.34	15
Study B	1.9	2.14	22
Study C	1.2	0.51	15
Normal fall	1.2	0.72	26
Normal witer	1.2	0.60	51

Implanted trout spent most of their time (86%) in runs, followed by eddies (8%), riffles and pools (3%), and backwaters (<1%). There was little evidence to indicate that trout use different habitats under different flows. Implanted trout were located furthest from shore (23 m) during the 5000 cfs flows and closest to shore (12 m) during the 11,000 cfs flow. Although we were unable to measure the depth that trout utilize, we did measure the

maximum depth at each trout location under existing flow conditions. Depths utilized ranged from 0.3 to 8.1 m with a mean of 1.2 m (Table 3.9), and differed among flows (K-W test, $X^2 = 12.61$, $P < 0.05$, $n = 196$).

Mean current velocity where fish were located was 0.16 m/s at the bottom, 0.28 m/s at midwater, and 0.47 m/s at the surface (Table 3.10). Velocities where trout were

TABLE 3.9.--Mean bottom, midwater and surface velocities and standard deviations (SD) of locations of implanted trout.

Study Flow (cfs)	Velocity (m/S)	SD	n
<i>Bottom velocity</i>			
5,000 Constant	0.10	0.06	27
11,000 Constant	0.27	0.14	5
Study B	0.14	0.09	10
Study C	0.30	0.18	3
Normal Winter	0.21	0.14	19
<i>Mid-water velocity</i>			
5,000 Constant	0.16	0.13	29
11,000 Constant	0.38	0.23	6
Study B	0.33	0.22	9
Study C	0.45	0.26	3
Normal Winter	0.38	0.24	19
<i>Surface velocity</i>			
5,000 Constant	0.28	0.36	55
11,000 Constant	0.29	0.21	12
Study B	0.32	0.25	10
Study C	0.79	0.36	14
Normal Fall	0.55	0.31	20
Normal Winter	0.67	0.39	41

TABLE 3.10. Mean distance traveled per hour over a 24 hour period by implanted trout.

Trout No.	Flow (cfs)	Mean Dist. (m)	SD	Cases
3	1,900-19,000 fluc.	32.6	27.33	22
4	1,200-15,200 fluc.	32.5	26.35	23
6	5,000 constant	26.2	24.06	23
10	15,000 constant	20.0	12.82	24

located were different between study flows at all three depths (K-W test, $P < 0.01$). Mean velocities at 5,000 cfs constant flow were lower than during other study flows for all depths. From visual observations, it appeared that trout spent most of their time between the bottom and midwater. It was not possible to determine the exact depth of our fish with radios.

Predominant and secondary substrates were noted by visual observations at the sites where fish were located. Sand was the most commonly used substrate (59%), followed by gravel (20%), cobble (8%), rubble and silt (6% each), and boulder (1%). Secondary substrates were gravel (48%), rubble (17%), cobble (16%), sand (11%) and boulder (9%).

The percent of substrate surface covered with aquatic vegetation (mostly *Cladophora*) at trout locations ranged from 0 to 95% with a mean of 40% (SD=30, $n=161$). Percent cover did not vary among flows (K-W test, $X^2=10.0$, $n=156$, $P=0.08$).

Discussion

Trout Spawning

Rainbow trout spawning activity occurred in Glen Canyon from late December, 1990 through April, 1991. Although the degree to which natural reproduction contributes to the trout fishery in Glen Canyon is not clear, there were fair numbers of naturally reproduced trout captured in August and November, 1991 electrofishing samples (S. Morgensen, unpublished data). Earlier studies by Maddux et al. (1987) estimated the contribution of naturally produced trout at 27% under predominantly high steady flows. Trout use spawning gravels ranging in size from 6.35 mm to 101.6 mm but prefer 13 to 38 mm gravels (Raleigh et al 1984). The size of gravel used and the depth to which the redd is dug vary with the size of the fish (Milner et al. 1981).

In Glen Canyon, D50 ranged from 28 mm at -4.0 mile bar, to 59 mm at -6.1 mile bar. This was larger than the D50 of 12.5-23.5 mm which Kondolf et al. (1989) reported from studies done in the Pacific Northwest. They reported a D50 of 33 mm for redds in tributaries to the Colorado River in the Grand Canyon, 22 mm for unspawned tributary gravels, 10.5 mm for samples from -4 mile and -8 mile redds, and 16 mm from -12 mile unspawned gravel.

Geometric mean substrate diameter showed a similar gradation throughout the reach. The D_g ranged from 34.6 mm at -14.0 mile bar, to 16.5 mm at -8.9 mile bar, to 14.1 mm at -4.0 mile bar. The average D_g in redds in the South Fork Salmon River, Idaho was 13-35 mm (Chapman 1988), and Kondolf et al (1989) reported that D_g ranged from 5.2 to 24.5 mm for the Colorado River.

Spawning gravels in Glen Canyon have apparently increased in size since 1984 (Kondolf et al. 1989). Differences may be partially attributed to their small sample size, three samples compared to 60 for our study, and to the difference between redds and unspawned gravels. However, we suspect that gravels have actually gotten larger as the reach continues to armor. There is no source for replenishment of gravel between the dam and Lee's Ferry.

Percent of fines can be an important factor in egg survival and fry emergence. Fine materials less than 0.2 mm permeate to the bottom of redds and choke eggs, while sands of approximately 0.5 mm diameter form a beneficial seal which blocks penetration by finer materials (Chapman 1988). Dissolved oxygen has been shown to be inversely related to the percentage of fines less than 0.85 mm (Chapman 1988).

Percent of fines does not appear to be a significant problem for trout spawning in Glen Canyon. Mean percent fines < 0.85 mm ranged from 8.5% at -6.1 mile bar to 17.7% at -8.9 mile bar. Higher values for -8.9 and -14.0 mile bar are biased by collections from the furthest downstream transects which had more fine sediments but were not used by spawning trout. Kondolf et al. (1989) estimated that less than 14% of fines < 0.85 mm and less than 30% of fines < 3.35 mm were needed for successful alevin emergence. Chapman (1988) reported 100% emergence success when 10% of fines were < 3 mm, and 60% emergence success when 20% of fines were < 3 mm. Mean percent fines < 3.35 mm ranged from 13-23% in our study.

The bar at -6.1 mile was an anomaly in the continuum of substrate size from larger upstream to smaller downstream. This bar was unique among the four in being located

midchannel instead of adjacent to the shore. It had the highest median gravel diameters, and a higher embeddedness rating and a lower percentage of fine material than -8.9 mile bar.

The majority of the spawning activity which we observed occurred at -4.0 mile and -8.9 mile bars. These two bars had the smallest D_g 's, 14.1 and 16.5 mm, and the lowest embeddedness ratings, 1.3 and 1.5. Only 30 redds were observed at -6.1 mile bar, and none were seen at -14.0 mile bar.

Suitable spawning gravels and redds were observed at all elevations. There was no apparent correlation between density of redds and elevation (discharge level). Density of redds was weakly correlated with smaller substrate size; 83% of the redds observed were above the 5,000 cfs discharge level.

In addition to scouring of spawning gravels, fluctuating flows can disrupt spawning (Burt and Mundie 1986). In the Campbell River, British Columbia, below John Hart Dam, chinook salmon (*Oncorhynchus tshawytscha*) stopped digging redds when discharge increased or decreased; flow decreases were more disruptive than increases. The degree to which trout spawning behavior is disrupted by fluctuating flows in Glen Canyon is unknown.

Stranding

Fluctuating flows below dams, especially when rapid rates of change are involved, can result in stranding of fish (Kroger 1973, Mundie 1991, Burt and Mundie 1986). Rainbow trout adults and fry are stranded by fluctuating flows in Glen Canyon. During the December 1989 to March 1991 survey period, there were 11 areas where adult trout became stranded and 10 areas where we observed stranded fry. Discharges at the time of isolation ranged from 4,000 cfs to 11,000 cfs. The status of stranding pools may change over time. Recent surveys have revealed changes in the location and size of stranding pools.

More adult trout became stranded during the spawning period than during the remainder of the year. Most of the areas where adult trout become stranded were known spawning sites. For this reason the impact of stranding on the trout population may be greater than numbers of stranded trout would suggest.

Most of the stranded trout fry we observed were at two locations, -4.0 and -10.4 mile. This is probably a reflection of better alevin emergence and early fry survival at these locations than at other locations along the river. Most stranding of trout fry occurred in the summer.

Movement

Half of the trout we followed with radio telemetry remained in the general location where they were caught and released. This high affinity of trout for particular locations was observed during other portions of this study (stranding, mark and recapture).

Trout in his study moved an average of 114 m between weekly observations, and 32 to 130 m per day depending on the flow regime. Trout traveled shorter distances during constant 11,000 cfs flows and "B" study flows (5,000-15,000 cfs) than during normal high fluctuations and 5,000 cfs constant flows. This was contrary to what Bowen (1991) found in the Green River below Flaming Gorge, where trout moved less during fluctuating flows than during constant flows.

There are several factors which may explain the greater movement of trout at 5,000 cfs constant discharge. Channel morphology and discharge in Glen Canyon have resulted in the deposition of gravels and rocks used by trout for spawning and cover at elevations associated with moderate discharge levels. Trout tend to be territorial (Hunter 1991). Fluctuating flows may result in trout being forced out of their territories and into territories of other fish. Resulting increases in aggressive encounters may increase fish movement.

Swimming and foraging energetics may be another explanation. Lower velocities were experienced at 5,000 cfs discharge, therefore less energy would be needed for stationary swimming (maintaining position), allowing more available energy for random swimming. Also, if invertebrate drift is less at 5,000 cfs, fish may move further to feed. Behavioral responses can only be hypothesized since we have no information on fish activities relative to movements.

There is a small amount of evidence from our 24 hour and daily telemetry trials to suggest that fish may travel less during constant flows, (11,000 and 15,000 cfs) than during fluctuating flows. Johnson et al. (1987) stated that trout shifted from random swimming to stationary swimming during higher discharges. Moderate constant flows may provide the right combination of current velocities and substrates for trout to establish and maintain territories.

Habitat characteristics measured where trout were located were similar to other studies (Raleigh et al. 1984, Gosse 1982, Gosse and Gosse 1985, Schrader 1989, Bowen 1991). Bowen (1991) found that there was no significant association between discharge and use of depth, substrate, fish elevation, cover or distance from the surface. He also found that there was no significant relationship between discharge and focal velocity. He estimated that only about 4% of the variation in focal velocity could be explained by discharge.

We found significant differences in distance from shore, maximum water depth, current velocity, and substrates between study flows. We found that trout in Glen Canyon used depths from 0.3 to 8.1 m, but were most often found in < 2 m of water. This may be a function of the availability of preferred sand and gravel substrates at shallow depths under moderate to high discharge levels.

Modal focal velocities for stationary swimming rainbow trout in the Colorado River were 0.30-0.35 m/s in the winters of 1984-85 (Gosse and Gosse 1985). This compares favorably with the columnar velocities measured in this study.

Gosse (1982) noted lower velocities of 0.7-0.21 m/s for trout that were randomly swimming than those that were stationary swimming (0.12-0.41 m/s) in the Green River below Flaming Gorge. This was similar to what we found for velocities during the 5,000 cfs constant discharge when fish moved greater distances compared to other flows.

Because of our small sample sizes, our habitat use findings should be considered preliminary. As more fish are implanted and tracked, our ability to resolve flow effects will improve. Ultimately we hope to express the short-term costs to trout of flow fluctuations in energy units. Only then can we evaluate the relative importance of displacement compared to other direct (spawning disruption, stranding) and indirect (food base) effects of Glen Canyon Dam.

Appendix 3.1. Cumulative size distributions for gravel samples from spawning bars in the Lee's Ferry Reach.

Transect No. and River Mile	Cumulative Percent Finer than Indicated Size (mm)											
	0.045	0.25	0.5	1.0	2.0	3.18	6.35	12.7	25.4	50.8	76.2	152.5
1A -4.0 Mile Bar	0.1	3.3	9.3	18.1	24.4	28.1	38.9	52.5	80.9	100.0	100.0	100.0
1B -4.0 Mile Bar	0.0	1.5	6.2	14.8	20.0	22.9	32.3	47.4	78.5	93.5	100.0	100.0
1C -4.0 Mile Bar	0.1	2.2	5.6	12.0	18.1	21.5	31.0	43.4	66.2	96.4	100.0	100.0
5A -4.0 Mile Bar	0.1	2.0	4.5	12.3	18.5	22.0	32.4	45.2	72.1	100.0	100.0	100.0
5B -4.0 Mile Bar	0.0	0.7	2.0	7.5	11.4	14.0	21.0	30.6	45.5	71.6	100.0	100.0
5C -4.0 Mile Bar	0.0	1.5	4.5	13.6	19.5	23.2	32.3	43.5	67.1	93.7	100.0	100.0
9A -4.0 Mile Bar	0.0	0.6	1.8	7.3	11.8	14.8	22.7	32.2	46.1	69.5	86.8	100.0
9B -4.0 Mile Bar	0.0	0.8	3.0	8.1	12.5	14.8	20.8	30.7	44.8	73.5	100.0	100.0
9C -4.0 Mile Bar	0.0	2.9	7.6	17.6	24.0	27.6	37.2	48.5	68.4	98.6	100.0	100.0
13A -4.0 Mile Bar	0.0	0.8	2.4	7.6	12.9	17.6	25.0	34.9	45.9	70.4	88.0	100.0
13B -4.0 Mile Bar	0.0	0.9	3.2	9.3	11.5	12.7	16.4	23.4	36.2	57.9	63.5	100.0
13C -4.0 Mile Bar	0.0	1.7	5.1	14.4	18.0	19.9	25.4	34.3	48.2	70.0	82.7	100.0
17A -4.0 Mile Bar	0.0	0.5	3.9	9.9	13.8	15.5	19.8	26.0	35.6	51.3	72.4	100.0
17B -4.0 Mile Bar	0.0	1.6	5.8	9.5	11.8	13.0	17.7	26.2	39.6	66.7	79.5	100.0
17C -4.0 Mile Bar	0.0	0.8	1.9	6.8	9.8	11.4	16.2	22.8	32.4	43.3	65.3	100.0
5A -6.1 Mile Bar	0.0	1.7	6.4	15.5	16.9	17.7	21.9	31.1	48.9	68.1	77.5	100.0
5B -6.1 Mile Bar	0.0	1.1	3.9	9.8	11.4	12.6	17.0	24.0	37.2	52.1	63.4	100.0
5C -6.1 Mile Bar	0.0	1.7	5.5	11.5	13.8	15.1	19.8	26.2	39.8	39.8	66.6	100.0
7A -6.1 Mile Bar	0.0	1.2	4.3	9.2	10.4	11.5	14.3	18.7	28.6	45.7	58.2	100.0
7B -6.1 Mile Bar	0.0	1.1	3.3	7.4	8.2	8.6	10.5	14.9	24.6	34.0	39.1	100.0
7C -6.1 Mile Bar	0.0	1.0	4.6	7.5	8.5	9.2	11.8	16.4	25.1	34.2	37.4	100.0
9A -6.1 Mile Bar	0.0	1.8	5.8	9.8	11.0	11.8	14.5	19.9	29.9	45.8	45.8	100.0
9B -6.1 Mile Bar	0.0	0.9	3.4	7.4	8.6	9.4	12.4	16.9	25.8	37.2	50.1	100.0
9C -6.1 Mile Bar	0.0	0.8	2.6	6.3	7.5	8.3	10.9	16.5	30.2	43.4	59.5	100.0
11A -6.1 Mile Bar	0.0	2.0	7.5	14.2	15.7	16.5	20.4	28.9	43.4	64.3	75.2	100.0
11B -6.1 Mile Bar	0.0	0.6	1.7	8.4	10.0	11.1	14.4	19.7	28.8	47.8	59.4	100.0
11C -6.1 Mile Bar	0.0	1.1	5.9	16.5	18.5	19.6	23.0	28.8	41.6	81.8	100.0	100.0
12A -6.1 Mile Bar	0.0	0.9	4.6	10.2	11.1	11.7	14.2	20.0	30.9	41.1	44.7	100.0
12B -6.1 Mile Bar	0.0	2.2	5.9	10.0	11.3	11.9	16.8	25.1	37.0	59.4	76.1	100.0
12C -6.1 Mile Bar	0.0	0.9	2.4	9.5	10.9	12.1	16.0	24.4	36.5	57.4	71.1	100.0

Appendix 3.1 (continued). Cumulative size distributions for gravel samples from spawning bars in the Lee's Ferry Reach.

