MONITORING AND RESEARCH: THE AQUATIC FOOD BASE IN THE COLORADO RIVER, ARIZONA DURING 1991-2001

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Abiotic Parameters

Discharge at Lees Ferry..... A1

Water Quality

Glen Canyon	Rkm	-23.2	A2
Lees Ferry	Rkm	0.0	A10
Two-Mile Wash	Rkm	3.1	A18
Gauge Above LCR	Rkm	98.4	A26
Tanner Canyon	Rkm	108.8	A34
127 Mile Rapid	Rkm	202.9	A42
205 Mile Rapid	Rkm	328.8	A50

Biotic Estimates

Cobble Habitats

Lees Ferry cobble	Rkm	0.8	A58
Two-Mile Wash	Rkm	3.1	A70
LCR Island cobble	Rkm	98.6	A82
Tanner cobble	Rkm	109.6	A94
127 Mile Rapid	Rkm	202.9	A106
205 Mile Rapid	Rkm	328.8	A118

Pool Habitats

Lees Ferry	Rkm	0.0	A130
Two-Mile Wash	Rkm	3.1	A142
60 Mile Rapid	Rkm	95.7	A154
Tanner Canyon	Rkm	108.8	A166
127 Mile Pool	Rkm	203.2	A178
Spring Canyon	Rkm	326.4	A190

Drift CPOM

Glen Canyon	Rkm	-23.2	A202
Lees Ferry	Rkm	0.0	A212
Two-Mile Wash	Rkm	2.9	A222
Gauge Above LCR	Rkm	98.4	A232
Tanner cobble	Rkm	109.6	A242
127 Mile Rapid	Rkm	202.9	A252
205 MIle Rapid	Rkm	328.8	A262

Drift FPOM

Glen Canyon	Rkm	-23.2	A272
Lees Ferry	Rkm	0.0	A280
Two-Mile Wash	Rkm	2.9	A288
Gauge Above LCR	Rkm	98.4	A296
Tanner cobble	Rkm	109.6	A304
127 Mile Rapid	Rkm	202.9	A312
205 Mile Rapid	Rkm	328.8	A320

INTRODUCTION

Impoundment of the Colorado River by Glen Canyon Dam (GCD) has caused significant and profound change within the lower trophic levels of the Colorado River through Grand Canyon (Blinn and Cole 1991, Haden 1997, Webb et al. 1999). Impoundment has disrupted the primary carbon source (allochthonous to autochthonous production), the temperature regime (seasonally warm to stenothermically cool) and the hydrologic patterns (from low daily variation to high daily variation). The resultant benthic community is comprised of the few species of invertebrates and algae that can thrive under these contrived and unstable environmental conditions. Cladophora glomerata, a filamentous green alga, underpins carbon production in this ecosystem system (Blinn and Cole 1991). Although it is considered a weed in other situations (Benenati et al. 1998, Blinn et al. 1998), Cladophora provides an important structural host for epiphytic diatoms that sustains grazing primary consumers (Benenati et al. 2000). The invertebrate community is a low diversity assemblage of alien nearctic taxa (Blinn et al. 1991, Sublette et al. 1998, Shannon et al. 2001).

In 1991 the Northern Arizona Food Base Project began a sustained effort to document changes in the benthos throughout the length of the river in Grand Canyon in response to the operations of GCD. This alien food base assemblage has developed against a background of changing flow scenarios since GCD was completed. During 1963 until 1983 as Lake Powell filled, daily flow variation ranged from 85 - 935 m^3/s for hydro-power production and very little information on the benthic community was gathered at this time. Arizona Game and Fish Department was actively introducing new species into the tailwaters (Stone and Rathbun 1969) and low abundance of downstream invertebrates were reported by Carothers

and Minckley (1981). A prolonged period of sustained high discharge from GCD (1133 - 2690 m^3/s) occurred during 1983; unfortunately, the effects of this discharge on the benthos were not well documented (Blinn and Cole 1991). The Bureau of Reclamation conducted experimental flows and ramping rates (142 - 935 m^3/s) in 1990 - 91 to examine their effect on all aspects of the river ecosystem (Patten 1991). In late 1992, federally mandated reductions in daily flow fluctuation were implemented (142-567 m^3/s) with reduced ramping rates; however these Interim Flows were later modified to higher daily fluctuations in the Record of Decision (ROD) for the GCD Environmental Impact Statement in 1995 (BOR 1995). Following the ROD a seven day spike flow of 1275 m^3/s was released in Spring 1996 (Shannon et al. 2000) and a combination of three-day spikes (793 m^3/s) and three months of steady flows (227 m^3/s) were released in 2000 (see chapter 7).

The NAU Aquatic Food Base was awarded a monitoring and research cooperative agreement with the Grand Canyon Monitoring and Research Center in 1998 that included the following objectives:

Objective 1: Monitor the effects of the GCD Environmental Impact Statement ROD modified low fluctuating flows on the benthic community in the Colorado River between GCD and Diamond Creek. (Seven sites - annual collections in March, June, and October).

Objective 2: Monitor the effects of modified low fluctuating flows from GCD on the organic drift in the Colorado River between GCD and Diamond Creek. (Seven sites - annual collections in March, June, and October).

Objective 3: Assess the benthos and drift of major tributaries in Grand Canyon National Park. (12 sites - bi-annually in January)

Objective 4: Construct an aquatic/riparian food web using stable isotope analysis.

In 1999 our agreement was modified to a reduced monitoring effort, one collection period in June and our focus was on manuscript preparation of existing data, continued work on the stable isotope objective, and the creation of fifth objective.

Objective 5: Preliminary analyses on the use of Cladophora, Oscillatoria, and total plant carbon as indices for general community health of the regulated Colorado River below Glen Canyon Dam, Arizona.

These project objectives were designed to gather data to inform stakeholders in the Grand Canyon Adaptive Management Program who were interested in the keystone relationship between the aquatic food base and higher trophic levels, in particular, humpback chub and rainbow trout. Our agreement was modified again in 2000 so we could monitor the effects of the 2000 ecological restoration flows effects on the aquatic food base and continue to meet the above stated five project objectives.