Transect No. and River Mile	Cumulative Percent Finer than Indicated Size (mm)											
	0.045	0.25	0.5	1.0	2.0	3.18	6.35	12.7	25.4	50.8	76.2	152.5
1A -8.9 Mile Bar	0.9	60.6	99.6	99.9	99.9	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1B -8.9 Mile Bar	0.0	2.9	12.7	19.9	23.1	25.0	33.4	45.4	61.5	88.8	100.0	100.0
1C -8.9 Mile Bar	0.0	2.0	11.0	19.9	23.1	25.7	35.6	47.4	63.2	88.2	100.0	100.0
5A -8.9 Mile Bar	0.0	3.0	12.7	16.8	19.2	20.8	26.5	34.4	47.0	78.2	89.0	100.0
5B -8.9 Mile Bar	0.0	1.2	10.9	17.2	20.1	22.1	29.5	39.4	52.4	73.7	85.8	100.0
5C -8.9 Mile Bar	0.0	1.4	7.0	11.0	13.8	15.4	21.2	29.4	40.4	72.5	100.0	100.0
9A -8.9 Mile Bar	0.0	1.3	8.7	18.6	20.9	22.0	25.7	31.1	38.0	55.2	75.4	100.0
9B -8.9 Mile Bar	0.0	0.5	5.9	10.9	12.3	13.5	17.8	24.3	32.3	49.4	69.7	100.0
9C -8.9 Mile Bar	0.0	1.1	7.2	14.0	18.0	20.7	26.9	34.4	43.9	61.3	96.8	100.0
13A -8.9 Mile Bar	0.0	1.0	6.8	12.3	13.8	15.4	22.2	31.8	44.7	59.3	70.2	100.0
13B -8.9 Mile Bar	0.0	1.1	6.5	11.7	13.2	14.1	18.4	26.0	39.0	53.2	71.0	100.0
13C -8.9 Mile Bar	0.0	0.7	5.7	13.5	16.1	17.8	23.2	31.1	40.1	57.5	81.9	100.0
18A -8.9 Mile Bar	0.0	4.2	10.8	13.4	15.2	17.0	23.2	32.0	45.0	65.8	91.6	100.0
18B -8.9 Mile Bar	0.0	0.2	1.9	4.2	5.4	6.2	9.2	13.2	19.1	33.3	42.8	100.0
18C -8.9 Mile Bar	0.0	0.6	3.3	6.3	7.9	8.8	12.5	18.2	28.4	41.3	47.6	100.0
1A -14.0 Mile Bar	0.2	57.9	91.1	99.0	99.8	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1B -14.0 Mile Bar	0.8	21.2	33.7	36.1	36.8	37.3	39.8	43.3	48.4	56.6	71.3	100.0
1C -14.0 Mile Bar	0.1	3.4	8.0	9.6	10.2	10.7	12.6	15.1	19.2	30.7	49.4	100.0
4A -14.0 Mile Bar	0.1	4.2	14.4	19.4	21.0	22.3	27.6	34.3	41.1	52.6	55.1	100.0
4B -14.0 Mile Bar	0.0	1.8	8.4	12.4	14.6	16.0	21.1	28.3	37.7	54.3	54.3	100.0
4C -14.0 Mile Bar	0.0	1.2	4.5	7.4	9.2	10.3	13.7	17.6	22.5	29.4	35.0	100.0
7A -14.0 Mile Bar	0.0	1.6	7.1	10.2	11.7	13.0	17.0	23.1	32.5	51.2	56.7	100.0
7B -14.0 Mile Bar	0.0	0.6	2.5	4.2	5.0	5.6	7.4	10.3	16.5	31.1	32.9	100.0
7C -14.0 Mile Bar	0.0	1.3	4.6	7.4	9.3	10.4	14.4	20.1	28.3	41.4	57.0	100.0
10A -14.0 Mile Bar	0.0	0.5	2.1	3.1	3.5	3.8	4.7	6.4	9.3	14.6	23.0	100.0
10B -14.0 Mile Bar	0.0	1.9	6.7	9.8	11.3	12.3	15.8	21.2	31.8	52.1	52.1	100.0
10C -14.0 Mile Bar	0.0	2.5	7.6	10.4	12.3	13.4	16.9	21.5	28.7	40.9	51.1	100.0
13A -14.0 Mile Bar	0.0	2.0	9.5	13.3	14.2	14.7	17.0	22.0	31.1	44.3	68.8	100.0
13B -14.0 Mile Bar	0.0	1.1	5.2	8.4	9.3	9.8	12.5	17.7	26.5	40.9	47.7	100.0
13C -14.0 Mile Bar	0.0	2.3	5.5	7.8	8.7	9.5	12.3	16.9	25.6	44.4	48.4	100.0



4. Native Fishes

Robert W. Clarkson and D. Alan Kinsolving

During their evolutionary history, native fishes of the Colorado River Basin have been subjected to periods of major disturbances such as vulcanism, flooding, and drought that resulted in localized extirpations of entire aquatic faunas (Minckley et al. 1986). Recent changes to aquatic habitats of the Colorado River drainage, including emplacement of impassible hydroelectric dams and introductions of alien predator and competitor species, have also resulted in regional losses of native fishes. The difference between historic and recent events, however, is that historically the opportunity for reinvasion from unaffected sub-drainages within the basin ensured that such localized extinction events were temporary. Recent environmental and biological transformations have been of such widespread geographic distribution (basin-wide) that suitable refugia populations from which reinvasion could occur are essentially nonexistent. In addition, the environmental disturbance created by dams and introductions of exotics is of such duration (longer than the life-span of fishes) that native fishes cannot simply endure until better conditions arrive for completion of their life cycles.

Perhaps the most unique group of native fishes of the Colorado River Basin, the large-bodied "big river" fishes, are highly adapted for life in the variable, sometimes harsh environment of the larger rivers (Minckley 1973, 1991). This fauna includes Colorado squawfish (*Ptychocheilus lucius*), bonytail chub (*Gila elegans*), humpback chub (*G. cypha*), and razorback sucker (*Xyrauchen texanus*). All are on the federal endangered species list and, with the possible exception of humpback chub, all probably require larger, relatively pristine mainstem habitats for completion of their life cycles. Although such reaches may still exist, biological alterations (species introductions) may preclude their continued suitability for native fishes. That the big river species formerly occurred in all major river systems in the basin but now reproduce in only a few sub-drainages illustrates the spatial scale of these recent changes.

Three species of the native fish fauna in Grand Canyon, Colorado squawfish, bonytail chub, and roundtail chub (*G. robusta*), have been recently extirpated. The species that remain (humpback chub; speckled dace, *Rhinichthys osculus*; flannelmouth sucker, *Catostomus latipinnis*; bluehead sucker, *Pantosteus discobolus*), with the possible exception of the rare razorback sucker, likely persisted because they utilize tributaries largely unaffected by Hoover and Glen Canyon dams for successful completion of their life cycles.

All successfully spawn in tributaries (Carothers et al. 1981, Kaeding and Zimmermann 1983, Maddux et al. 1987, Maddux and Kepner 1988, Kubly 1990), and progeny either remain in tributaries or enter mainstem rearing habitats for completion of later life stages (Maddux et al. 1987, Carothers et al. 1981). Adults of many native species are found in tributaries throughout summer and autumn, after their which occurrence in catches declines coincident with equilibration between mainstem and tributary water temperatures (Suttkus and Clemmer 1979, Carothers et al. 1981, Maddux et al. 1987).

Thus, the Colorado River and its tributaries in Grand Canyon form part of an integrated whole, and a complete understanding of the effects of Glen Canyon Dam on the native fish fauna requires an understanding of both mainstem and tributary environments. The major focus of the Department's GCES native fishes research program is to investigate the interrelationships between mainstem and tributary aquatic habitats of Grand Canyon in terms of the distribution, abundance, and life history requirements of early life stages, with particular attention to endangered humpback chub and potential interactions with exotic species. Studies described in this section are primarily directed at quantifying the varied physical, chemical, and biological conditions to which native fishes are exposed in the mainstem and tributaries of Grand Canyon, and at describing how younger and smaller fishes attempt to cope with them. Particular attention is paid to rearing habitats within the Colorado River mainstem and the Little Colorado River, the latter being the only known spawning site and a major rearing habitat for humpback chub.

Our studies are largely concerned with the following areas of investigation: (1) changes in abundance, movements, and reproductive periodicity of native fishes in the LCR. This aspect of the Department's native fishes program, which is concentrated in the period of humpback chub reproduction, was initiated as a monitoring study in 1987 following the cessation of Phase I field efforts, and is meant to measure the long-term status of native fish populations; (2) movements, distributions, behaviors, and habitat utilization of smaller [< 150 mm total length (TL)] fishes in the mainstem and LCR. We hope to obtain measures of the amount of passive transport and active movement of fishes from tributary to mainstream habitats, and thus the potential relative contributions of mainstem and tributary reproduction to fish populations in Grand Canyon; (3) longitudinal biological and physical-chemical zonation in the LCR, with particular reference to differential distributions of native species. The upper 6 km perennial reach of the lower LCR presently is solely inhabited by speckled dace, and if humpback chub population augmentation is to be considered, the extent to which various structural, hydrological, and limnological attributes of the LCR limit the

rates, and spawning initiation of native fishes in the mainstem and LCR in relation to the history of hydrologic, thermal, and chemical conditions they have experienced. Knowledge of age structure, growth rates, and survivorship to a given age is fundamental to our understanding of the life history of native fishes in Grand Canyon. We intend to differentiate histories of young native fishes in relatively warm tributary waters from those that entered the cold mainstream at some point in their lives through examination of otoliths and length-frequency distributions, and to relate these movements to tributary and mainstream hydrologies; (5) diel changes in water chemistry (quality) and habitat transformation of mainstem backwaters in response to daily temperature and flow cycles. A better knowledge of the physical-chemical dynamics and variability of backwater habitats may eventually assist in determining the relationship between available habitat and population densities of native fishes, and in developing strategies for habitat improvement; and (6) changes in water chemistry parameters and structure of the fish community in other tributary streams. The composition and structure of the fish communities in different tributaries is indicative of environmental conditions in the streams and reflects their potential for rearing and population augmentation.

Methods

Because of the ongoing nature of both mainstem Colorado River and Little Colorado River native fishes research, samples and data are at various stages of analysis, and many could not be presented at this time. However, because of the integrated nature of our study designs, all methodologies are detailed but results are not always discussed.

Mainstem Colorado River

During the period of research flows (see Chapter 1), one or two water quality monitoring sondes (Hydrolab DataSonde Model 3) were emplaced at 12 tributary, backwater and mainstem locations for periods ranging from 20 to 74 hours. Water temperature, pH, conductivity and dissolved oxygen (as percent saturation and mg/l) were recorded at 15 min intervals. Because stable flows are uncommon and unpredictable, the majority of DataSonde data were collected during periods of stable water in order to obtain information that would be difficult or impossible to obtain after the termination of research flows.

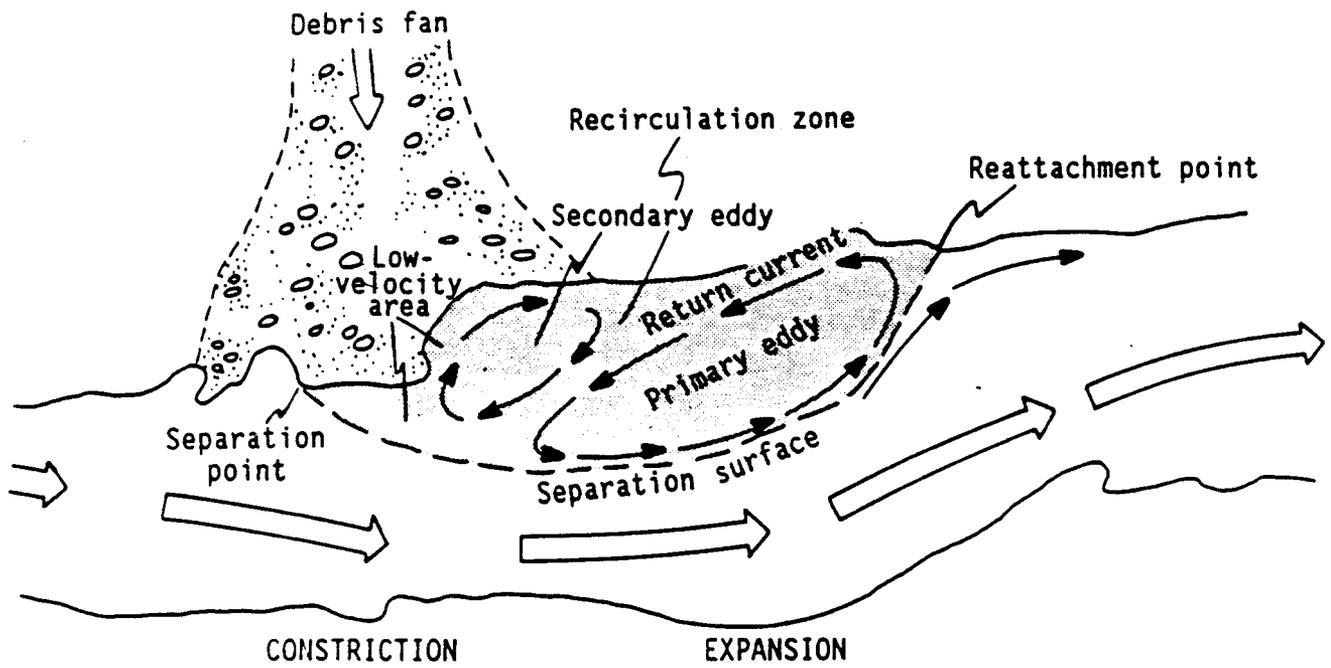
Down-river research trips took place during March/April, May, July and September of 1991, resulting in a total of 69 field days. Mainstem sampling was concentrated in

shallow, slow water nearshore areas known to be used for rearing by native fishes. The most conspicuous of these habitats is the backwater complex (Figure 4.1), which is typically associated with alluvial, fine-grained sediment deposits formed by recirculation zones (eddies) downstream from abutments of talus or bedrock or by debris fans at tributary mouths (Schmidt and Graf 1988). There are three sub-habitats in this complex: (1) the backwater, formed by the primary eddy return channel, where current speeds are lowest and conditions most divergent from the mainstream; (2) the backwater eddy, or secondary eddy, where current speeds and mixing are intermediate; and (3) the mainstream eddy, or primary eddy, where current speeds are fastest, and mixing results in conditions virtually identical to the mainstream.

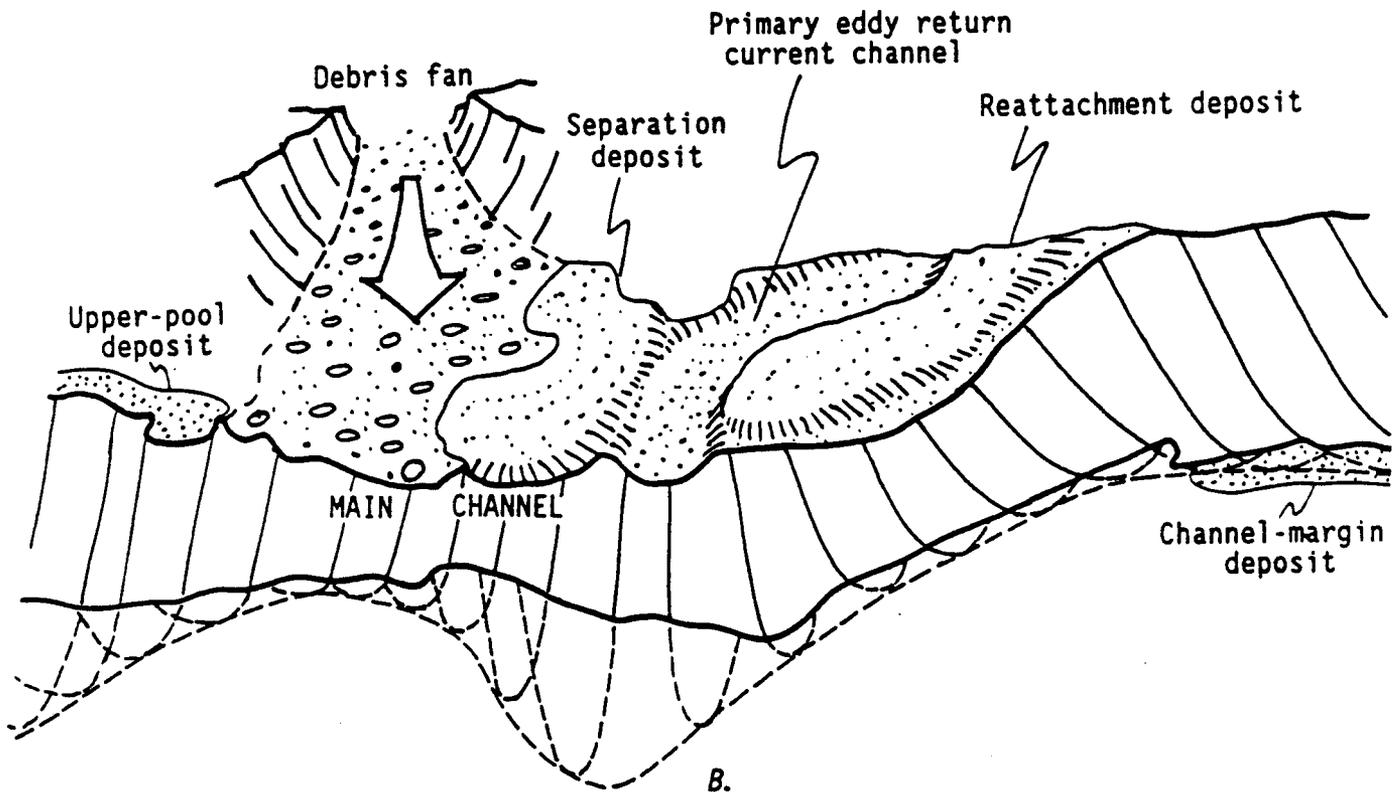
At opportunistically sampled sites, fishes were captured using either a straight or bag seine (3-10 m long, 1.6-3.2 mm mesh, 1-1.5 m high). Effort was recorded in m² of water seined and collected fish were identified, measured and enumerated following each seine haul. Unidentified fishes were preserved in 10% formalin or 95% ethanol for later identification in the lab. At each site the habitat type, dominant substrate, water temperature and site morphology were recorded.

At intensively sampled sites, fishes were captured by two methods. In the backwater portion of the site, block nets (3.2-6.4 mm mesh) were emplaced as necessary in order to prevent fish escape from the site. The site was then electrofished using one or two handheld probes powered by a Coffelt VVP pulsator and a 5000 watt generator. Following electrofishing, the site was seined using either straight or bag seines (as above), depending on site topography and size. Electrofishing and seining continued until no further fish were captured. During those times of year when very small (<25 mm) fish were present, the site was also seined using a 0.8 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.

Intensively sampled sites were mapped in one of two ways. The first method used an alidade and plane table in order 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. Precisely surveyed sites were mapped using a Leitz Total Station to generate maps that could later be tied to the Geographical Information System.



A.



B.

FIGURE 4.1.--Drawing showing morphological features associated with the backwater habitat complex (from Schmidt and Graf 1988). A. Flow patterns at high water; B. Exposed bed deposits at low water.

Water temperature and current speed were recorded at 10-30 evenly spaced locations along the longest axis of the backwater and at one location in the mainstream. Both measurements were taken at 0.6 depth. Water temperature was measured to ± 1 C using a digital type K thermocouple thermometer; current speed was measured to ± 0.01 m/sec using a Marsh-McBirney Model 201D electromagnetic flow meter. Dissolved oxygen (as percent saturation) and water turbidity (in nephelometric turbidity units) were each measured at one location per habitat type.

Prior to shocking and seining the site, 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 through a 45 μ m mesh plankton net. Sediment core samples were taken using a 50 cm³ minicore sampler. Sediment, benthos and plankton samples were preserved in 5-10% formalin for later laboratory identification and analysis.

Larval drift nets 3 m long, with 750 μ m mesh net, 500 μ m mesh bucket and 0.25 m² opening were deployed in nearshore mainstem and tributary locations. Current velocities were taken at the mouth of the net immediately after net deployment, and before retrieval. Mean of the two sets of readings was used in calculations of volumes filtered. Drift was preserved in 5% formalin, and sorted to invertebrate family, fish species, fish eggs, and algae-detritus categories in the lab. Because March and early April Paria River sampling took place during a period when no current meter was available, those samples were treated qualitatively, and analyzed only as presence-absence data.

Little Colorado River and Other Tributaries

Quarterly inflatable kayak trips from Blue Springs (RKM 21) to near the mouth were undertaken to characterize seasonal and longitudinal variations of water quality. Water temperature, conductivity, pH, and dissolved oxygen were measured with a Hydrolab Surveyor 3. 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 end point, 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.

Two base camps were established on the LCR, one above the mouth at RKM 1.9 on May 1, 1991, and the other at the confluence with Salt Trail Canyon at RKM 10.5 on May 15. Four, 2-3 person crews were rotated weekly between the two camps. Thirteen hoop

nets (2-3 m long, 6.4 mm-mesh, 1.0 m diameter of the largest hoop) were deployed between RKM 0.1-1.2, and six between RKM 9.1-11.6. Hoop nets and irregular trammel net sets (23-30 m long, 38-51 mm inner mesh, 254-381 mm outer mesh, 1.5-1.8 m high) were situated at or close to sites previously utilized during May 1987-1990 as part of the Department's annual monitoring program. Hoop nets were checked twice daily (except on weekly crew-transfer days) and fished nearly continuously through June 30. Sampling intensity was decreased to 3-8 day periods once or twice monthly after that date. Seines (1-10 m long, 0.8-6.4 mm mesh, 1-1.5 m high), fine-meshed dip nets, and minnow traps (0.5 m long, 800 μ m mesh) were also employed extensively.

Larval drift nets as described above were deployed in duplicate or triplicate at each camp every other day during May-June, and at less frequent intervals thereafter. Sampling intervals encompassed daytime, crepuscular, and nighttime periods. Opportunistic drift sampling at other sites in the LCR and at other tributary mouths was also undertaken.

Post-larval fishes collected by other means were identified to species, weighed to ± 1 g if longer than approximately 75 mm, and measured to ± 1 mm TL. Fishes were examined for presence of external parasites, abrasions, and other external anomalies. Humpback chub ≥ 150 mm TL were tagged with passive integrated transponders for mark and recapture. Beginning in October, other native species were similarly marked. Samples of native fishes were preserved in 10% formalin and 95% ethanol for diet analyses and ageing, respectively. Unidentified larvae were identified in the lab using keys of Snyder (1981) and Snyder and Muth (1990). Numbers of taxa and life stages of invertebrates in guts of native fishes were obtained by dissection of preserved specimens. For each fish, the presence and approximate numbers of internal parasites were recorded.

Other than from the LCR, tributary confluence zones were sampled qualitatively using seines or a bank shocker. Most tributaries were seined as often as possible in locations where fish capture was probable. Because of the qualitative nature of tributary sampling, effort was not calculated.

Behaviors of young-of-year fishes in the LCR (A.T. Robinson, unpublished manuscript) were evaluated using the time-bound focal animal sampling method of Altman (1974). Observations were of larval and post-larval young-of-year chub, dace, and suckers in a variety of nearshore habitats < 0.5 m in depth. The focal animal was identified *in situ* or collected and identified following a continuous 5 min period. The amount of time spent on six behavioral activities (feeding, swimming, schooling, chasing, being chased, and other) was recorded during sunrise, midday, and late afternoon periods. Time budgets for

behaviors and occupation within vertical zones of the water column were arc-sine transformed prior to application of parametric statistical analyses.

A network of 3-10 points encompassing the areas sampled by nets was measured for depth, current velocity, substrate, and cover features to characterize habitats used by fishes in the LCR. Depths and flows were measured using either a Marsh-McBirney Model 201D or Swoffer Instruments Model 2100 Series current velocity meter/wading rod combination. Substrates were classified to major categories of clays, silts, sands, gravels, cobbles and boulders according to criteria and terminology of the American Geophysics Union (Lane 1947). In addition, travertine (consolidated), calcium carbonate (unconsolidated floc), and detritus substrate categories were established. Features of aquatic habitats potentially used as cover by fishes, including turbidity, turbulence, depth > 0.5 m, shore ledges and undercut banks, overhanging vegetation, dense instream vegetation, large boulders, and upstream, undercut travertine dams, were also recorded.

Results

Water Quality and Hydrology

Mainstem Colorado River--DataSonde traces from 13 locations in backwater and mainstream areas were examined. The traces showed changes in water quality parameters over periods ranging from 18 to 36 hours during both stable and fluctuating stage during controlled research flows in April and May. It appeared that dissolved oxygen levels were incorrect for many early traces, possibly due to calibration error, and that actual levels were somewhat lower. However, because relative (within trace) changes are probably correct, they were retained for further analysis. Selected Sonde locations and habitat types are shown in Figure 4.2. In general, for stable water periods, both backwater and mainstream locations showed a daily cycle with water temperature, dissolved oxygen and pH reaching their peaks in late afternoon, and falling to their lowest levels prior to dawn. Mainstream locations showed considerably less daily variation than did backwater locations in all parameters and generally showed increasing variability with downstream distance. Even during stable flows each backwater showed different trends, and the amplitude, timing and periodicity of all traces were dissimilar. During periods of fluctuating flows, both backwater and mainstream traces became chaotic and difficult to interpret.

Traces for a backwater and associated mainstream eddy (RM 201.6, river right) during stable flows are reproduced in Figure 4.3. Water temperature in the connected

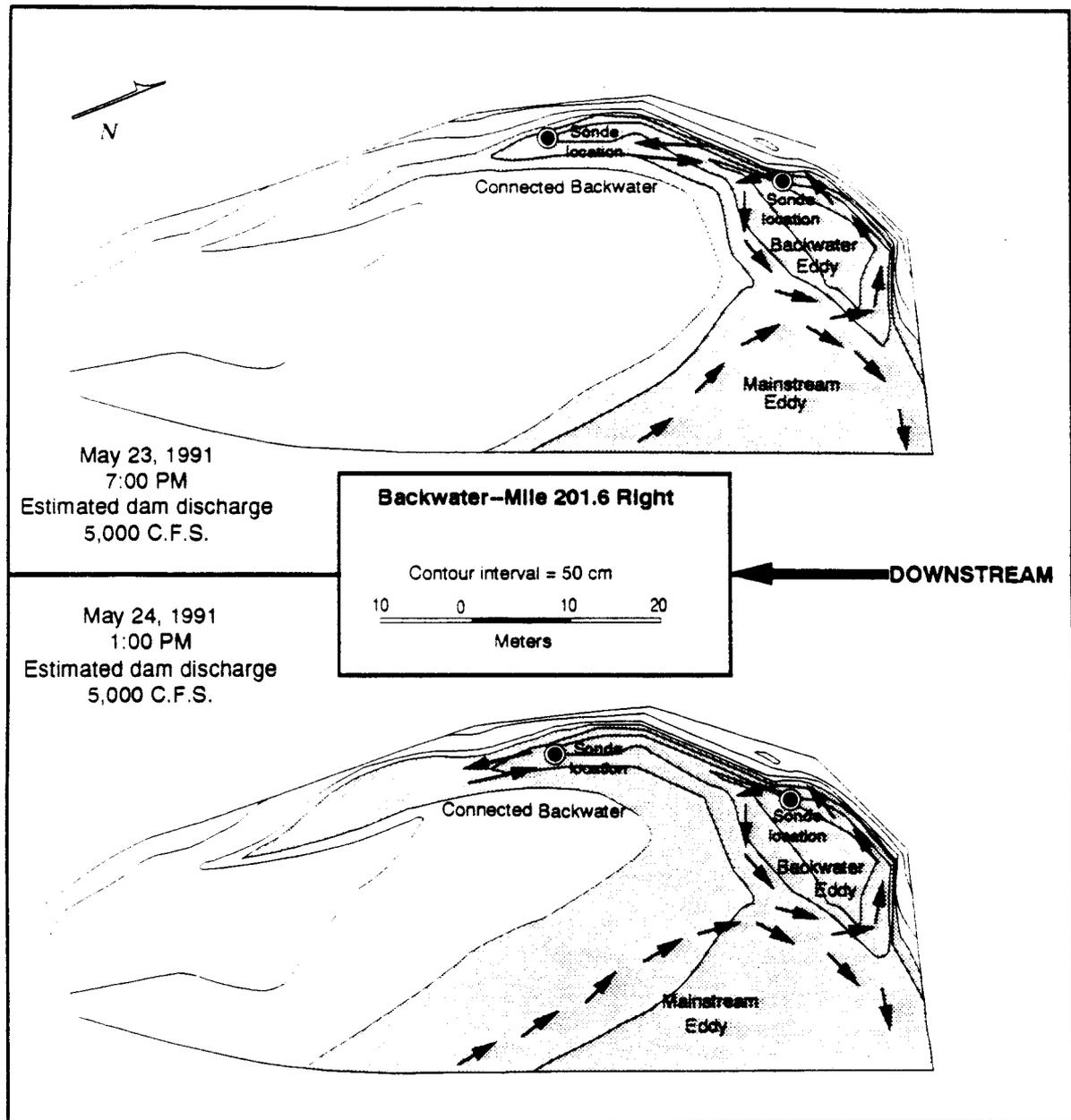


FIGURE 4.2.--Map of the backwater at mile 201.6. Site was surveyed at approximately 1700 hrs on May 23rd 1991 using a Leitz Total Station. Wetted perimeter at times other than time of survey was calculated from the associated Data Sonde trace.

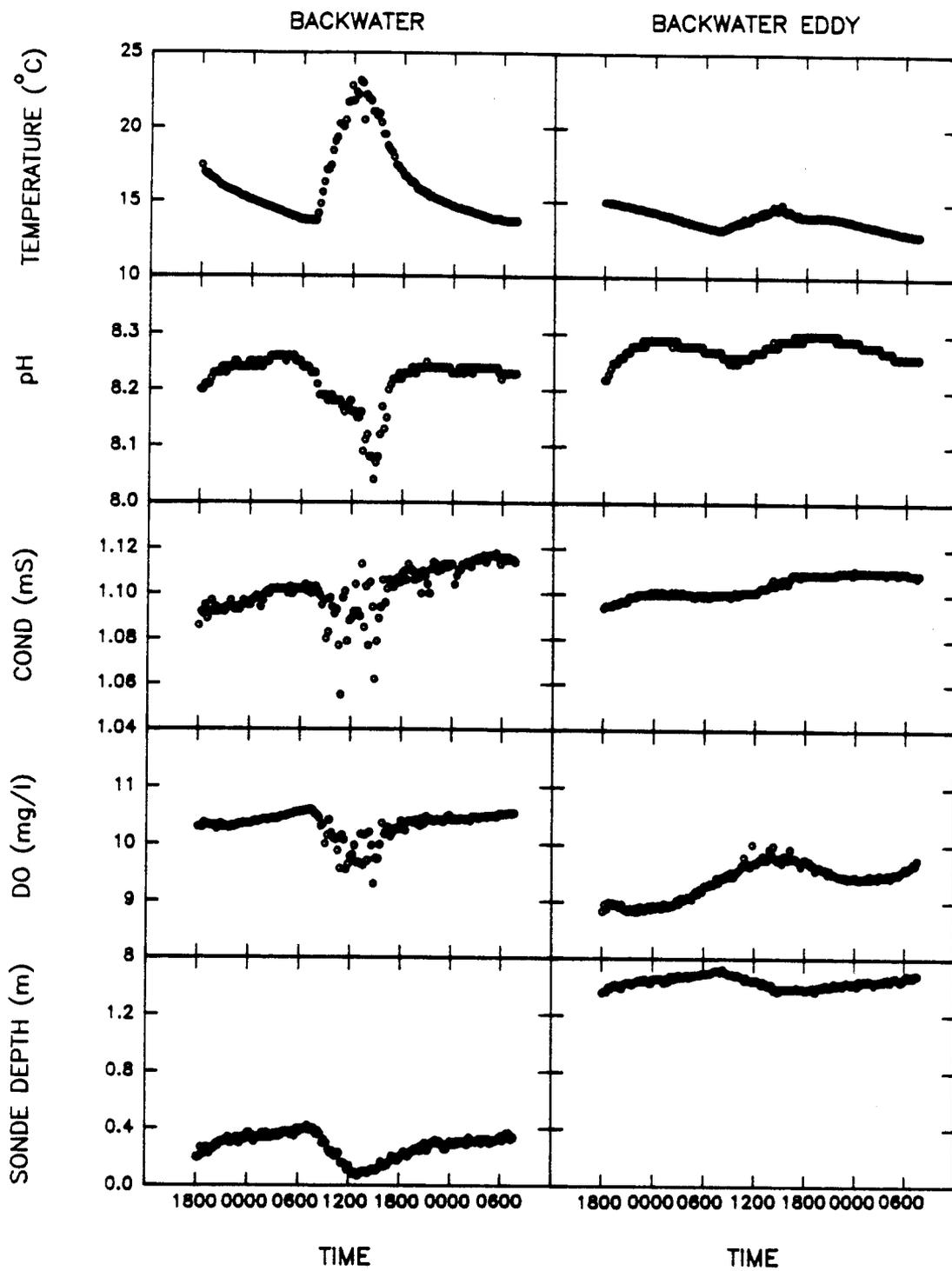


FIGURE 4.3.--Datasonde traces from the backwater and associated backwater eddy at mile 201.6.

backwater warmed extensively during the day and fell to near river levels at night. Both dissolved oxygen and pH levels reached their lowest points early in the afternoon. This was the reverse of most backwaters, and can probably be explained by low productivity in this particular location due to a lack of suitable substrates (shifting unstable sands) for algal colonization resulting in virtually no autochthonous production of oxygen by photosynthesis. During those periods when dissolved oxygen, temperature or pH in the backwater differed greatly from the river, the traces showed increased noise due to surges of water from either further up the backwater or from the mainstream passing the sonde.