This report delineates the results we obtained while pursuing these five project objectives. **Objective 1** results, which are described in Chapters 5, 7, 8, 9, and 10, highlight the ongoing instability of the biomass and composition of the aquatic food base. Also see Benenati et al. (2000) for a description and analysis of the abrupt changes in the phytobenthic community since 1995. **Objective 2** results, included in Chapters 2, 3, 6, and 9, demonstrate the importance of monitoring organic drift in relationship to fish population dynamics. Also see Benenati et al. (2001) for a description of zooplankton drift patterns. **Objective 3** results are described in Chapter 4 and demonstrate the importance of monitoring tributaries for effects within the watershed, yet also outside the main stem

corridor and National Park boundaries. Also see Oberlin et al. (1999) for a complete description of the phytobenthic communities and processes within 12 Grand Canyon tributaries. **Objective 4** involved the application of stable isotopes analysis in understanding the linkages between the aquatic food base and higher trophic levels, results of these efforts are contained in Chapters 3, 6 and 11. Also see Shannon et al. (2001) and Pomeroy et al. (2001) for food web analysis in the Colorado River. **Objective 5** topics are presented in Chapters 1, 2, 3, 6, 10, and 11. Readers of this report should note that the chapters pertaining to Objective 5 are very much management driven and do contain "null data" results which are not applicable to peer-review for journal publication. However, the work is reported in this technical report to provide GCMRC staff and the Adaptive Management Program stakeholders information regarding the current state of knowledge which will also serve to help develop further experimental and monitoring techniques. Each chapter is written to stand alone.

Summary

In conclusion, the data from our objectives provide evidence of strong linkages between the aquatic food base and fishes of the Colorado River. This includes native fish. We have shown that the food base responds negatively to peaking (or load-following) hydropower flows and therefore, this same response applies to native fish and their habitat.

The 1995 Environmental Impact Statement on the operations of GCD predicted "potential major increase" for the aquatic food base (p58 Table II-7) with the implemented Modified Low Fluctuating Flow alternative. This increase has not happened and in fact, the food base is very unstable

(Table 1). Also, the Modified Low Fluctuating Flow alternative has a base flow of 142 m^3/s at night and 227 m^3/s from 7 am to 7 pm. We have found that varial zone exposure during the day, night, summer, or winter has the same effect - desiccation and death of the food base. Aquatic organism need to be continuously submerged in order to be viable. In light of these published facts, it would be prudent to raise the minimum baseflow to 227 m^3/s. (See Blinn et al. 1995, Benenati et al. 1998).

Descending hydrographs of spring and fall are the best periods for growth of the aquatic food base. We recommend a decade of the Seasonally Adjusted Steady Flow alternative, with spring beach building flows as the climate permits and unlimited hydropower ramping within 10% of the predicted seasonal mean. We feel these flows in combination with alien fish suppression and thermal modification of GCD could make Grand Canyon a sanctuary for native fishes of the Colorado River basin.

Table 1. Average biomass and density estimates in the Colorado River from Lees Ferry (rkm 0.8) to 205 Mile Rapid (rkm 328.8) in June from 1991 - 2001. MAMB is an abbreviation for miscellaneous algae, macrophytes, and bryophytes.

Year	Cladophora gAFDM/m^2	MAMB gAFDM/m^2	Invertebrates #/m^2	Snails #/m^2
1991	2.7	0	150	2
1992	0.7	0.04	191	4
1993	1.5	0.08	197	4
1994	5.2	1.5	738	13
1995	12	1.5	427	6
1996	7	15	1160	58
1997	3.8	6.2	2500	970
1998	6.1	6.6	4773	3336
1999	5.2	8.0	2237	640
2000	2	38.0	1116	37350
2001	6.2	36.1	995	2624

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Chapter 1: Cladophora, Oscillatoria, total plant carbon, and macroinvertebrate biomass as an indicator of aquatic invertebrate community health of the Colorado River below Glen Canyon Dam, Arizona.

INTRODUCTION

Cladophora glomerata serves as a keystone species in the food web in the tailwaters below Glen Canyon Dam (GCD). Previous studies on the tailwaters below GCD have repeatedly shown that C. glomerata is the preferred habitat for the alien macroinvertebrate assemblage in the regulated river in comparison to other available habitats including other green filamentous algae and Oscillatoria, aquatic bryophytes, and macrophytes (Blinn and Cole 1991, Blinn et al. 1992, Angradi 1994, Shannon et al. 1994, Shaver et al. 1997, Stevens et al. 1997, Ayers and McKinney 1998, Benenati et al. 1998, Shannon et al. 1998, Benenati et al. 2000). The highly branched filaments of C. glomerata provide a large surface area for the colonization of epiphytes, as well as, habitat for invertebrate reproduction and a refugium from predators (Stevenson and Stoermer 1982, Leskinen and Hallfors 1990, Dodds and Gudder 1992, Hardwick et al. 1992, Blinn et al. 1998).

Stakeholders comprising the Grand Canyon Adaptive Management Program (GC-AMP) have a management goal to "Protect or improve the aquatic food base so that it will support viable populations of desired species at higher trophic levels" (see GC-AMP Strategic Plan). This goal is supported by four management objectives that strive to maintain the post-dam phyto-benthic community. These management criteria can collectively be referred to as stream health according to the definition of "... an ecosystem that is sustainable and resilient, maintaining its ecological structure and function over time while continuing to meet societal needs

and expectations" (Meyer 1997). The stakeholders have not yet determined any numerical values or indices to evaluate if the goals and management objectives have been met. Due to the critical role of C. glomerata in the food web of the regulated Colorado River below GCD (see Blinn et al. 1998), we propose that this green filamentous alga be considered as a potential index for invertebrate community health in the Colorado River throughout Grand Canyon. An index based on algal biomass would provide an inexpensive and less time consuming way to monitor lower trophic levels in the Colorado River.

We compiled and analyzed phytobenthic data collected from cobble bars from 1991 through 1996 by the Northern Arizona University Aquatic Food Base Program. The relationships between C. glomerata, Oscillatoria and total invertebrate biomass were analyzed for a potential health index. Total plant carbon biomass (autochthonous and allochthonous) and invertebrate biomass were also examined.

METHODS

Collections: The data presented in this report result from 6 years of effort between 1991 and 1996 by the Northern Arizona University Aquatic Food Base Project (Blinn et al. 1992, Blinn et al. 1993, Blinn et al. 1994, Blinn et al. 1995a, Shannon et al. 1996, Shannon et al. 1997). These data sets contained 1,122 data points starting in January 1991 and continued through 1996. Although this project has had various objectives over the last decade, many of the sampling sites and methodologies have remained constant throughout. The data used for these analyses have been taken from the data base and represent common sites and common collecting methods throughout the period, although there may not be an uniform

representation of sites or uniform number of sample periods between years.

Collection trips (between 1 - 6) were made down the Colorado River each year. The number of collections per year reflected the available funding for food base research and the project objectives at the time. A summary of the number of collections for each calendar year is given in Table 1. Samples were taken from cobble bars at 11 different sites between Lees Ferry (rkm 0) and Diamond Creek (rkm 360). Sites were located along the length of the river to determine the influence of distance from GCD (rkm = -26.0) and the influence of tributaries on the aquatic benthos (Table 2).

Samples were taken with a modified Hess substrate sampler on cobble substrates. Samples were collected by stirring the benthos with a metal trowel for 30 sec. Benthos dislodged from the substrate was flushed into the collection net portion of the sampler and transferred to plastic containers for further processing. Samples were taken from the permanently wetted area of the cobble bar as opposed to the varial zone which is subject to regular de-watering due to fluctuating flows from GCD. Previous studies have shown that the varial zone has a different benthic community composition and limited standing mass compared to the permanently wetted area (Blinn et al. 1995a, Shaver et al. 1997, Benenati et al. 1998). The cobble bar at each site was divided into 3 transects approximately 30 m apart. Two randomly spaced samples were taken at each transect to give a total of 6 samples for each site. Collections in 1991 have only 3 samples per cobble bar since half the samples were used for taxonomic purposes during that period.

Samples were sorted within 48 hr of collection. Samples were originally sorted into 11 different biotic categories as described by Blinn et al. (1995b). Samples were dried to a constant weight at 60°C then weighed and ashed for 1 h at 500°C to estimate ash-free dry mass (AFDM). During the later part of the study, AFDM was estimated from dry weight using regression equations for each benthic category. For the purpose of these analyses, the original 11 categories were reduced to 4 broad categories: total macroinvertebrates, C. glomerata, Oscillatoria spp., and detritus. Some analyses compared total primary carbon to other categories. Total primary carbon is composed of all algae and detrital categories in the phytobenthic community. All analyses are based on AFDM m^{-2} standing mass of each category.

Statistical methods: We used simple linear regression to test the hypothesis that carbon sources (C. glomerata, Oscillatoria spp., detritus, total carbon, or a ratio of Oscillatoria standing mass to C. glomerata standing mass) would be good predictors of invertebrate standing mass in the Colorado River. Regression models were tested with one predictor at a time rather than in multiple regression models since the objective of this research is to provide information that will help simplify field collections and processing methods rather than build predictive models from multiple predictors. Each Hess sample represents a single sample and no attempt has been made to look at relationships within a specific site.

All data were transformed using a 4th root transformation to improve homoscedascity (Sokal and Rolf 1992). Data were further refined by removing all samples with zero values. For each analysis we attempted to improve the fit of the linear equation by removing outliers from the

analysis. Outlier points were identified using a Cooks-D coefficient (Sokal and Rolf 1992). Data were analyzed using JMP IN® Ver. 3.2.1 statistical software (SAS Institute, 1989).

RESULTS AND DISCUSSION

Our analyses indicated that C. glomerata has a strong potential of serving as a functional index for invertebrate community health in the regulated Colorado River below GCD. This is based on the strong positive relationship between C. glomerata AFDM and total invertebrate AFDM ($R^2 = 0.415$, $p < 0.001$) in the tailwaters of GCD (Fig. 1). Total carbon was also a positive and signficant predictor of invertebrate AFDM ($R^2 = 0.39$, $p < 0.001$) however less of the variance in invertebrate biomass could be explained by total carbon alone (Fig. 2).

In contrast, there was no relationship between Oscillatoria spp. AFDM, and total invertebrate AFDM ($R^2 = 0.009$; Fig. 3). This is not surprising since Oscillatoria spp. only becomes numerically important in the regulated Colorado River in highly stressed regions of the tailwaters such as the varial zone and during periods of turbidity (Shaver et al. 1997, Benenati et al. 1998). Furthermore, C. glomerata communities contribute an order of magnitude more potential energy to the ecosystem than Oscillatoria spp. mats (Shaver et al. 1997).

Other workers have found a strong relationship between organic carbon standing crop and invertebrate abundance, biomass, and production in streams (Wallace et al. 1999). These same relationships apply to linkages between algae and terrestrial plant carbon mass (standing organic plant carbon) and macroinvertebrates (Winterbourn 1990). Filbert and Hawkins (1995) reported a strong relationship between drifting mass of

invertebrates and condition of rainbow trout in the Green River, Wyoming. Therefore, since invertebrates make up a large proportion of the diet of native and nonnative fish (Valdez and Ryel 1995, McKinney and Persons 1999) in the tailwaters of GCD, this index should provide good insight into the overall health of the Colorado River below GCD. However, Wallace and Webster (1996) proposed that "effective fisheries management must account for fish-invertebrate linkages and macroinvertebrate linkages with resources and habitats" and the relationship between standing mass of the relatively new assemblage of aquatic invertebrates, non-native fishes and native fishes remains unclear.

Therefore, it may be feasible to use either C. glomerata mass and/or standing carbon mass as a simple, but functional index, for aquatic invertebrate community health in the regulated Colorado River while continuing to test how native and non-native species interact within the context of the post regulation food base. This index could provide the basis for a long-term monitoring program designed to determine general condition of the aquatic community in the Colorado River below GCD. An index could be developed with stakeholder input or the slope of the present line could be compared with future collections to determine if there are any shifts in the dependence between macroinvertebrates and a particular carbon source.

Table 1. List of sample trips for each calendar year, number of sites and number of samples per site used in analysis of relationship of primary

Calendar year	# trips/year	# sites/trip	# samples/site
1991	6	11	3
1992	1	11	6
1993	4	11	6
1994	4	11	6
1995	2	11	6
1996	3	11	6

Table 2. Location and names of cobble bar sample sites used in analysis of the relationship between primary carbon sources to aquatic invertebrate standing mass in the Colorado River below Glen Canyon Dam, AZ. Lees Ferry, AZ is designated as rkm 0.0, Glen Canyon Dam is located at rkm -26.0.

Name	Location (RKM)	Comments
Lees Ferry	0.8	Continuous clear water, no tributary influence
Two Mile Wash	3.1	Below influence of Paria R. tributary
South Canyon	50.8	Below influence of Paria R. tributary
Nankoweap	83.2	Above Nankoweap Ck.
Little Colorado	98.7	Above influence of Little Colorado R.
Tanner	109.6	Below influence of Little Colorado R.
Phantom Ranch	142.4	Below influence of Bright Angel Ck.
Kanab	232.0	Below influence of Kanab Ck.
Upset Rapid	240.0	Below influence of Kanab Ck.
205 Mile Rapid	328.9	Below influence of Kanab Ck.
Gorilla Island	352.0	Below influence of Kanab Ck.