The associated mainstream eddy trace showed very different patterns and reduced magnitude of daily fluctuations (Figure 4.3). The most extreme difference between mainstream and backwater locations was in levels of dissolved oxygen. In the river, oxygen levels peaked near 1500 hrs, when backwater levels were at their lowest. Changes in water level were probably due to daily changes in rates of evapotranspiration, because dam discharge during this period was relatively constant.

DataSonde traces from backwaters at RM 60.66 right and 60.85 left during strongly fluctuating flows in early May of 1991 are reproduced in Figure 4.4. Maps of the backwaters in which they were located are shown in Figures 4.5-4.6. In spite of the close physical proximity of these backwaters to one another, the traces are very different for most parameters. Because these traces were made during a period of widely fluctuating flows, neither backwater had a chance to warm a great deal since the previous high release, causing only a slight reduction in water temperature when the backwater was invaded by the river.

Little Colorado River and Other Tributaries--Pronounced gradients of several water quality parameters were apparent from longitudinal surveys of the LCR (Figure 4.7). Conductivity of the LCR was 4,012 $\mu\text{S}/\text{cm}$ in the Blue Spring outflow, increased to 4,726 μS at RKM 14.9 above Atomizer Falls, and dropped to approximately 4,600 μS downstream. pH was 6.0 in Blue Spring at RKM 21 and continually increased downstream to a high of 7.8 near the mouth. The rate of increase was greatest between Blue Spring and RKM 15. Dissolved oxygen also increased rapidly downstream from Blue Spring (3.7 mg/l) to RKM 14.9 (7.7 mg/l), after which it remained relatively steady near 7.5 mg/l. Carbon dioxide exhibited a similar, but opposing, pattern of marked change between Blue Spring (670 mg/l) and RKM 14.9 (280 mg/l). CO_2 levels declined to 163 mg/l near the LCR terminus.

Alkalinity and turbidity displayed a trend contrary to CO_2 , with the reach between Blue Spring and RKM 14.9 relatively constant at 700-740 mg/l CaCO_3 and 1-9 N.T.U.,

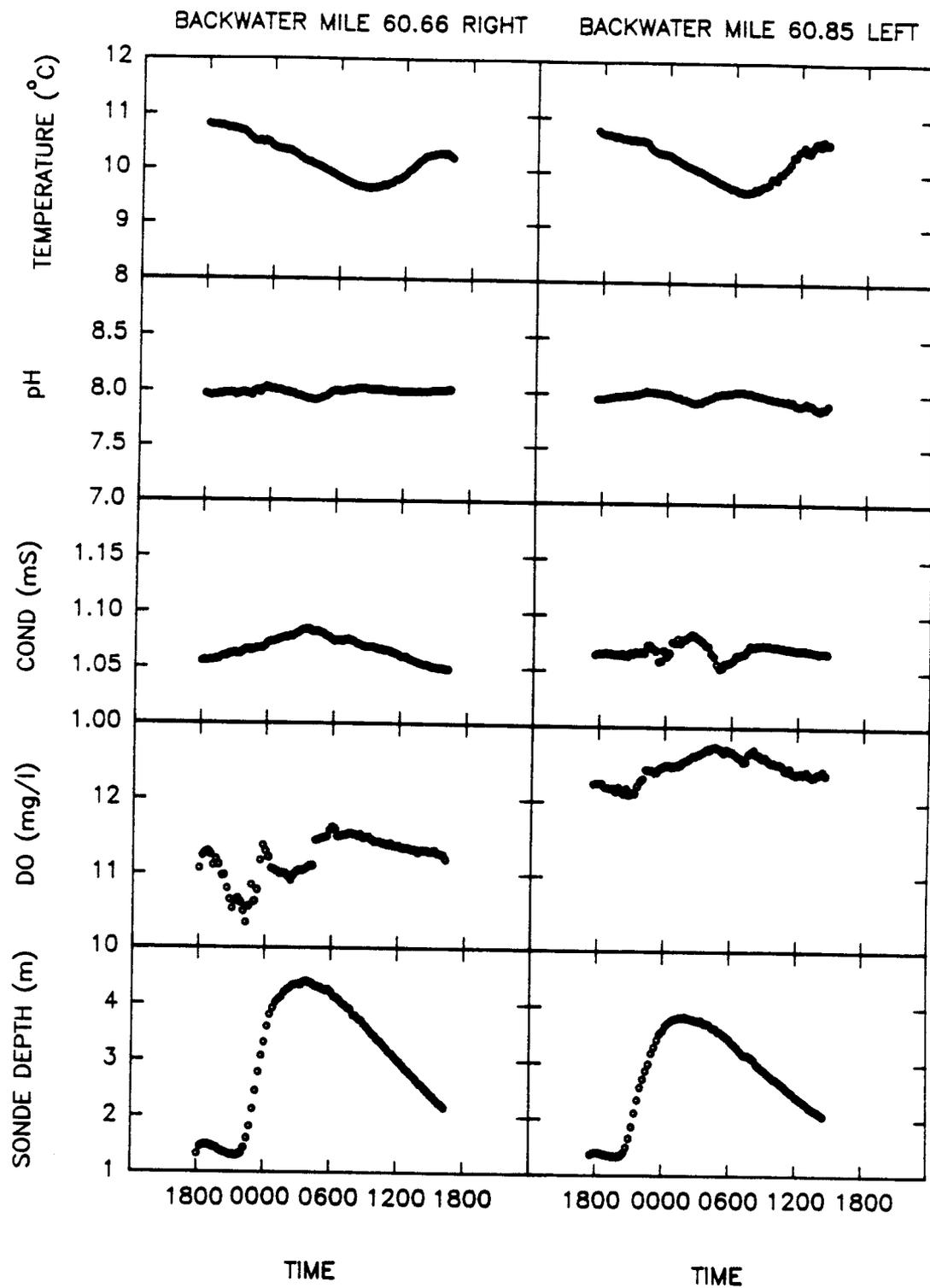


FIGURE 4.4.--Datasonde traces from backwaters at miles 60.66 and 60.85.

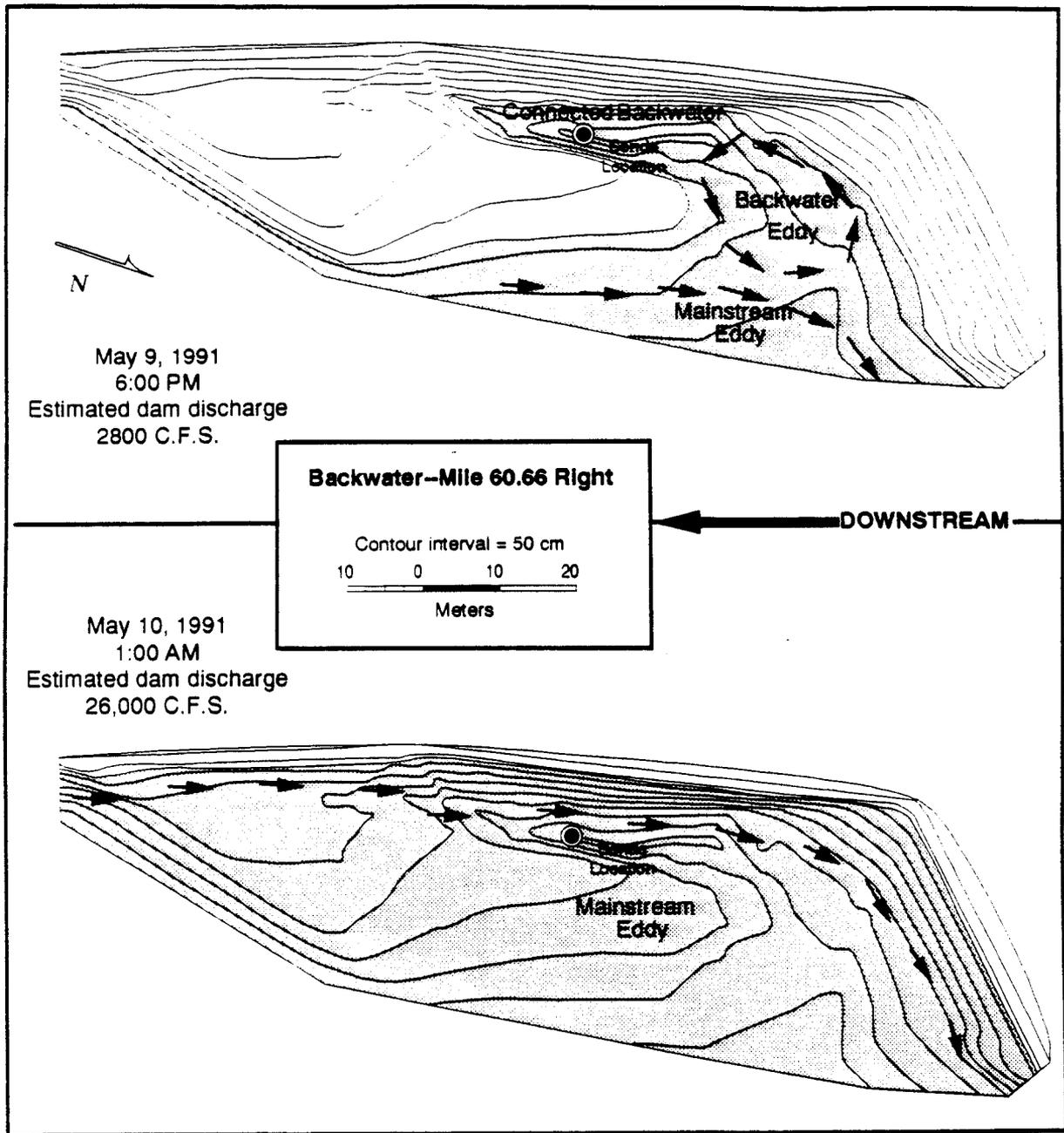


FIGURE 4.5.--Map of the backwater at mile 60.66. Site was surveyed at approximately 2:00 pm on May 9th 1991 using a Leitz Total Station. Wetted perimeter at times other than time of survey was calculated from the associated Data Sonde trace.

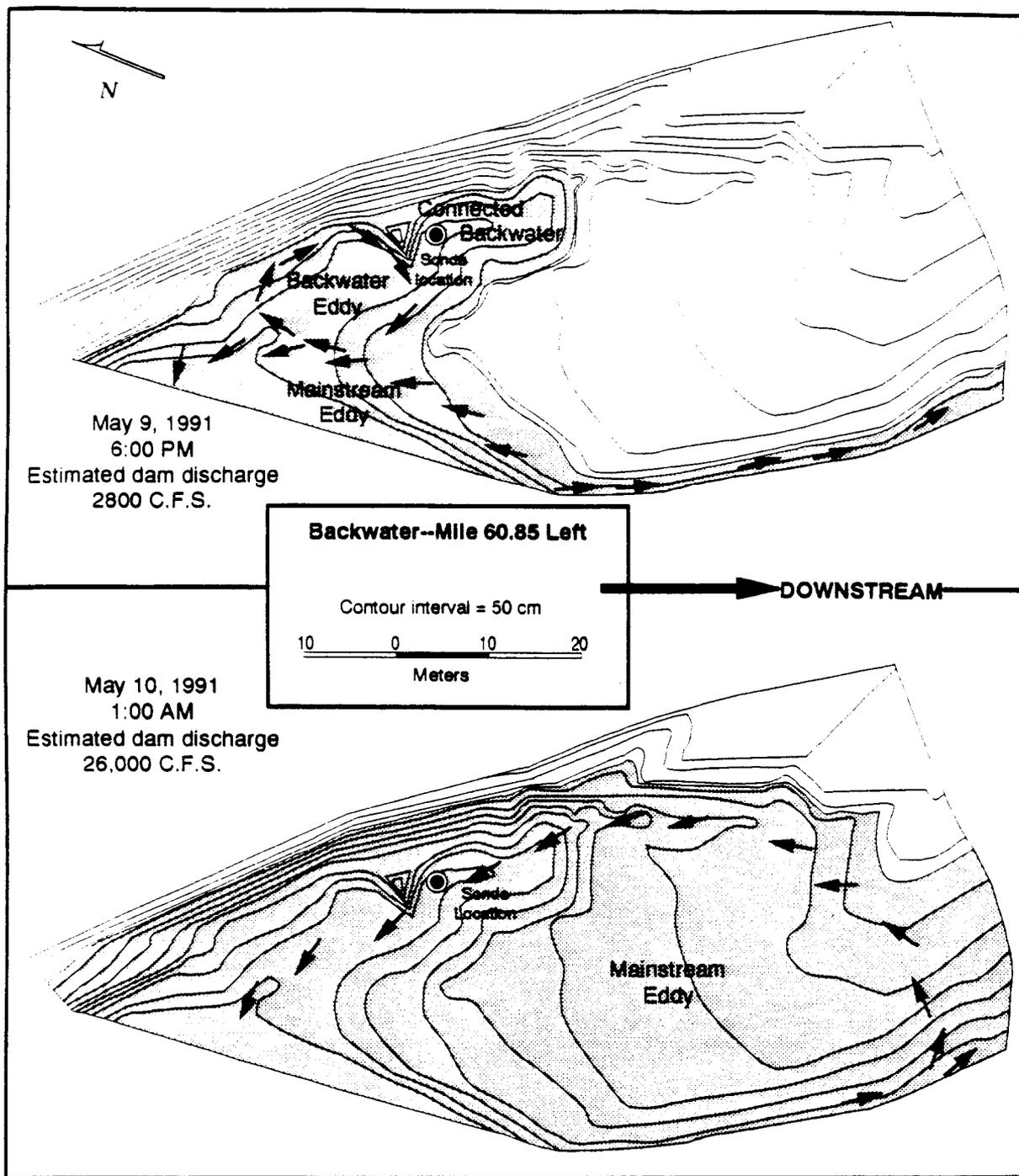


FIGURE 4.6.--Map of the backwater at mile 60.85. Site was surveyed at approximately 5:00 pm on May 9th 1991 using a Leitz Total Station. Wetted perimeter at times other than time of survey was calculated from the associated Data Sonde trace.

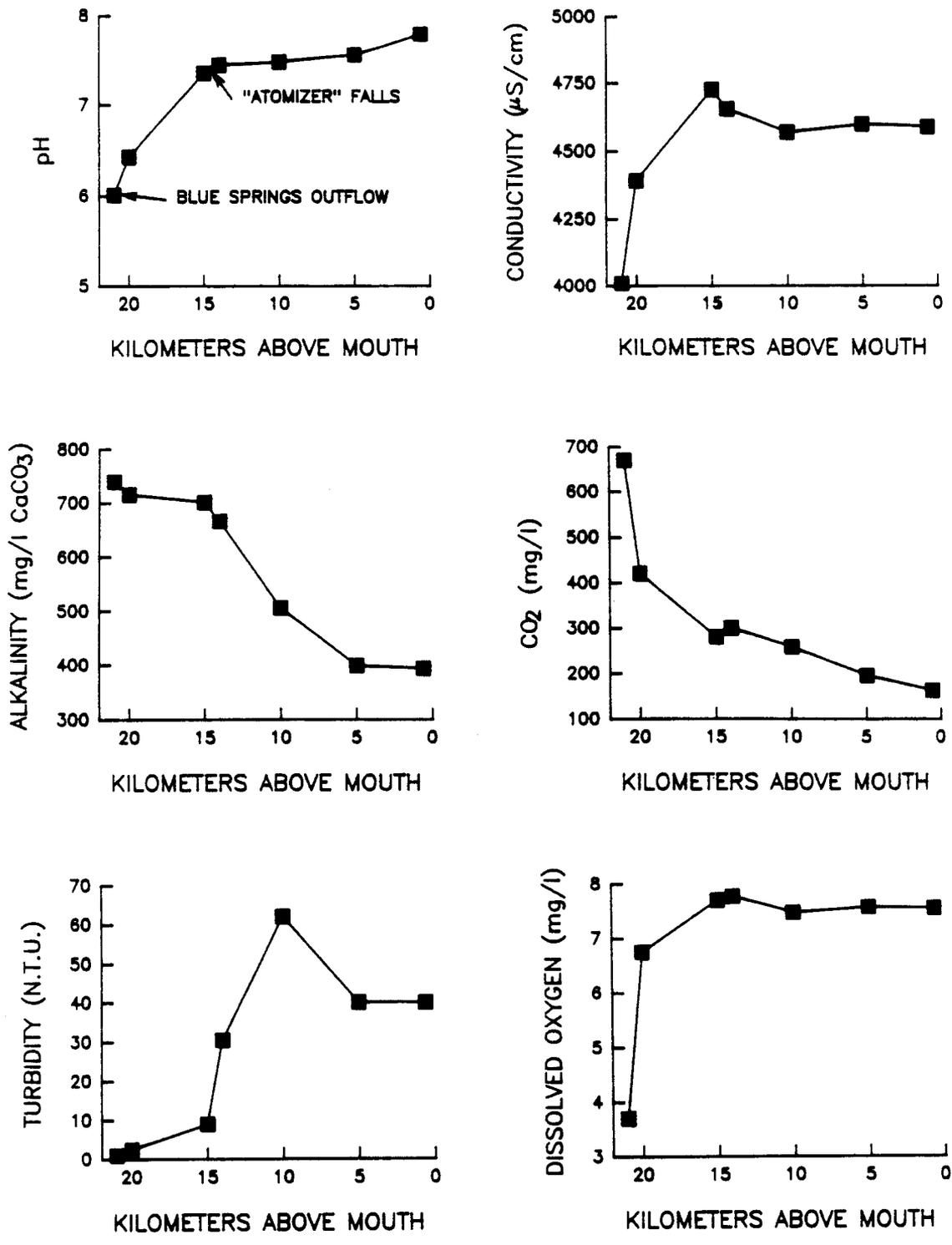


FIGURE 4.7.--Longitudinal patterns of selected water quality parameters from the Little Colorado River, October 1991.

respectively (Figure 4.7). Below RKM 14.9, alkalinity levels dropped precipitously and reached 393 mg/l near the mouth, while turbidity rose to 62 N.T.U. in 5 km. Turbidity decreased to 40 N.T.U. below RKM 10.