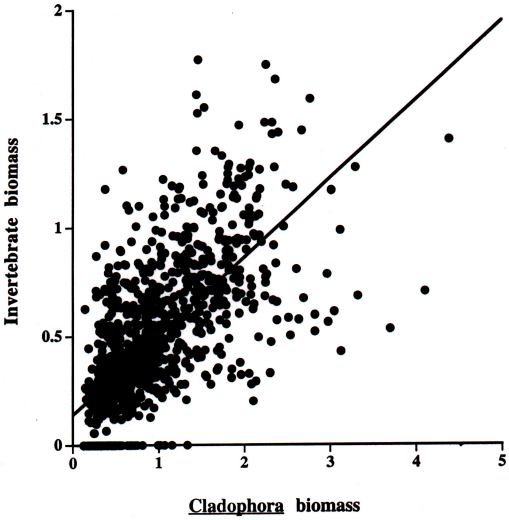

Figure 1. Relationship between Cladophora glomerata and invertebrate biomass in the Colorado River below Glen Canyon Dam, AZ. n=1046; R^2=0.44; Y=0.361X+0.141. Data is 4th root transformed AFDM $g \cdot m^{-2}$. Samples with predictor values > 0 have been included in analysis.

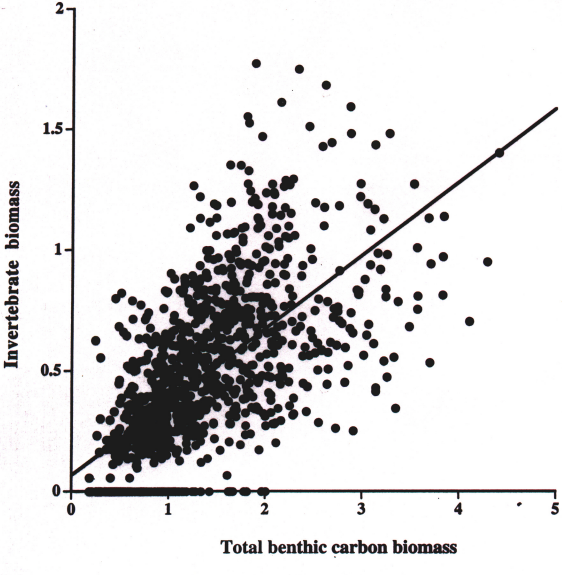

Figure 2. Relationship between benthic carbon and invertebrate biomass in the Colorado River below Glen Canyon Dam, AZ. n=1118; R^2=0.38; Y=0.303X+0.068. Data is 4th root transformed AFDM $g \cdot m^{-2}$. Samples with predictor values > 0 have been included in analysis

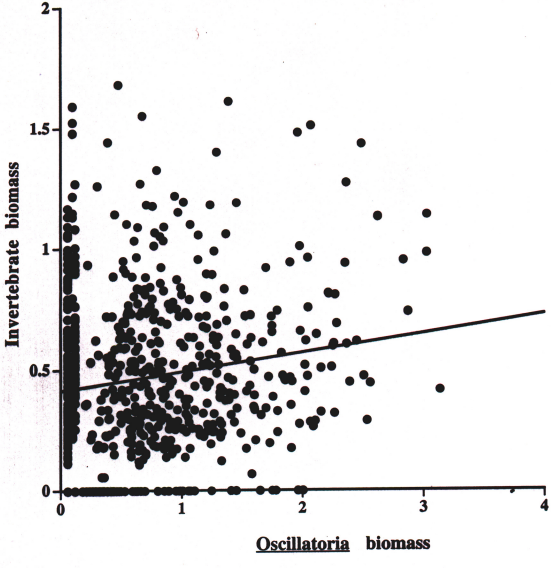

Figure 3. Relationship between Oscillatoria spp. and invertebrate biomass in the Colorado River below Glen Canyon Dam, AZ. n=692; R^2=0.02; Y=0.79X+0.413. Data is 4th root transformed AFDM $g \cdot m^{-2}$. Samples with predictor values > 0 have been included in analysis.

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Chapter 2: Patterns in benthic standing mass and rainbow trout populations in the Colorado River at Lees Ferry, AZ from 1991-1999.

INTRODUCTION

It is widely recognized that growth and maintenance of fish populations is partially dependent on an adequate supply of energy (Wooton 1990, Hewett and Johnson 1992). However the relationship between food availability and fish population variables are often mitigated by factors such as habitat availability for various life stages, competition, predation or parasite infestations (Chapman 1966, Hiscox and Brockson 1973, Slaney and Northcote 1974, Wooton 1990, McKinney et al. 2001a). Invertebrates comprise nearly 100% of the animal matter in rainbow trout (Onchorynchus mykiss) diets in the Colorado River at Lees Ferry, Arizona (Angradi 1994, McKinney et al. 1999a, McKinney and Speas 2001). Changes in standing mass of the benthic community of this reach may be expected to have effects on the growth rates (Wooton 1990), health, condition (McKinney et al. 2001a), and density of the trout population.

The objective of this study was to examine relationships between trout prey items (benthos and drift) and the condition, density, and growth of rainbow trout in the Lees Ferry reach of the Colorado River between Lees Ferry (Rkm 0.8) and Glen Canyon Dam (Rkm -26.0). By necessity, our approach has been a post hoc analysis of data collected under two separate research programs with different research goals. Arizona Game and Fish Department has monitored rainbow trout in this reach since 1991 and Northern Arizona University Aquatic Food Base lab has monitored the aquatic community at Lees Ferry for the same period. While the two projects were not designed to be integrated, the methodologies for both projects have remained consistent for the duration of the sampling period.

The methods and extent of the data sets combined with the close proximity of the sample sites make these data sets a logical choice for this type of ad hoc analysis.

METHODS

We used correlation analysis to test the hypothesis that food base is related to rainbow trout condition and density. Food base variables include invertebrate drift (mean AFDM $g \cdot m^{-3}$), standing mass of invertebrates, and algae (mean AFDM $g \cdot m^{-2}$) from cobble substrates at our Lees Ferry site (0.8 km). Response variables were mean relative condition (Kn) and mean catch per unit effort (CPUE) of rainbow trout from the Lees Ferry tailwater. Arizona Game and Fish Department collected CPUE data by single-pass electrofishing at 9-15 randomly selected transects during 1991-1999 using standardized methods (see McKinney et al. 1999a). Benthic and drift variables were collected on 26 dates from 1991 through 1999, while fish data were collected during 30 sampling trips conducted by Arizona Game and Fish Department. Catch per unit effort is measured as fish · minute EF^{-1} caught by electro-fishing and Kn is:

$$W/W' * 100$$

(Anderson and Nuemann 1996) where W is observed weight of individual fish and W' is weight predicted by a standard weight equation ($10^{(-4.6 + 2.856\log10(length))}$) derived from Lee's Ferry fish measurements (McKinney et al. 2001b).