Nutrient levels did not display longitudinal patterns. PO_4^{3-} levels were only 0.04 mg/l in the ephemeral mainchannel flow above Blue Springs, jumped to 0.15 mg/l in the Blue Springs outflow, and fluctuated between 0.11-0.18 at mainchannel sites downstream. Outflow from Big Canyon, the largest tributary drainage below Blue Spring, was 0.58 mg/l for this nutrient, but only 0.05 mg/l from springs immediately below Salt Trail Canyon at RKM 10.4. Nitrate values ranged from 0.12-0.22 mg/l NO_3^- -N, but distributions were otherwise unremarkable when compared to the range of values encountered by Grimm et al. (1981) for desert streams in the Gila River Basin to the south.

Mean daily discharge of an ephemeral reach of the LCR at Cameron, Arizona, ca. 65 km above Blue Spring, is shown in Figure 4.8. For representation of discharge in the study area, flow values in Figure 4.8 should be adjusted upward by a minimum of 217-223 cfs, the estimated discharge at Blue Spring (Johnson and Sanderson 1968). Sustained high flows from upland snowmelt occurred between late February and April, and smaller spates occurred in late summer resulting from "monsoonal" convection storms.

Fish Distribution, Abundance and Movements

Mainstem Colorado River--The frequency with which various species were captured varied widely in different sections of the river (Figure 4.9). With the exception of speckled dace, native fishes were very rare or absent in sections 1 and 2 (above the Nankoweap Basin). Both bluehead sucker and flannelmouth sucker appeared considerably more frequently below the Nankoweap Basin, in section 3, with humpback chub appearing in the assemblage only downstream from the LCR. Below the LCR, the frequency with which most native species were encountered varied widely, but without apparent pattern. Humpback chub occurrence, however, showed a clear and precipitous decline with increasing distance below the Little Colorado River, with a slight increase in the lowermost sections near Diamond Creek.

All species occurred more frequently in connected backwater areas than in either backwater eddy or mainstream locations (Table 4.1). With the exception of rainbow trout, which were most abundant in backwater eddy locations, all species also were more abundant in connected backwaters than in other areas. A total of 18 isolated backwaters was sampled, but no fishes were encountered.

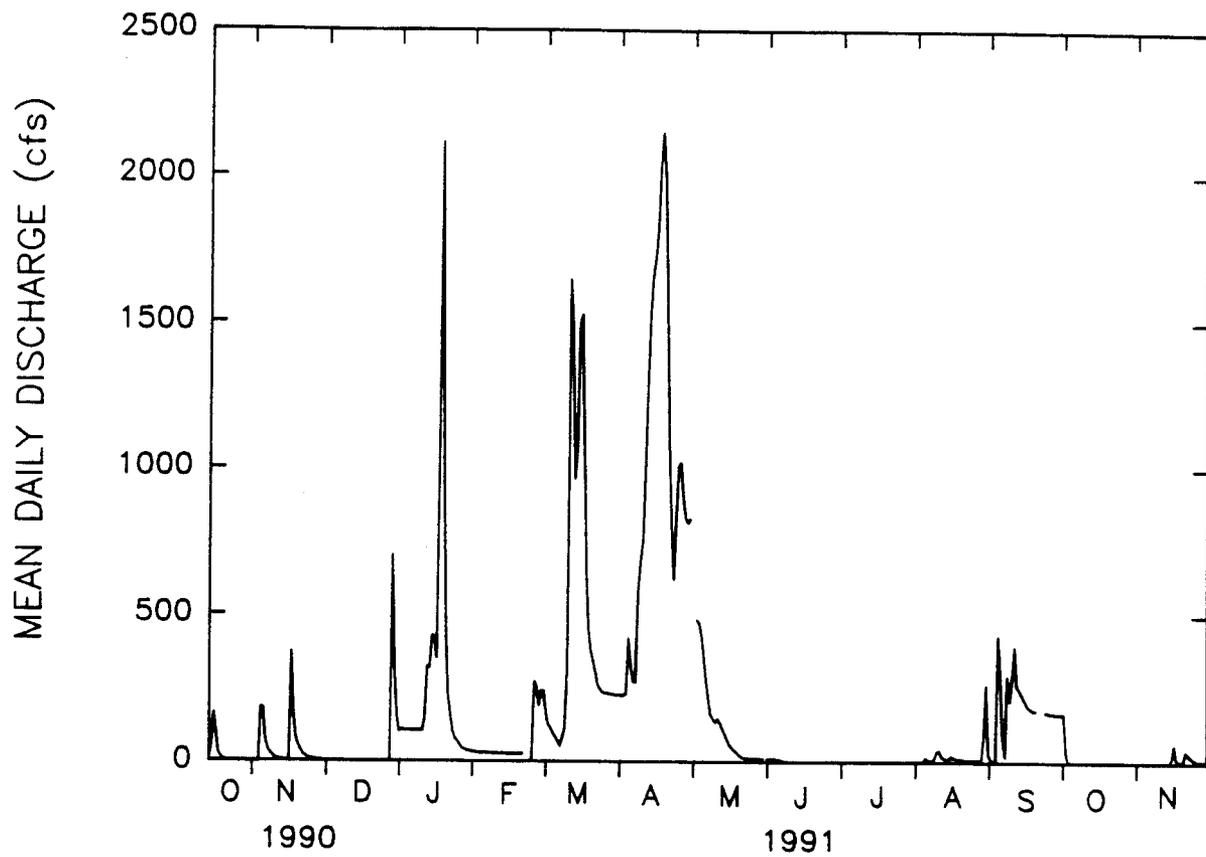


FIGURE 4.8.--Mean daily discharge (cfs) of the Little Colorado River at Cameron, AZ, October 1990-November 1991.

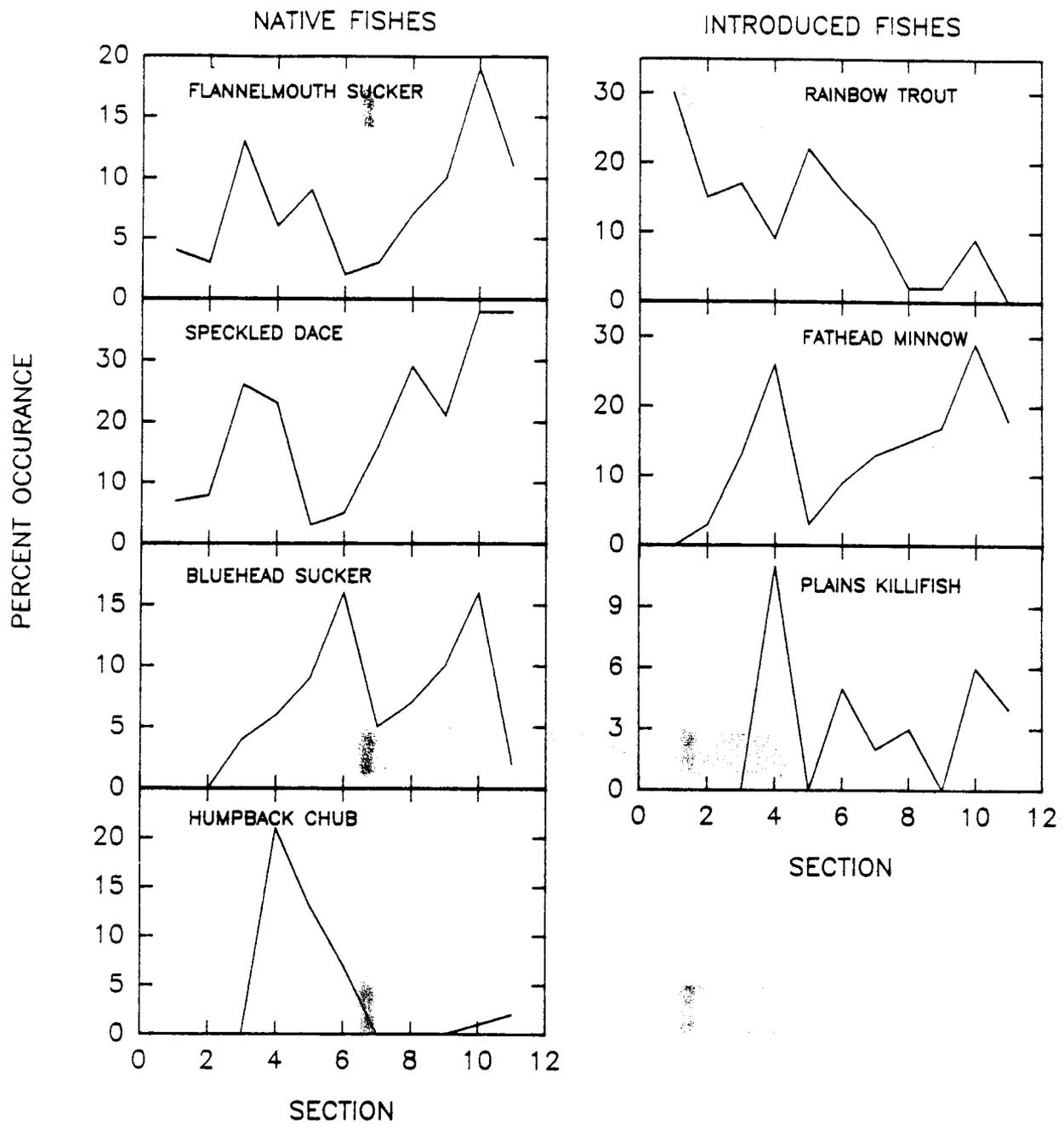


FIGURE 4.9.--Trends in species occurrence for native and introduced fishes frequently encountered in the mainstem Colorado River. Boundaries of river sections are shown in Figure 1.3.

TABLE 4.1.--Occurrence and abundance of fishes by major habitat type. Percent occurrence is the percentage of sites of that habitat type in which the given species was encountered. Mean abundance is the mean number of individuals of the given species that were caught at each site where they were encountered.

Species	Backwater Eddy		Connected Backwater		Mainstream		Total
	% Occ.	Mean Abund.	% Occ.	Mean Abund.	% Occ.	Mean Abund.	
Rainbow trout	8	5	16	2	5	2	101
Brown trout	0	0	1	1	0	0	2
Common carp	0	0	5	3	1	1	41
Humpback chub	4	1	8	9	3	3	177
Fathead minnow	12	1	29	5	4	2	326
Speckled dace	8	1	39	12	10	7	1181
Bluehead sucker	4	1	12	3	6	2	125
Flannelmouth sucker	4	5	17	5	3	4	226
Black bullhead	0	0	1	1	0	0	1
Channel catfish	4	1	0	0	1	1	2
Plains killifish	0	0	6	1	2	4	40
Striped bass	0	0	0	0	1	1	1

Little Colorado River and Other Tributaries--Of 5,386 post-larval fishes caught in hoop and trammel nets, seines, and minnow traps between May and November, 1991, in the LCR, speckled dace accounted for 56.8% of the catch by numbers, followed by humpback chub (29.7%), bluehead sucker (4.6%), and flannelmouth sucker (4.5%). Exotic species [channel catfish (*Ictalurus punctatus*), carp (*Cyprinus carpio*), fathead minnow (*Pimephales promelas*), rainbow trout (*Oncorhynchus mykiss*), yellow bullhead (*Ameiurus natalis*), and plains killifish (*Fundulus kansae*)] together comprised less than 1% of the catch. The remainder was accounted for by early post-larval fishes that have not been identified.

Trammel nets were the only gear that departed substantially from this general pattern of relative abundance; flannelmouth sucker comprised 50.6% of the catch by this technique, followed by humpback chub (34.2%) and bluehead sucker (12.7%). Because of their small size, dace were not expected in catches from trammel nets.

Daily mean catch rates for humpback chub using all data from May-June hoop net sets (mean number of chub caught per net) ranged between 0.3 and 2.7, and were generally comparable to rates from previous years (Kubly 1990). Daily modified Schnabel population estimates (Ricker 1975) of humpback chub ≥ 150 mm in the lower 1200 m of the LCR using May-June hoop and trammel net mark-recapture data showed a pattern of increasing numbers similar to those in 1987-88 reported by Kubly (1990). The 1989 pattern of decreasing population size over time (Kubly 1990) stands alone among the four annual population trends. The final population estimate for 1991 was considerably less than those estimated in previous years. Estimates of the population size of humpback chub > 150 mm in the lower 1200 m of the LCR since 1987 have ranged from 700-2,900.

Hoop and trammel net recaptures did not detect large scale movements of humpback chub in the LCR during May and June. Individuals captured two or more times over periods exceeding one month generally moved only a few hundred meters, and often were recaptured in the same net over a several week period.

Assemblage composition of other tributary streams was examined by totaling all collections from all trips in order to provide data on coarse patterns of species dominance in the various major tributaries (Table 4.2). With the exception of Bright Angel and Tapeats creeks, which were dominated by rainbow trout, and Kanab Creek, which was dominated by flannelmouth suckers, all tributary streams were dominated by speckled dace. In those tributaries where introduced species were first or second in order of abundance (Nankoweap, Clear, Bright Angel, Crystal and Tapeats creeks), faunal diversity was low (one or two species). Where native fishes dominated the assemblage, faunal diversity was generally higher. Because of the seasonal nature of the sampling regime (no winter samples) and the bias of this project towards smaller fishes, these patterns may not be accurate representations of true patterns of species dominance and diversity in the tributary streams.

Age and Growth

Mainstem Colorado River--Analyses of humpback chub length frequency distributions collected in the mainstem revealed that fish in the 30-80 mm length interval between March and July were likely not from the 1991 cohort, whereas those < 30 mm probably were

TABLE 4.2.--Total numbers of fishes captured in tributary streams, 1991, excluding the LCR. HBC = humpback chub, SPD = speckled dace, RBT = rainbow trout, BHS = bluehead sucker, FMS = flannelmouth sucker, PKF = Plains killifish, FHM = fathead minnow.

Stream	HBC	SPD	RBT	BHS	FMS	PKF	FHM
Paria River	0	384	2	0	18	0	0
Nankoweap Creek	0	12	9	0	0	0	0
Clear Creek	0	7	5	0	0	0	0
Bright Angel Creek	0	3	18	0	0	0	0
Crystal Creek	0	22	0	0	0	16	0
Shinumo Creek	5	322	3	9	6	1	0
Tapeats Creek	0	0	17	0	0	0	0
Kanab Creek	0	27	0	36	14	16	21
Total	5	987	54	45	38	33	21

(Figure 4.10). The frequency distribution of September mainstem chubs likely represent a combination of 1991 cohort fish that relatively recently had entered the mainstream and 1990 cohort individuals that over wintered in the mainstem. Small sample sizes in Figure 4.10 rendered growth estimations difficult for mainstem humpback chub.

Flannelmouth sucker length-frequency plots (Figure 4.11) showed that fish < 150 mm encountered during March likely represented the prior summer's cohort (approximately eight months old); these fish had a mean length of 61 mm. The same cohort can be seen in May where they have reached a mean length of 76 mm, an increase of 15 mm. By July, two cohorts can be seen; young-of-the-year fish with a mean length of 37 mm, and age-1+ fish with a mean length of 104 mm. By September, young-of-the-year fish have reached an average length of 58 mm, and age-1+ fish appear to have reached a length greater than 150 mm and no longer appear with any regularity in the samples.

Bluehead sucker length frequency plots (Figure 4.12) do not show any obvious trends or year-class boundaries. These fish probably originated from a number of tributaries, where spawns took place at different times, and growth rates were very different, making the tracking of any given cohort virtually impossible.

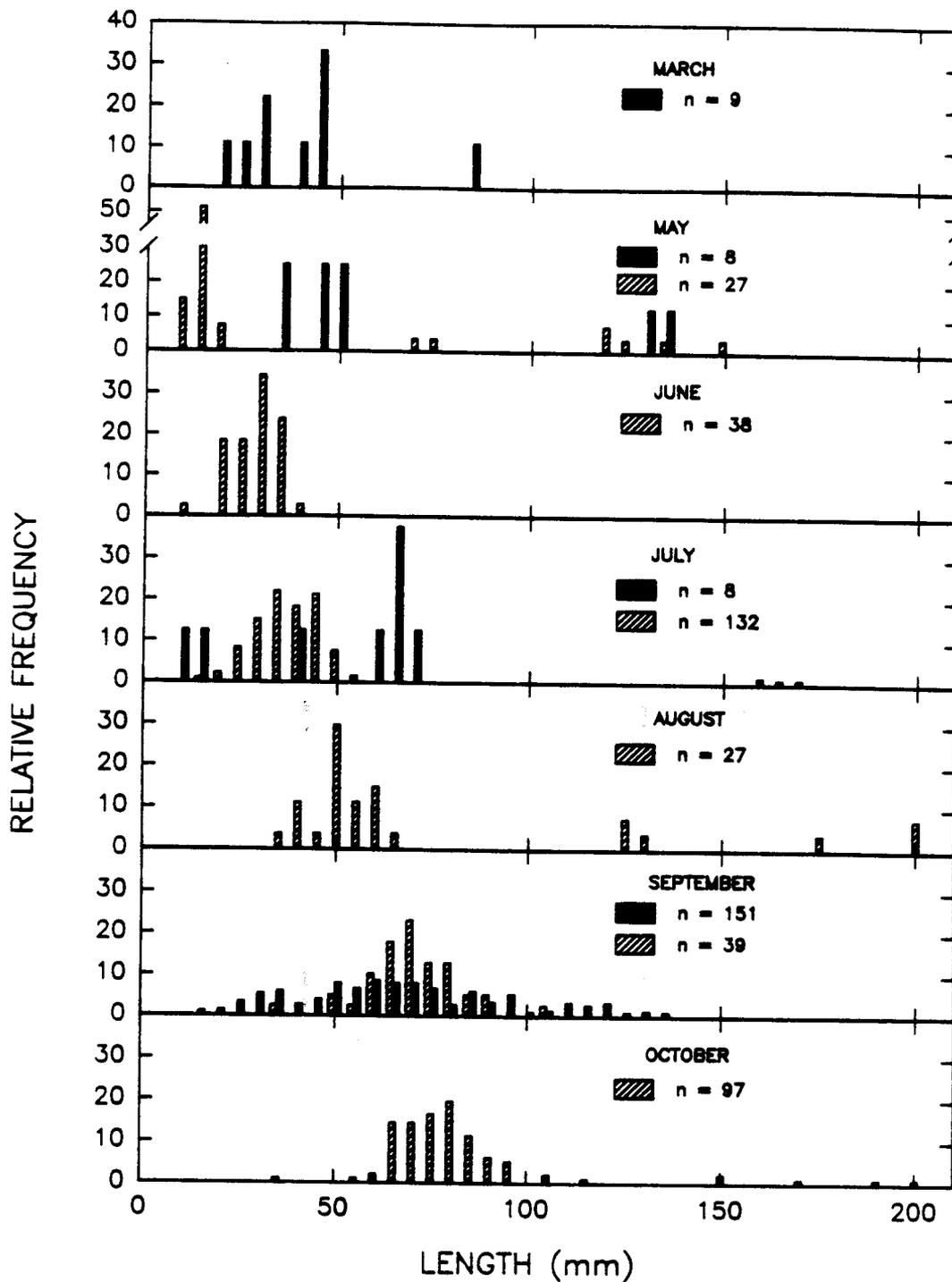


FIGURE 4.10.--Length frequency distribution for humpback chub captured in the mainstem Colorado River and Little Colorado River, 1991. Solid bars denote mainstem collections, hatched bars denote LCR collections.

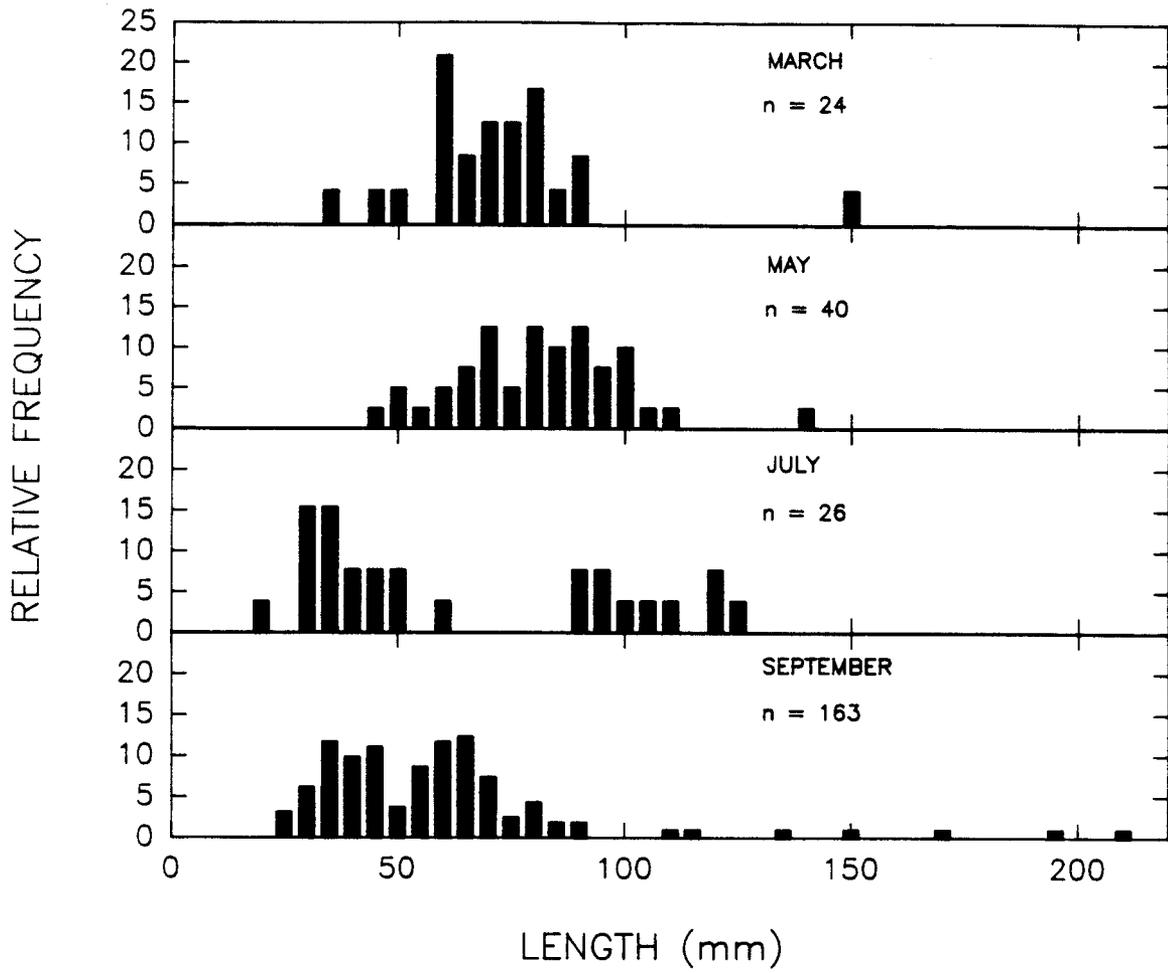


FIGURE 4.11.--Length frequency distribution for flannelmouth sucker captured in the mainstem Colorado River, 1991.

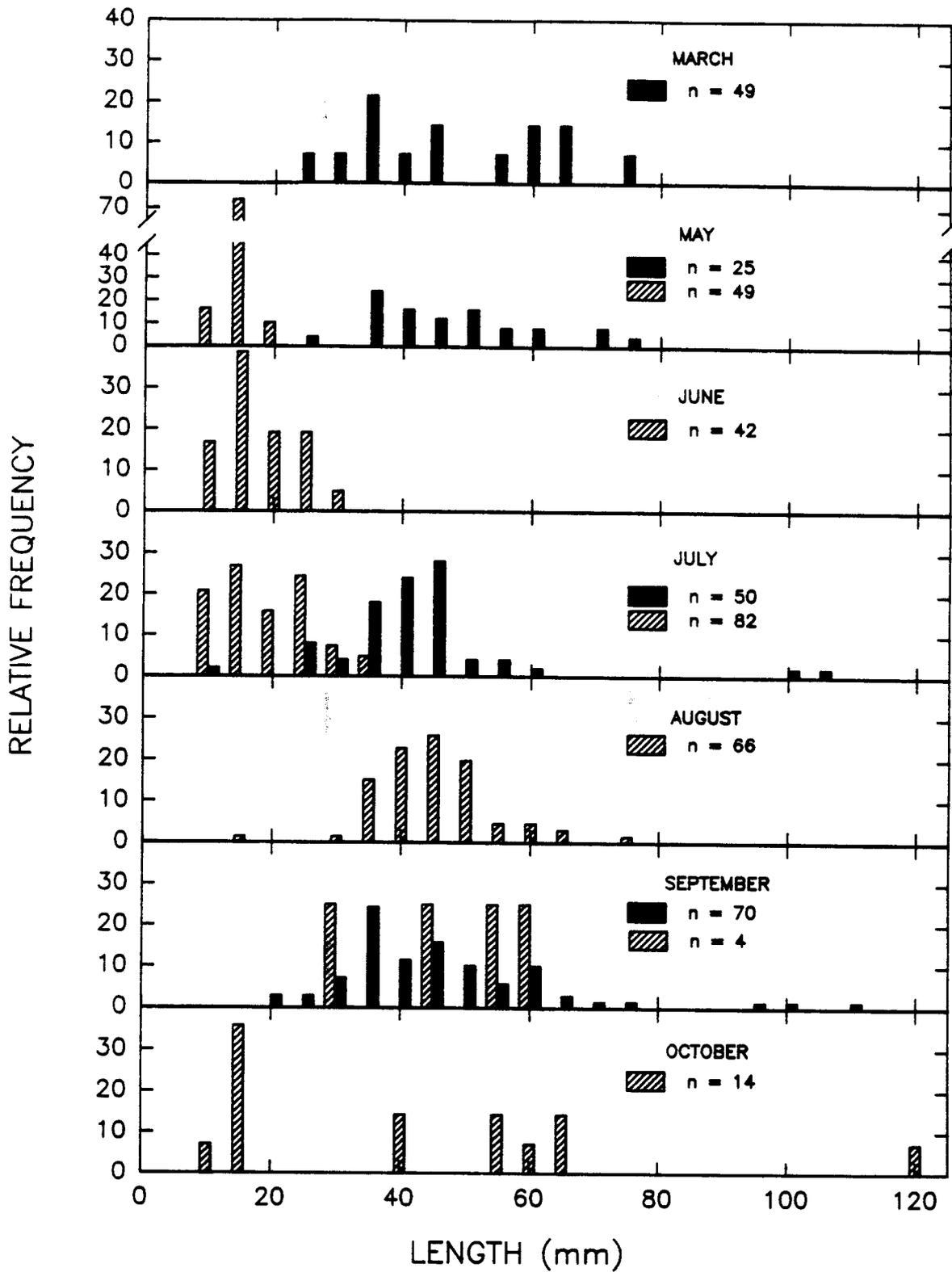


FIGURE 4.12.--Length frequency distribution for bluehead sucker captured in the mainstem Colorado River and Little Colorado River, 1991. Solid bars denote mainstem collections, hatched bars denote LCR collections.

Little Colorado River and Other Tributaries--All native species except razorback sucker spawned successfully in the LCR in 1991 as evidenced by representation of larvae in collections. Based on their dates of appearance in collections and drift (see below), it is likely that humpback chub spawned as early as April and possibly into June (Figure 4.10). Bluehead suckers apparently had two major periods of spawning based on large collections of young in May through July and October-November (Figure 4.12). Maddux et al. (1987) also reported early autumn spawning for this species. Larvae of speckled dace appeared beginning in mid May and remained through July, indicating either multiple spawning periods or a single protracted period of spawning (Figure 4.13). The relatively few collections of flannelmouth sucker larvae (from drift samples only) spanned the period of mid May through late June.

Growth of the 1991 humpback chub cohort in the LCR as determined by length-frequency analysis exceeded a mean of 10 mm/month through October (Figure 4.10). Mean length of this age class was approximately 75 mm in October.

Growth of the age-0 speckled dace cohort in the LCR was more difficult to assess from length frequency distributions (Figure 4.13). It appears that lengths of age-0 and age-1+ fish began to overlap by August, and age distributions thereafter are impossible to distinguish. Also problematic were rates of growth of age-0 bluehead sucker in the LCR (Figure 4.12), although in this case inadequate sample sizes and a protracted spawning period(s) were the reason. The distributions shown in Figure 4.12, however, all likely represent young-of-the-year except for the 120 mm specimen taken in October.

Drift and Benthos Analyses

Mainstem Colorado River--To date, a total of 41 drift samples have been examined for larval fish and fish eggs. Samples were taken from tributaries (The Paria River, Nankoweap Creek, Shinumo Creek and Kanab Creek) and mainstem locations during March, April, May, June and July. All four samples taken from the Paria River on April 3, and one of the samples taken on March 27 had flannelmouth sucker eggs present. None of the other tributary or mainstem samples had either larval fish or eggs.

Abundance and occurrence data for macroinvertebrates encountered during the analysis of benthos samples are shown in Tables 4.3 and 4.4. Samples taken from mainstream eddy habitats were extremely depauperate, with only three out of 26 samples having any aquatic organisms. Connected backwater samples were much richer in macroinvertebrates, and were dominated by chironomids and oligochaetes. All frequently

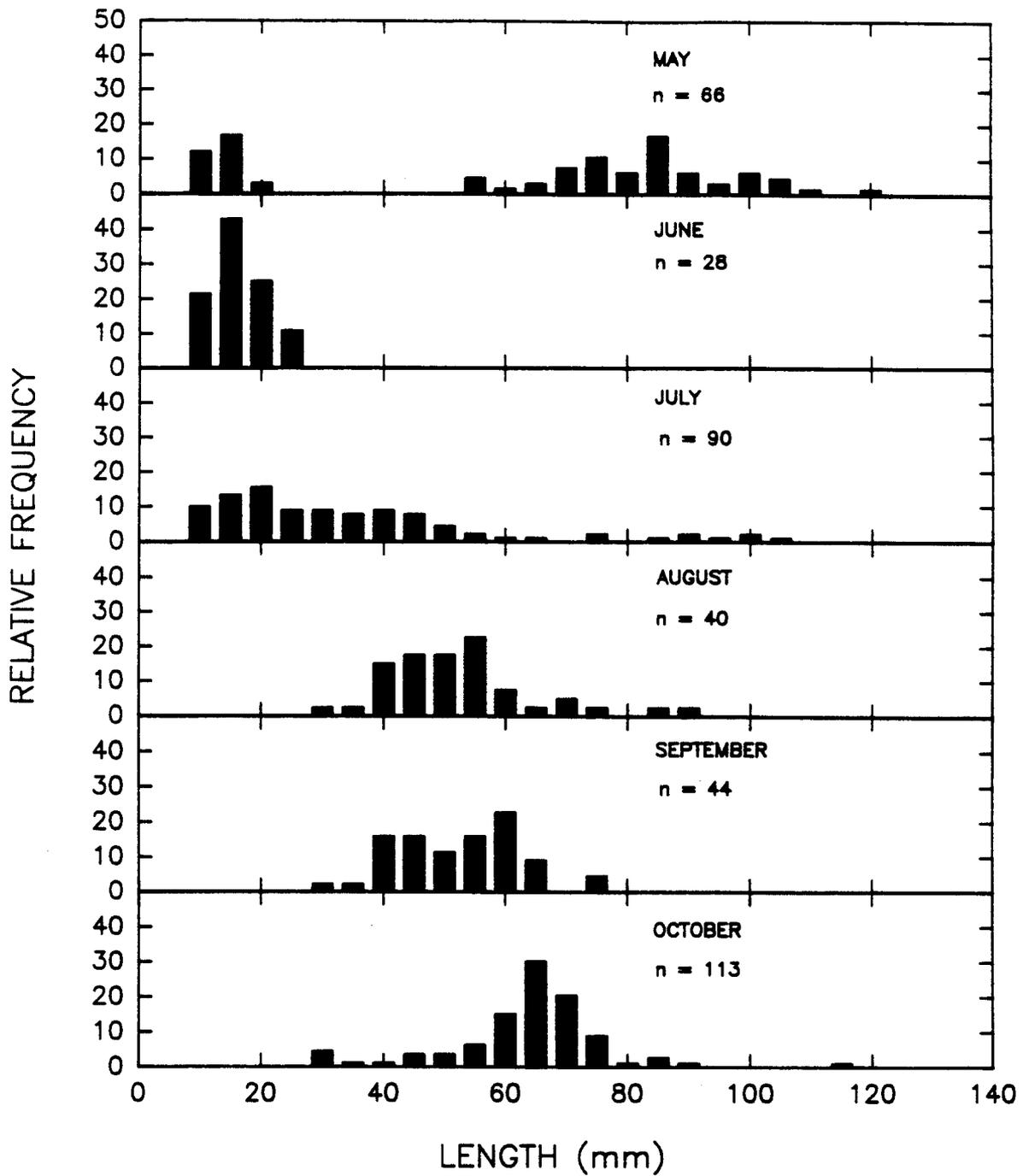


FIGURE 4.13.--Length frequency distribution for speckled dace collected by seine and dip net from the Little Colorado River, 1991.