Since data was collected under two different programs, not all sample dates coincide. Fisheries data was matched to benthic data from the closest benthic sampling date previous to fisheries data collection. Benthic sampling dates were from 1 week to 2 months previous to fisheries

sampling. Data was analyzed using correlation techniques in JumpIn ver. 3.2.1 (SAS Institute 1996). Due to multiple pair-wise comparisons, pair-wise significance levels were tested against an experiment wide alpha of 0.05 using the Dunn-Sidák method (Sokal and Rolf 1992).

Log-transformed benthic, drift, and CPUE independent variables were also utilized jointly in a step wise multiple regression analysis to identify degrees of association of each variable with trout instantaneous growth rates. We assumed that CPUE data was an unbiased index of trout population size in the tailwater (McKinney et al 1999a, 2001b). Trout growth was indexed by observed instantaneous growth rates of recaptured stocked trout, which had been batch-marked with coded wire tags in the hatchery. These fish were stocked annually by AGFD beginning in 1992. Instantaneous growth (Busacker et al. 1990) was calculated as:

$$\ln(TLr) - \ln(TL_m) / (t_r - t_m)$$

where TL is total fish body length (millimeters), t is time (days), and subscripts r and m refer to recapture and marking occasions, respectively.

Lengths of marked fish in the growth analysis were the average length of cohorts as measured in the hatchery. Mean length at recapture was 324 mm, indicating that most growth observations were made on adult fish. To aid in interpreting response of growth rates among sub-adult fish, we fit cohort-specific lengths at recapture over time with logistic growth curves, where predicted length at time t is expressed as:

$$K / (1 + (K - TL_0) / TL_0)* e^{(-r*t)}$$

(Freund and Littell 1991) where K is the expected mean length at very large t, TL_0 is total length at t = 0 (stocking), and r is the intrinsic rate of growth. We used r as an index of juvenile fish growth rates, because it essentially describes growth of fish prior to the asymptotic phase associated

with adulthood (Freund and Littell 1991). Data were available only for five estimates of r (stocked cohorts recaptured in 1993-1995, 1997, and 1998). We did not use r estimates in analysis, but rather compared trends in r over the duration of the study period with trends in growth observed in adult fish.

RESULTS

Both invertebrate standing crop and rainbow trout CPUE showed a pattern of increase from 1991 through 1997, followed by declines from 1998 through 1999 (Fig. 1). However, there was too much variation within the general pattern for a significant correlation except with invertebrate drift, which is closely correlated with benthic standing mass (Table 1). The correlation between CPUE and invertebrates standing mass was improved by deleting dates that had >10 $g \cdot m^{-2}$ standing mass invertebrates and were not sustained from one sample period to another ($R = 0.43$, $p = 0.034$, $n = 25$), however this comparison was still nonsignificant at the adjusted alpha level. Standing mass of these trips was dominated by gastropods as opposed to amphipods and chironomids.

Step wise multiple regression revealed that declines in instantaneous trout growth rates were negatively correlated with trout density ($R^2 = 0.29$, $p = 0.048$, $n = 22$), but addition of invertebrate benthic standing mass and drift variables to the model did not explain significant amounts of the remaining variance. Trout density (LnCPUE) generally increased from 1991 through 1999 (Fig. 2).

Growth rates of sub-adult trout (as indexed by intrinsic growth rate r) increased from 1993 through 1998, although the trend is weak ($R^2 =$

0.63, $p = 0.059$, $n = 6$). In contrast, adult growth (indexed by instantaneous growth) declined during the same period (Fig. 2).

DISCUSSION

Hydrologic conditions created by varying releases from Glen Canyon Dam during 1991-1999 simultaneously enhanced conditions for rainbow trout and invertebrates in the Lees Ferry reach. These findings are very similar to those of McKinney et al. (1999a, 2001a), who concluded that increases in trout density were due primarily to increases in survival and recruitment of wild-spawned fish resulting from increased daily minimum flows and reduced daily discharge variability from 1991 through 1997, which also coincided with increases in benthic standing mass.

Linkages between benthic and fishery variables are probably restricted to invertebrate consumption by sub-adult (<300 mm) rainbow trout. McKinney and Speas (2001) demonstrated that diel energy intake by sub-adult (ca. < 300 mm) trout in the tailwater was usually sufficient to promote growth, making these fish the most likely to show a response to variations in food availability. Adult (≥ 300 mm) RBT, however, rarely exceeded maintenance energy intake levels, suggesting competition for invertebrate food resources effectively limited growth rates beyond maturity. In the present study, subtle increases in intrinsic (juvenile) growth rates during 1992-1998 reflected improved growth (and perhaps survival) conditions for sub-adult fish. Increased food availability was among these improved conditions.

Effects of varied food quantities on trout growth should be greatest when water temperatures are optimal for growth (Elliot 1976, Hewett and Johnson 1992, Filbert and Hawkins 1995), or about 17 ° C for rainbow

trout (Hokanson et al. 1977). Water temperatures in the Lees Ferry tailwater are relatively constant and arguably sub-optimal (8-10 °C) for growth of rainbow trout (McKinney and Speas 2001), so direct linkages between variance in benthic standing stocks and trout population are inherently difficult to quantify. Compounding this difficulty is the strong possibility that competition for spatial resources (optimal foraging habitat and resulting stress incurred from increased fish densities in these areas; Chapman 1966, Slaney and Northcote 1974, Jenkins et al. 1999) could override or obscure benefits of increased food availability.

Improved survival of juvenile trout led to over-recruitment to adulthood, which progressively depressed growth rates beyond maturity. Trout growth has apparently been decoupled, to a large extent, from changes in the food base, so causes of depressed growth rates must also be ascribed to competition of some form of non-food resources such as habitat. McKinney and Speas (2001) observed no substantial change in median diel energy intake by any size class of trout during 1991-1997 despite an increase in benthic standing mass during that same period, and percentages of maximum consumption rates for fish of all sizes never exceeded 30%. Growth rates of adult fish declined as relative densities increased, while growth rates of juvenile fish remained the same or increased slightly. Competitive asymmetries of this sort among age or size classes have been described in detail by Walters and Post (1993). While food availability and adult fish growth appear decoupled in the Lees Ferry reach with high fish densities were high and benthic standing mass, sites downstream of Lees Ferry may be interacting differently. In areas where benthic standing mass is chronically reduced and fish densities are lower we suspect that trophic linkages might be more simplistic.