TABLE 4.3.--Percent occurrence (% of sites in reach where collected) and mean density (no./m² at sites where collected) of invertebrates in Petite Ponar dredge samples by Colorado River reach.

	REACH 20 (N=14)		REACH 30 (N=12)		REACH 40 (N=8)		REACH 50 (N=32)	
	% Occ.	Mean Density	% Occ.	Mean Density	% Occ.	Mean Density	% Occ.	Mean Density
Chironomidae	50	27	8	22	12	43	6	43
Simuliidae	7	22	0	0	0	0	0	0
Oligochaeta	57	977	17	194	25	86	9	22
Nematoda	21	65	0	0	0	0	6	66
<i>Gammarus</i>	7	22	8	21	12	22	3	66
Terr. Diptera	0	0	8	22	12	22	0	0
Ephemeroptera	0	0	0	0	12	22	0	0
Coleoptera	0	0	0	0	12	22	0	0
Formicidae	0	0	0	0	0	0	3	22
Tricoptera	0	0	0	0	0	0	3	22
Physidae	14	32	0	0	12	43	3	22

encountered organisms (oligochaetes, chironomids and nematodes) occurred most often above the LCR.

Little Colorado River and Other Tributaries--Drift samples from the LCR generally contained substantial numbers of dipteran (predominantly Chironomidae) larvae, pupae, and adults, lesser numbers of ephemeropteran nymphs and trichopteran larvae, and many other taxa of less frequent occurrence. Larval fishes were found in 16% of 25 samples analyzed from May, 44% of 27 samples from June, and 25% of 8 samples from other periods. Fish eggs were found in 24% of May samples, 37% of June samples, and were absent in other months. Relatively low numbers of eggs and larvae were found on a per unit volume basis ($\ll 1/m^3$), with the exception of a single 12-hr sample from July 6-7 that contained 139 speckled dace larvae 5.8-7.0 mm TL. Assuming a river discharge of approximately 7 m³/s and equal distribution of larvae across the river (but see Valdez et al. 1985 and Bestgen et al. 1985), over 100,000 dace larvae drifted past RKM 0.33 between 1800-0600 hrs based on this sample. The proximity of this site to the Colorado River mainstem likely indicates that substantial transport from the LCR occurred. Valdez (1989) reported the presence of

TABLE 4.4.--Percent occurrence (% of sites in habitat type where present) and mean density (no./m² at each site where collected) of invertebrates in Petite Ponar dredge samples by Colorado River habitat type.

	Connected Backwater (N = 38)		Mainstream Eddy (N = 24)	
	% Occurrence	Density	% Occurrence	Density
Chironomidae	26.3	64	0.0	0
Simuliidae	<0.1	22	0.0	0
Oligochaeta	29.0	399	<0.1	22
Nematoda	<0.1	50	<0.1	22
<i>Gammarus</i>	<0.1	36	<0.1	22
Terr. Diptera	0.0	0	<0.1	22
Ephemeroptera	<0.1	22	0.0	0
Coleoptera	<0.1	22	0.0	0
Formicidae	<0.1	22	0.0	0
Tricoptera	<0.1	22	0.0	0
Physidae	10.5	32	0.0	0

approximately 500-750 larval humpback chub in a large pool at the confluence of the LCR in May, 1989, also suggesting considerable transport of larval native fishes from the LCR.

Foraging and Food Habits of Fishes

Little Colorado River and Other Tributaries--Many components of LCR drift were utilized for food by young-of-year humpback chub (Table 4.5). All 15 chub (21-56 mm TL) stomachs examined from May 1989 contained chironomids, and 60.0% had ephemeropteran nymphs, 46.7% simuliid larvae, and 40.0% empidid larvae. Highest frequency of occurrence of invertebrate categories in guts of 40 young-of-year chub (13-35 mm TL) examined from May 1990 were for chironomid (62.5%) and ceratopogonid larvae (12.5%), and ephemeropteran nymphs (10%). Feeding habits of other species have not yet been examined. Of particular note was the high incidence of Asian fish tapeworm (*Bothriocephalus acheilognathi*) in stomachs from 1990, and their absence in 1989.

Behavioral analyses support the contention that chub 11-55 mm TL are largely drift feeders (A.T. Robinson, unpublished manuscript). Out of 115 five minute behavioral

TABLE 4.5.--Frequency of occurrence of invertebrates in guts of humpback chub collected from the LCR in May, 1989 and 1990. Lengths of specimens ranged from 21-56 mm in 1989 (n=15) and 13-35 mm in 1990 (n=40). Sim=Simuliidae larvae, Dip=Diptera adults, Chi=Chironomidae larvae and pupae, Tri=Trichoptera larvae, Emp=Empididae larvae, Eph=Ephemeroptera nymphs, Cpg=Ceratopogonidae larvae, Thy=Thysanoptera adults, Tip=Tipulidae larvae, Hyo=Hymenoptera adults, Tap=Cestoda adults, Oti=Other unidentified, Clc=Cladocera adults.

Year	Sim	Dip	Chi	Tri	Emp	Eph	Cpg	Thy	Tip	Hyo	Tap	Oti	Clc
1989	47	13	100	7	40	60	27	27	13	7	0	0	0
1990	0	20	60	0	0	10	12	2	0	0	80	2	2

observation periods for humpback chub and 89 for sucker spp., chub foraged on the bottom less, on plants less, and on the surface more than suckers (ANOVA; $P < .01$), and chub utilized surface, upper, and middle pelagic zones of the water column more than lower zones (Figure 4.14).

Discussion

In many major river systems, tributary inputs increase base flows, add sediment, and increase seasonality of flow and temperature regimes downstream from hydroelectric installations. These inputs, coupled with pulse attenuation, can cause a rapid downstream reduction in the effects of upstream hydroelectric development and a correspondingly rapid change in the fish community (Kinsolving and Bain, unpublished manuscript; Schlosser 1985, Zimmermann and Ward 1984, Ward and Stanford 1983). In Grand Canyon, however, tributary inputs are relatively minimal (except sediment). Entrenchment of the Colorado River within a canyon somewhat reduces bank storage and pulse attenuation, and steep canyon walls reduce solar radiation, causing the river to warm slowly even during the warmest months. This is reflected in the slow rate of change in the fish community. Few species show a steady increase or decrease in occurrence with distance below Glen Canyon Dam, and the localized influence of tributary streams appears to have as large a role in structuring the fish community as does the declining influence of Glen Canyon Dam. However, in spite of the slow rate of community change, change does occur. By Diamond Creek, the riverine fish community has changed a great deal, from one dominated by

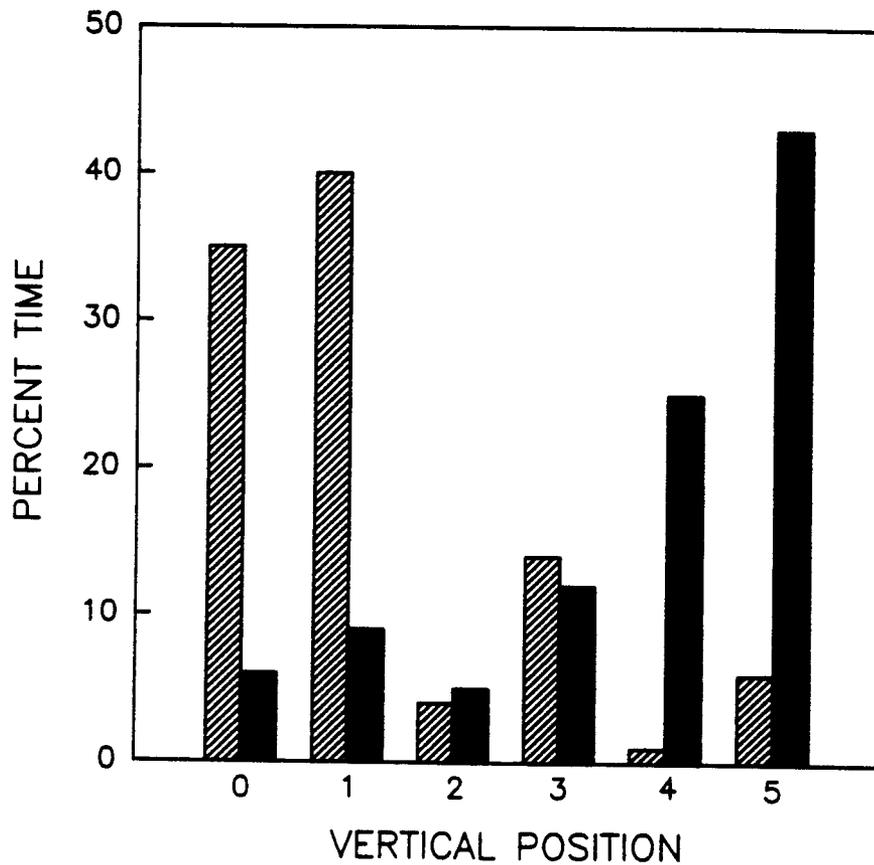


FIGURE 4.14.--Time budget for post-larval age-0 humpback chub and sucker spp. behaviors from the Little Colorado River, 1991. Vertical zone designations are as follows: 0=in contact with bottom; 1=close to but not in contact with bottom; 2=lower one-third of water column above position 1; 3=middle one-third of water column; 4=upper one-third of water column but not at or near surface; 5=at or near surface. Solid bars denote humpback chub, hatched bars denote sucker spp.

introduced, coldwater salmonids to one dominated by a mix of introduced and native catostomids and cyprinids.

The distribution of humpback chub in Grand Canyon has contracted since closure of Glen Canyon Dam. Holden and Stalnaker (1975) reported collecting 11 specimens in the Lee's Ferry reach in 1967. By the late 1970s, catches there became rare, but chub were considered most common in the vicinity of Tiger Wash near RM 25 by Carothers et al. (1981). The present distribution of chub in the mainstem is now nearly exclusively below the LCR confluence (Maddux et al. 1987; R.A. Valdez, personal communication). Range contractions may have occurred through attrition of populations that formerly spawned in the mainstem prior to closure of Glen Canyon Dam. Population estimates in the lower LCR, first estimated in 1980 (Kaeding and Zimmerman 1983), have not yet shown downward trends (Minckley 1988, 1989; Kubly 1990).

Based on our preliminary data and those from other researchers, it is difficult to generalize about movement patterns of humpback chub between the mainstem Colorado River and LCR. Radiotelemetry data obtained by BioWest, Inc. (1991 trip reports) demonstrate that some "staging" at the LCR mouth occurs in late winter and spring, and sporadic movements into lower reaches of the LCR occur soon afterward, ostensibly associated with spawning efforts.

Our and Arizona State University's mark-recapture data (P.C. Marsh, personal communication), however, indicate that longitudinal movements within the LCR are not commonly of great distances that would be expected if they were associated with spawning "runs." Our population estimates from 1991 suggest that numbers near the mouth were still increasing seemingly well beyond the time of major spawning. Decreases in catch of large humpback chub from hoop nets during autumn of 1991 (P.C. Marsh, personal communication; AGFD data) suggest movements back out of the LCR in autumn. Recaptures of LCR-marked fish in the mainstem may support the latter contention (W.J. Masslich, personal communication).

At this time we cannot definitively discern among the following possible scenarios concerning humpback chub populations in Grand Canyon: (1) A single migratory population of adult chub enters the LCR in spring to spawn and also spends part of the summer there, and then reenters the mainstem to overwinter; (2) A separate, resident LCR "population" is supplemented in spring and summer by individuals that overwinter in the mainstem; or (3) A complex facultative use of the LCR and mainstem by humpback chub that varies by individual among seasons or years depending on environmental conditions at the time.

Although we presently consider the third scenario best supported by existing data, further research is needed before firm conclusions can be reached.

In general, fish distributions in tributaries are reflective of geomorphic categories developed by Hamblin and Rigby (1968). Trout tend to dominate, or be co-dominant in higher gradient, cooler, spring-fed streams. Catostomids tend to be abundant only in warmer, more seasonally variable streams with large drainage basins such as the Paria River, Kanab Creek and the LCR. The two major exceptions appear to be Crystal and Shinumo creeks. Crystal Creek is a small, tributary-fed stream in which trout are not present during the summer months, probably because of high summer water temperatures and poor access. Shinumo Creek, another smaller spring-fed tributary stream, has a diverse fauna of both native and introduced fishes.

In terms of direct utilization, it appears that the most important tributary streams other than the LCR for native fishes are Shinumo Creek and Kanab Creek, at least in lower reaches. Both offer only a short reach that is exploitable year-round. Kanab Creek dries frequently during the summer and autumn less than 3 km above the confluence zone, but is used extensively for spawning by suckers and dace. Shinumo Creek has a barrier falls less than a kilometer above the confluence, but is used extensively by a wide variety of native and non-native fishes. It is possible that humpback chub spawn in Shinumo on occasion, though small (<25 mm) chubs captured there may all represent spawn from the LCR. In any event, it is one of the few suitable rearing habitats for humpback chub in the inner gorge area.

Our continuing limnological analyses of the LCR and other tributaries are intended to ascertain the potential for augmentation of humpback chub and other native fish populations in Grand Canyon. It has been theorized that Atomizer Falls near RKM 15 on the LCR may serve as a physical catalyst for certain chemical events in the river, and as a potential barrier to fish passage. Our data suggest that the series of falls does effect pronounced changes in alkalinity and turbidity, but that observed longitudinal gradients of other water quality parameters (pH, conductivity, carbon dioxide, dissolved oxygen) are greatest in the reach above. Water quality conditions immediately above Atomizer are not drastically different from conditions below, suggesting that chemistry alone (at least parameters we measured) does not preclude presence of humpback chub and other natives. Speckled dace presently occupy the reach between the falls and Blue Spring, and squawfish, bonytail chub and bluehead sucker were taken historically at Grand Falls, approximately 120 km upstream (Miller 1963, Minckley 1973). It is possible that the falls presently act only

as a physical barrier to upstream fish movements, and that humpback chub, if ever formerly present, were eliminated from the reach sometime in the past. If this is the case, the potential for physical modification of travertine formations at Atomizer may be all that is necessary to allow expansion of populations into a reach that represents fully 1/4 of the available habitat longitudinally. These studies may prove important for consideration of other tributaries for population augmentation as well.

Inspection of humpback chub length frequency distributions in Figure 4.10 reveals the consequences of rearing in cold (mainstem) vs. warm (LCR) environments. Chub collected from the mainstem in March, prior to spawning in the LCR, must represent fish approaching one year of age that mostly were reared and overwintered in the mainstem. These fish were too large to be the result of an early mainstem spawn. Likewise, the smaller group of chub from mainstem collections in May that exceed lengths of age-0 fish recently spawned in the LCR (those < 25 mm) also ostensibly represent 1990-spawned fish. The smallest specimens from the mainstem in July (< 25 mm), however, were likely age-0 fish that earlier moved from the LCR and grew more slowly. Preliminary ageing data from otolith lapilli support this contention (Hendrickson 1991).

In September, the number of chub collected from the mainstem increased dramatically (Figure 4.10). Since most of these fish were captured a short distance below the LCR, it is likely that they represented mostly young-of-the-year LCR-raised fish. If this is the case, it is interesting to note that they are generally larger at an estimated age of five months than chub encountered in the mainstem in March that were approaching their first year of life. The frequency distribution of September mainstem chub lengths (Figure 4.10), therefore, is likely a combination of 1991 cohort fish that had recently entered the mainstem and 1990 cohort individuals that overwintered in the mainstem.