Our analysis indicates that sudden, unsustained variations in the food base are not correlated with increases in trout populations. Much of the increases in benthic mass are associated with increases in the density of snails, which may not be easily digested by trout and are less likely to be entrained in the drift. In addition, conditions that favor the rapid increase of benthic standing mass may not be sustained for long enough periods to cause associated increases in fish density. This finding is consistent with that of McKinney et al. (1999b), who concluded that sudden reductions in benthic standing mass due to scouring had little direct influence on trout diets. While CPUE and Kn have shown significant trends of the Lees Ferry trout community over the last decade, they are poor variables to measure the short-term effects of food base variation on the trout community. The relatively poor fit of the data may also be a function of the post-hoc nature of this study which attempted to integrate two data bases collected under programs with different goals. The nature of the link between food availability and the fish community requires further study, especially if native/nonnative fish interactions are to be included. We suggest that physiological parameters such as RNA/DNA ratios (Bulow et al. 1981), more detailed analyses of growth and/or consumption (see McKinney et al. 1999b), or others (see McKinney et al. 2001a) may provide a better measure of short-term effects to the fish community.

Table 1. Pair wise correlation of benthic variables and rainbow trout parameters collected at Lees Ferry from 1991 through 1999. Correlation coefficients are Pearson's R. * Significant at experiment wise alpha = 0.05 adjusted by Dunn Sidák method.

		R	n	p
Cladaphora standing mass (AFDM $g \cdot m^{-2}$)	Invertebrate standing mass (AFDM $g \cdot m^{-2}$)	0.58	30	0.0006*
Invertebrate drift (AFDM $g \cdot m^{-3}$)	Invertebrate standing mass (AFDM $g \cdot m^{-2}$)	0.75	21	0.0001*
Invertebrate drift (AFDM $g \cdot m^{-3}$)	Cladaphora standing mass (AFDM $g \cdot m^{-2}$)	0.67	21	0.0010*
Trout condition (kn)	Invertebrate standing mass (AFDM $g \cdot m^{-2}$)	-0.09	30	0.6255
Trout condition (kn)	Cladaphora standing mass (AFDM $g \cdot m^{-2}$)	0.32	30	0.0849
Trout condition (kn)	Invertebrate drift (AFDM $g \cdot m^{-3}$)	-0.21	20	0.3660
Trout catch per unit effort (cpue)	Invertebrate standing mass (AFDM $g \cdot m^{-2}$)	0.35	30	0.0577
Trout catch per unit effort (cpue)	Cladaphora standing mass (AFDM $g \cdot m^{-2}$)	0.14	30	0.4433
Trout catch per unit effort (cpue)	Invertebrate drift (AFDM $g \cdot m^{-3}$)	0.46	20	0.0416
Trout catch per unit effort (cpue)	Trout condition (kn)	-0.14	30	0.4543

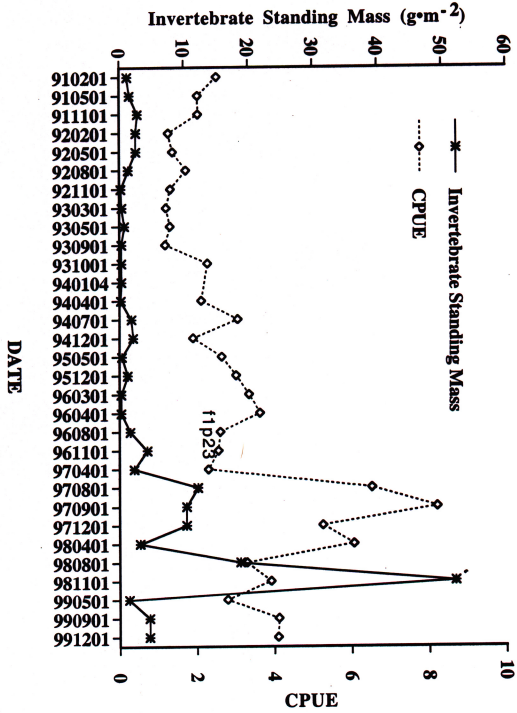

Figure. 1. Catch per unit effort (CPUE; fish per minute electrofishing in the 25 km Lees Ferry tailwater) and invertebrate standing mass (AFDM g·m-2 at Rkm 0.8) from 1991 through 1999.

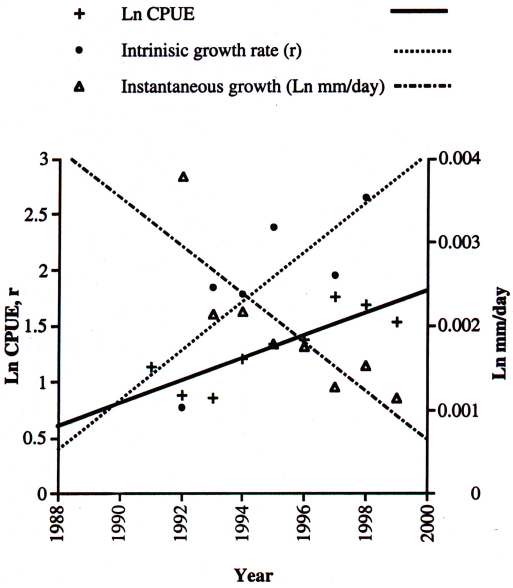

Figure 2. Catch per unit effort (+, left axis) intrinsic growth coefficient (•, left axis) and instantaneous growth rates (Δ, right axis) of rainbow trout in the Lee's Ferry tailwater, 1991-1999. Lines depict linear trends which show that intrinsic growth (juvenile growth) and catch per unit effort (density) increased while intrinsic growth (adult growth) declined.

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Chapter 3: Food resource limitations and movement of the humpback chub an endangered cyprinid fish in the Little Colorado River, Arizona, USA

INTRODUCTION

Migration of fish among distinct habitats distributed over a broad geographic range to meet life history requirements confounds conservation efforts for many diadromous and marine species (McDowall 1992, Musick et al. 2000). Different life stages of a population may depend on successfully moving among a complex of connected habitats in order to fulfill energetic requirements for successful reproduction and recruitment (McDowall 1992, 2001; Northcote 1996). The degradation of key habitat components may have more profound consequences for population dynamics beyond simple reduction in habitat size, particularly if the energetic needs for a portion of the population or life history stage are compromised. Thus, when one life stage using one habitat is adversely affected by anthropogenic impacts such as habitat disturbance, barriers to migrations, over harvest etc., the status of the population or species may be jeopardized (McDowall 1992; Musick et al. 2000). Within the confines of freshwater systems, anthropogenic impacts to vulnerable migratory species may be more pronounced, including degradation and destruction of habitats, sedimentation, pollution, imposition of barriers (dams and locks), changes in hydrological regimes (dams and diversions), and over exploitation (Northcote 1996; Billard and Lecointre 2000).