The sudden appearance of numerous young humpback chub in September collections from the mainstem was coincident with spates in the LCR (Figure 4.8). Floods have been shown to be of little negative consequence to native fish populations in general, and in fact may be beneficial through differential depletion of populations of non-native species (Minckley and Meffe 1987), as a necessary cue for spawning of some species (Tyus 1986, John 1963, Copp 1989), or through indirect effects on channel morphometry and riparian vegetation (Campbell and Green 1968, Tyus and Karp 1991). Nevertheless, larvae and small post-larvae are likely more susceptible to downstream transport during flood events (John 1964, Harvey 1987, Minckley and Meffe 1987), and the late August-September floods in the

LCR may have been responsible for some of the increase in mainstem catches during September.

The consequences to fishes of rearing in colder waters include increased early-life mortality and decreased survival to sexual maturity (Kaeding and Osmundson 1988), reduced condition, lipid stores, and size that results in elevated overwinter mortality for young-of-the-year fishes (Thompson et al. 1991), and lowered egg production by adults (McAda and Wydoski 1983).

How much of the tributary production of native fishes enters the mainstem via drift or displacement? Our LCR data suggest a potential for high, although temporally limited, larval fish drift rates. Drift rates reported for the same and related species by Valdez et al. (1985) in the upper Colorado River and Bestgen et al. (1985) in the upper Gila River in New Mexico are considerably higher overall than ours, and further analyses of LCR samples may corroborate their findings.

It is unknown how far larval native fishes drift, but certainly those near the termini of tributaries are susceptible to transport into the mainstem. Although much of the fish production in the longer LCR, Paria, and Kanab tributaries may not be susceptible to such losses, larvae produced in other tributaries certainly are. At this time it is difficult to provide a quantitative assessment of the transport of larval and young-of-the-year fishes from tributaries to mainstem, although it is certain that those that do enter the mainstem experience elevated mortality and other debilitating effects.

Our results clearly show that thermally warmed backwater habitat is more frequently utilized by young native fishes during summer months than are other available habitats. This was quite possibly the case prior to the construction of Glen Canyon Dam, as has been demonstrated on other unregulated rivers (Kinsolving and Bain, unpublished manuscript). Backwater habitats offer numerous advantages to young fishes such as higher zooplankton and algal densities, low current velocities, and refugia from large, predatory fishes (Kinsolving and Bain, unpublished manuscript). However, following construction of Glen Canyon Dam, these habitats became the only portion of the mainstem offering water warm enough for successful rearing.

At this time, mainstem water quality studies are at too preliminary to draw conclusions. Studies have taken place only during warmer months, and the quantity of available data is insufficient to make broad generalizations concerning the dynamic interaction between backwaters, the mainstream, and flow regimes. However, data examined to date show clearly that these interactions are complex and that backwater

dynamics are affected by numerous factors. This indicates that though it is perhaps possible to quantify the absolute amount of shallow, slow water habitat using aerial photographs, it will be considerably more difficult to quantify the quantity and quality of rearing habitat that is both suitable for and available to native fishes.

Changes in patterns of species occurrence highlight a potentially important problem for the native fish community. Although native fishes generally increased downstream from Glen Canyon Dam, warmwater introduced species increased at least as much or more so. It is possible that populations of many native fishes began to decline well before the construction of Glen Canyon Dam, and that competition and predation from introduced species is at least as important a causal factor in the decline of many native species as the effects of Glen Canyon Dam (Minckley 1991). If this is the case, mitigation of flow and thermally related impacts must be carefully crafted so as to not encourage introduced fishes to the detriment of natives.

It appears that most introduced fishes, with the exception of striped bass and Plains killifish, were well established in either the mainstem Colorado or its tributaries prior to the construction of Glen Canyon Dam (Carothers et al. 1981), and that the dam has resulted in reductions in distributions and abundance of many introduced species, including red shiner, channel catfish and common carp. This was probably due primarily to changes in the thermal regime of the post-dam river.

All introduced fishes have the potential to impact populations of native fishes to some degree, either through competition or predation. The predatory nature of striped bass is well known, but at this time their impact is minimized by their limited penetration (both spatial and seasonal) into the Grand Canyon. Other species that may predate facultatively on native fishes, such as channel catfish, common carp and rainbow trout, are more widely distributed. In the Grand Canyon, native fishes have not been shown to be a major component of the diets of any of these fish (except for channel catfish in LCR hoop nets), though in other rivers smaller fish form an important seasonal component of both channel catfish and common carp diets (D.A. Kinsolving, unpublished data).

Potential competitors with native species include red shiner, Plains killifish, and fathead minnow. Red shiner have become extremely rare in Grand Canyon collections since closure of Glen Canyon Dam (Carothers et al. 1981, Maddux et al. 1987, AGFD data), and killifish and fathead minnow, although locally common, apparently have difficulty coping with floods or other disturbances in the system.

Potentially more problematic for native fishes in Grand Canyon is the recently discovered presence of the exotic Asian fish tapeworm. Its alarming frequency of occurrence and degree of infestation in stomachs of humpback chub (other species have not yet been examined), and the rapidity of infestation (it had not been found prior to 1990) likely portends sustained chronic effects in the foreseeable future. These effects, although not well studied, may include reduced growth, depressed swimming ability via elevated muscle fatigue, and other debilitating influences. Infestation in wild and hatchery populations of endangered woundfin, *Plagopterus argentissimus*, have wreaked havoc on recovery efforts for that species (Heckmann et al. 1986; J.J. Landye, personal communication).

5. Integration¹

We recognize that the separation of this report into three discrete research elements (ecosystem, trout, native fishes) is artificial. Each of the preceding chapters contains references to processes or resources outside the explicit scope of that chapter, but which influence or are influenced by some aspect of the research elements of concern in that chapter. Two aspects of this study account for its high degree of interconnectedness: (1) streams are linear systems and upstream events have downstream consequences, and; (2) there are multiple trophic levels that interact and respond to changes in the physical and chemical environment.

Proximal Effects

Glen Canyon Dam modifies the hydrology, sediment inputs, and water temperature of the Colorado River. Dam-induced changes in each of the three major physical components drives the river ecosystem to respond and adjust in numerous ways. Some responses are obvious and easy to comprehend, but many are subtle and difficult to comprehend. The latter group reflects the numerous interactions among the physical elements and the interactions between physical and biotic components which together form the ecosystem. Furthermore, the responses change temporally as the river adjusts and species enter or leave the ecosystem, and they change spatially as tributary influences and local climate act to modify the dam's influence.

An example of how the dam affects the physical environment of the tailwater, and the complexity of interactions between physical and biotic ecosystem components, is provided by considering the factors controlling productivity of the periphyton. In the continuously inundated zone below the dam, the filamentous green alga, *Cladophora glomerata*, and its epiphytic diatoms grow luxuriantly and provide food, substrate, and cover for invertebrates and fishes. Excepting possibly the deepest parts of the tailwater, light levels are sufficient to support high levels of productivity during much of the year. Extreme clarity in the tailwater is a byproduct of the settling out of more than 90% of the sediment entering Lake Powell.

Highest standing crops, and apparently greatest productivity, of *Cladophora* and its epiphytes occur on larger cobble and rubble substrates. Estimates of gross primary production for the mature periphyton assemblage (24-34 g O₂/m²/day in September 1991, J. Brock, personal communication) exceed all but a few previously reported values for large streams (Bott et al. 1985). The area of stream bottom covered by these coarse substrates is considerably greater at present than prior to the construction of Glen Canyon Dam because over time the clear release

¹ All authors of preceding chapters contributed to this chapter.

waters have scoured much of the finer sediment and transported it downstream (Pemberton 1976). Coarser substrates are more resistant to displacement by prevailing current velocities; thus, both sediment stability and water clarity are enhanced in the tailwater.

In addition to sufficient light and stable substrates, the tailwater periphyton requires dissolved nutrients to maintain productivity. The plant nutrients most often implicated as limiting primary productivity are forms of nitrogen and phosphorus. In the Colorado River, the latter occurs in particularly low concentrations, and it is suspect as the limiting nutrient. Most of the phosphorus entering Lake Powell is complexed with sediment and is removed by the reservoir before it can enter the tailwater. Thus, the dam enhances primary productivity in the tailwater through increased water clarity and provisioning of more stable, coarser substrates, but potentially limits this same productivity by retaining an essential nutrient in the reservoir.

There is some evidence that load following (peaking) dam operations compromise the tailwater's primary productivity by dewatering large areas of substrate. Based on 22 surveyed range lines in the Lee's Ferry reach, the area of stream bottom increases by more than 50% as discharge changes from 1,000 cfs to 31,500 cfs. If algae suffer mortality during dewatering, they may be more susceptible to entrainment and downstream transport. In this manner, dam operations may reduce local primary productivity and the standing crop of algae, accelerate the downstream movement of algae-derived organic matter, and alter its rate of processing. Periphyton losses during fluctuating flows may occur through physical removal by increased tractive forces during high flows, reduction in the rate of colonization following disturbance events, inhibition of photosynthesis during dewatering, and desiccation.

Downstream Effects

The potential importance to Grand Canyon aquatic resources of organic material exported from Glen Canyon is becoming obvious. Standing crops of benthic algae and invertebrates decline in a stepwise fashion below the Paria River and LCR. Unless inputs of organic matter from tributaries compensate for these reductions, food resources for fishes in Grand Canyon may be lacking. Unfortunately, confirming this relationship is difficult given the current emphasis on studying upstream and downstream reaches separately. Probably the two most important categories of potential effects are direct food inputs for fish populations, and dissolved and particulate nutrient inputs.

Direct food inputs are probably of relatively minor importance except perhaps directly below Lee's Ferry because coarse particles (including, for example, *Cladophora glomerata* debris, zooplankton, macroinvertebrates, and shad from Lake Powell) are usually transported

a relatively short distance (< 10 km) before they are retained by the channel bottom and processed, or are processed to finer sizes in the water column (e.g., Ward 1975, Webster et al. 1979). We emphasize, however, that, as for all the interactions considered here, this effect has a seasonal dimension. There may be periods when food items exported to Marble Canyon are critical to resources there.

We hypothesize that the export of fine particulate organic matter (FPOM), including processed CPOM, and nutrients from Glen Canyon has an important downstream effect. High turbidity and scouring caused by high suspended sediment loads, especially below the Paria and Little Colorado rivers (Kubly and Cole 1979), may limit autotrophic production for extended periods, and result in seasonal food limitation (Minckley 1991). The trophic economy at these times must increasingly rely on stored organic matter, terrestrial inputs, or on material exported from upstream or from tributaries. FPOM exported from upstream may be consumed directly by detritivorous fishes and invertebrates, or may otherwise yield it nutrients to benthic autotrophic production.

We hypothesize that fluctuating flows may benefit downstream communities by reducing the efficiency of organic matter processing in Glen Canyon and by decreasing the amplitude of seasonal export pulses. Reduced processing efficiency in Glen Canyon permits greater exports of organic particles useful to downstream organisms. Decreased seasonality of export increases the predictability of resource delivery for downstream communities.

There is also some evidence that downstream effects may include riparian and terrestrial organisms, e.g., bats and birds that forage on chironomids emerging from the river (H. Mizutani, personal communication). Until the Grand Canyon food web is better understood, seasonal variation in the importance of autotrophy versus heterotrophy will remain unknown.

Rainbow trout-Cladophora glomerata interactions

Several workers have commented on the relatively large amount of the algae *Cladophora* often found in the stomachs of Colorado River rainbow trout (Moffet 1942, Montgomery et al. 1986, Maddux et al. 1987, Chapter 2 of this report). Whether trout consume *Cladophora* for its inherent energy content, for the energy content of its epiphytes, or incidentally while foraging for invertebrates is still not clear. *Cladophora* is the most conspicuous component of the periphyton community in Glen Canyon. The extent and health of the periphyton community is directly linked to production of other important trout foods, particularly dipterans, and the amphipod, *Gammarus lacustris* (Leibfried and Blinn 1987, Pinney 1991). The trophic coupling of periphyton and trout in Glen Canyon cannot be overemphasized.

Cladophora may influence the spawning success of trout in Glen Canyon by trapping and stabilizing fine sediments (T. Angradi, unpublished data). In this way, the alga reduces the embeddedness of spawning gravels (see Chapter 3 of this report). However, a very dense growth of periphyton may inhibit successful spawning by trout (Skulberg 1984). Our observations suggest that algae does not interfere with trout reproduction in Glen Canyon because adult trout are able to cut redds through algal coverage, and because spawning gravels are generally smaller than substrates supporting the greatest accumulation of algae.

Depletion of interstitial dissolved oxygen caused by intense respiration of periphyton at night may affect trout eggs in redds surrounded by dense algal coverage, especially in areas with restricted circulation (i.e., stranding pools, dewatered spawning bars). Alternatively, algal coverage may enhance egg/alevin survival if it moderates intragravel temperatures and moisture content (Becker et al. 1982, Neitzel and Becker 1985). Research now underway may increase our understanding of these interactions (Montgomery 1990).

The importance of *Cladophora* as cover for young trout is unknown. Fry require near-zero velocity habitat (e.g., Moore and Gregory 1988). At high flows this cover is available in the form of inundated terrestrial vegetation. How and if fry are able to use in-channel cover, including *Cladophora*, to avoid displacement at low and fluctuating flows is unknown and unstudied in Glen Canyon.

Native Fishes

Some native fishes seem unable to successfully reproduce in the mainstem because of perennially low water temperatures, and severe reduction in successful hatching at these temperatures has been demonstrated for humpback chub (Hamman 1982, Marsh 1985). The ability to control the thermal regime of the Colorado River below Glen Canyon Dam by reducing daily flow fluctuations is limited and restricted largely to off channel, e.g. backwater, habitats used for rearing, but probably not spawning, by the chub. Removal of this bottleneck to successful reproduction for humpback chub will probably require engineering modifications to Glen Canyon Dam such as a multiple level withdrawal system.

Dam management to control tailwater temperatures might have the unintended effect of increasing the distribution and abundance of nonnative fishes. Just which species might be benefitted would depend upon the magnitude, timing, and duration of warming. Seasonally warmer waters would also change the dynamics and structure of lower trophic levels, particularly the diversity of aquatic insects, thus altering the type and availability of food resources available to Grand Canyon fishes. Although rainbow trout are considered coldwater

species, growth below Glen Canyon Dam could increase with higher temperature and greater diversity of their food base.

If warmer water temperatures resulted in the increased distribution or abundance of undesirable nonnative fishes, an additional management option, controlled floods, might well provide rapid checks on nonnative fishes, with a return to reduced temperature as a secondary measure. The control of hydrology and water temperature in the tailwater could prove to be an effective management tool for recovery of endangered fishes.

A disadvantage of controlled floods is the likelihood that sediment equilibrium could not be maintained. It has been hypothesized that Grand Canyon ecosystem processes are sediment driven and that the health of other ecosystem components, both biotic and abiotic, is reflective of and controlled by processes of sediment deposition and erosion. This is the philosophy behind the present interim flows. However, it is probable that this paradigm is overly simplistic and that the ecosystem, rather than being constructed in a linear fashion and dependent upon a single structural component, actually consists of a complex series of interrelated components and processes that interact on multiple levels. This is not to imply that sediment is unimportant, only that ecosystem structure and function is considerably more complex than the simple sediment-driven model would imply.

Controlled floods would have the added benefit, if applied during a time of sediment input, of building alluvial sediment deposits in Grand Canyon. We believe that this same process of beach building has an ecologically important counterpart in the scouring and rejuvenation of backwater rearing habitats for native fishes. Under steady or mildly fluctuating flow regimes these early successional habitats will fill with fine alluvial sediments and become palustrine habitats populated by semiaquatic plants.

If the combination of floods and seasonally warm water is to be used as a management tool for recovery of endangered fish in Grand Canyon, it is apparent that a fresh look at sediment augmentation is necessary. We recognize that augmentation could preserve the sediment equilibrium, but might, depending on input site and season, decrease primary productivity. We urge that the complexity of interactions among these management options not preclude their consideration. Compelling evidence suggests that successful mainstream reproduction of humpback chub will not occur in the range of water temperatures presently found in the Colorado River below Glen Canyon Dam.

Generality of Ecosystem Processes

An assumption throughout the GCES has been that the importance of the Glen Canyon reach is disproportionate to its length. Our results (Chapter 2 in this report) do not refute this assumption, but we feel that the current lack of data on ecosystem level processes in the Grand Canyon represents a gap in our understanding. The degree to which ecosystem structure and function (e.g., trophic linkages, processes, rates, trajectories) of the Glen Canyon reach resemble ecosystem structure and function in Grand Canyon is almost totally unknown. We feel that downstream communities probably depend on local processes (e.g., periphyton production, tributary and backwater inputs) at least as much as they depend on material resulting from upstream processes. The effects of dam operations on ecosystem features such as resistance and resilience of periphyton probably apply downstream as well.

Differences between Glen Canyon and Grand Canyon that may influence the generality of ecosystem processes include tributary inputs, pulse attenuation, differences in the taxonomic composition of the benthic flora and fauna, the magnitude and quality of terrestrial inputs, underwater light attenuation, substrate size distribution, channel retentiveness, sediment chemistry, and climate.

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