Movement of fish occurs for a variety of reasons throughout their life cycle. Hall (1972) suggested that the impetus for migration is best understood within the framework of energetic demands on the organism in question. While fish movement has been tied to optimization of foraging

or reproductive success, fish may also move to avoid unfavorable conditions (Northcote 1978). Hall (1972) showed that the movement of stream fishes is closely tied to maximization of energetic resources for the whole fish community. Fish populations that use different habitats for spawning, rearing of young and the maintenance of adults provide good examples of the maximization of energy use that result from migration of individuals (McKeown 1984). Additionally, movement may only be required of a specific portion of the population in order to maximize the energetic benefits (Northcote 1978). Failure of portions of the populations to move to different habitats at critical periods in the life history can result in reduced reproduction, increased mortality, and a reduction in population size.

Our study examined the food resources of a population of humpback chub (Gila cypha), a federally endangered cyprinid fish, endemic to the Colorado River and its tributaries in the southwestern USA, in order to better understand the energetic basis for movement and distribution patterns noted by previous researchers. The Little Colorado River (LCR) and adjacent reach of the Colorado River contain the largest remaining population of adult humpback chub in the Colorado River basin (Douglas and Marsh 1996). Natural thermal and flow regimes of the Colorado River in Grand Canyon has been dramatically altered by the installation and operation of Glen Canyon Dam, a large peaking hydroelectric facility located above Lees Ferry, Arizona. The once turbid, seasonally fluctuating, warm temperate river has been transformed into one characterized by clear, daily fluctuating flows and chronically cold temperatures (8-10˚C) and now supports a large non-indigenous trout population (Gorman et al. 2002). The LCR appears to serve as a thermal

refugia for humpback chub in Grand Canyon (Douglas and Marsh 1996); all humpback chub within the study population are dependent on the relatively warm LCR for spawning and rearing (Gorman and Stone 1999, Valdez and Hoffnagle 1999). Chronic cold temperatures of the post-impoundment mainstem Colorado River in Grand Canyon prevent successful spawning by this species (Hamman 1982, Kaeding and Zimmerman 1983) and growth in age-0 fish is greatly diminished at temperatures below 14˚C (Clarkson and Childs 2000). Adult humpback chub have been shown to move from the colder mainstem Colorado River into the warmer LCR to spawn (Kaeding and Zimmerman 1983, Gorman and Stone 1999, Valdez and Hoffnagle 1999). Many adult humpback chub move back out into the Colorado River after spawning is complete, however some adults remain and over-winter in the LCR (Douglas and Marsh 1996, Gorman and Stone 1999).

We hypothesize that large adult humpback chub move out of the LCR because of insufficient food resources even though this tributary provides a thermal regime that is better suited for growth of these fish compared to the mainstem Colorado River. The objectives of our study were to 1) quantify the seasonal food resources in the LCR in comparison to the mainstem Colorado River; 2) determine linkages within the LCR food web with multiple stable isotopes (^{13}C, ^{15}N, and ^{34}S); and 3) characterize the carrying capacity of the LCR for humpback chub through energetic modeling.

Study Site

The Little Colorado River originates on Mt. Baldy in eastern Arizona. It flows 412 km and drains 69,832 km^2 before joining the Colorado River

124 km below Glen Canyon Dam (Loughlin, 1983; Strength, 1997). This study was located in the lower 14.5 km of the LCR just above the confluence with the Colorado River (Fig. 1).

Impoundment, diversion, and land-use practices in the headwaters of the LCR have reduced base flow so that there is no surface flow as the river crosses the Painted Desert, AZ, except during substantial storm runoff. Perennial flow in the lower reach of the LCR is maintained by a series of springs emanating from the Redwall Limestone and Muav Limestone formations at 20-21 km above the mouth. Blue Springs is the largest of these springs and supplies approximately 56% of the 6.3 $m^3 \cdot s^{-1}$ base flow in this reach (Loughlin, 1983). Discharge from Blue Springs is characterized by high specific conductance (4075 µS) and high dissolved CO2 (>200 $mg \cdot L^{-1}$; Strength, 1997). As the spring discharge moves downstream, CO2 degasses with exposure to the atmosphere and photosynthetic activity. The loss of CO2 results in carbonate precipitation and travertine deposition, which are important geomorphic features of the lower reach of the river. The highest travertine dam formations (> 5 m) are located near the upstream boundary of the study area and form the Chute Falls complex (Fig.1). The distribution of humpback chub in the LCR is limited to areas downstream of these falls (Douglas and Marsh 1996).

Discharge above base flow in the LCR is stochastic and determined by seasonal cycles of precipitation. Periods exceeding base flow in the lower 21 km are normally bimodal with high flows resulting from winter precipitation and snow melt early in the year or localized convective

rainstorm activity in late summer (Gorman and Stone 1999). Suspended sediments are especially high during summer flooding events. Humpback chub are commonly found in the mainstem Colorado River from the confluence with the LCR to approximately 12 km downstream. In contrast to the warm LCR, the mainstem Colorado River is a stenothermal cool (8-10˚C) stream with temperature and discharge patterns controlled by hypolimnetic releases from Glen Canyon Dam that impounds Lake Powell. Because Glen Canyon Dam is a peaking power hydroelectric facility, discharge fluctuates on a daily basis from 142 to 707 $m^3 \cdot sec^{-1}$ to accommodate fluctuations in electrical demand.

Methods

Water Quality

We measured selected water quality parameters to examine physicochemical parameters that could be affecting abundance and distribution of the benthos. Discharge for the LCR was estimated from the U.S. Geological Survey gage at Cameron, AZ (86 km above the confluence). Discharge estimates for the LCR sampling sites below Blue Springs were estimated by adding the base flow discharge above the confluence (6.3 $m^3 \cdot s^{-1}$) to daily average flow at the Cameron, AZ gage (Gorman and Stone 1999). Mean daily water temperature was estimated from 15 minute interval temperature data taken at a site 1 km upstream from the confluence with the mainstem Colorado River. All other water quality parameters were collected at benthic sampling sites (km 14.5, 10.1, 0.9) when fieldwork was conducted. Dissolved oxygen ($mg \cdot L^{-1}$) and temperature (˚C) were determined using a YSI™ (Model 55) meter. Dissolved CO2 was measured using a HACH™ field titration kit or a CO2

microelectrode (O'Brien and Blinn, 1999) and pH was measured with an Oakton™ hand-held electronic meter. Water clarity was estimated to the nearest cm with a Secchi disk. Suspended particulates ($mg \cdot L^{-1}$) were estimated from grab samples taken from the top 0.3 m of the water column and turbidity was measured (NTU) in the field with a HACH™ portable turbidimeter. Grab samples were filtered through a Whatman™ GF/C glass filter and filtrates were dried and weighed to determine total particulate mass ($mg \cdot L^{-1}$). Additional water samples were collected, stored on ice, and transported to the laboratory where we determined total alkalinity (mg CaCO3 by titration) and specific conductance (µS).

Benthic standing mass and drift estimations

We outlined two basic objectives for our study of the LCR benthic community: (1) define the seasonal quantity and composition of the benthic community as a food resource for fish in the LCR, and (2) define the longitudinal distribution of the benthic community within the LCR. The first objective was met by sampling water quality, benthos, and aquatic drift at two different sites during June 1998, August 1998, October 1998, December 1998, April 1999, and June 1999. The first LCR site was located 14.5 km above the confluence and just upstream of the Atomizer/Chute Falls complex. The second LCR site was located 10.1 km above the confluence near Salt Canyon (Fig. 1). The second objective was addressed by including a third downstream site near the mouth of the LCR (km 0.9), April 1999 and June 1999. These three sites provided information on the longitudinal changes in water quality, benthos and aquatic drift (Fig. 1). To examine potential differences in food bases between the LCR and the mainstem Colorado River, we compared

invertebrate standing mass from sites in the LCR to a site in the mainstem Colorado River near the confluence of the two streams (Fig 1).

Benthos samples at each site were evenly stratified between hard (travertine dams) and soft (pool sediment) substrates. Hard benthic substrates were sampled using a Surber sampler (N = 6 at each site for sampling trip). Substrates were scraped for 30 seconds with a metal trowel to remove benthos. For each sample, depth (cm) and water velocity ($cm \cdot s^{-1}$) were measured with a Marsh-McBirney™ electronic flow meter. Soft sediments were sampled using a Petite Ponar dredge (N = 6 at each site for each sampling trip). Samples were collected along two transects running perpendicular to the stream edge. The three samples at each transect were taken with increasing distance from the stream edge to the center of the channel. Depth (cm) and relative distance from the stream edge were recorded for each sample. Additional benthic samples on soft and hard sediments were taken for taxonomic purposes.

Both fine particulate organic matter (FPOM; < 1 mm) and coarse particulate organic matter (CPOM; > 1 mm) drift were sampled. Collections were made in triplicate at the water surface. CPOM was collected in a rectangular net (0.135 m2, 0.5 mm mesh) and FPOM was collected in a 0.3 m diameter net with a 153 µm mesh. Velocity ($cm \cdot s^{-1}$) for each sample was measured with a Marsh-McBirney™ electronic flow meter for volumetric calculation.

All CPOM and benthic samples were sorted live within 48 h of collection. Samples were sorted into 5 different categories: miscellaneous macroinvertebrates (aquatic insects and other invertebrates), Cladaphora glomerata, cyanobacterial crust, detritus and miscellaneous algae, macrophytes and bryophytes. Abundance of specific taxa of invertebrates

(annelid worms, tubificid worms (oligochaetes), simuliids, chironomids, gastropods, ephemeroptera and trichoptera) were noted for each sample. Samples were dried, weighed, and combusted at 500˚C for 1 h to determine ash-free-dry-mass (AFDM).

FPOM samples were stored in 70% ETOH and sorted in the laboratory using a dissecting scope. Samples were sorted into the following categories: Copepoda, Cladocera, Ostracoda, miscellaneous invertebrates, and detritus. Samples of invertebrates were dried and weighed. Detrital AFDM was determined by combustion for 1 h at 500˚C.

Prior to statistical analysis, benthic data was log-transformed to improve homoscedascity. We used substrate type, sample date and site as predictor variables for response variables of estimates of mass of biotic categories using MANOVA techniques in SYSTAT 5.2.1 for the Macintosh (Systat, Inc., 1992). Specific univariate patterns within significant overall MANOVA tests were tested using post-hoc Tukey tests.

Energetic modeling

Energetic carrying capacity of the LCR, was estimated by constructing a bioenergetic model based on our estimate of the calories produced per kilometer by the benthos and drift for a one kilometer reach at the km 10.1 site and the caloric requirements for humpback chub. Our model was based on the caloric requirements for maintenance and not energy required for growth. The energetic requirements of humpback chub have not been studied, so we used values for a similar sized, congeneric species, which also inhabits southwestern rivers, the roundtail chub (*Gila robusta;* Shuman 1978). Caloric values per g·AFDM of standing mass and drift were estimated using caloric values from Cummins and Wuycheck (1971).

Caloric standing mass was converted to production per year using a production to biomass (P/B) ratio (Waters 1969, 1987). Area of each substrate type (hard or soft) and total surface area of the LCR channel for the kilometer reach surrounding the km 10.1 study site were estimated from intensive habitat sampling by O.T. Gorman (unpubl. data).

Our calculations follow the basic principles reviewed by Winberg (1956) and again by Mann (1978). Standard metabolic rate for G. robusta was estimated by O2 consumption (Shuman, 1978). Caloric requirements of this fish at rest were estimated by multiplying the oxygen consumption rate by the caloric equivalent of oxygen (4.63 kcal$\cdot$ l^{-1}; Brett and Groves 1979, Hillyard 1981). The caloric requirements of an active fish in the wild were estimated by multiplying the standard metabolic requirement by two (Rajagopal and Kramer, 1974). We corrected the caloric intake to calories actually used for metabolism (caloric intake - egestion as feces) with a multiplier of 0.8 (Winberg 1956). Annual caloric production$\cdot$$km^{-1}$ at the km 10.1 site was divided by the annual caloric requirements for G. robusta to estimate the biomass of fish supported by the food base in the LCR. Carrying capacity as defined by food availability was calculated as:

$$K = ((SC \cdot A \cdot C \cdot P) / (VO_2 \cdot 4.63 \cdot 2 \cdot 8760)) * 0.8$$

Where : K = carrying capacity of humpback chub ($g \cdot km^{-1}$)

SC = standing crop of invertebrates (AFDM $g \cdot m^{-2}$)

A = area covered by substrate type (m^{-2})

C = caloric conversion for invertebrates ($cal \cdot g^{-1}$ AFDM)

P = annual P/B ratio

VO_2 = Standard metabolic rate of G. robusta (ml $O_2 \cdot g^{-1} \cdot hr^{-1}$)

4.63 = caloric equivalent of O_2 ($kcal \cdot l^{-1}$)

2 = adjustment from standard metabolic rate to natural conditions metabolic rate

8760 = adjustment from hours to year

0.8 = adjustment for calories lost to egestion

Variability was incorporated into the model at several levels. Standing crop estimates were varied ±1 SE from the mean standing crop. Production to biomass ratios were varied from 2.5 to 5.0 to incorporate the full range of possible P/B ratios for the LCR invertebrate community and the standard metabolic rate of G. robusta was varied by ± 1 SE from the mean. The values were changed iteratively during mutiple runs of the model. Maximum and minimum values of K were reported.

Stable isotopes

Stable isotopes of carbon, nitrogen and sulfur were used to construct a food web for the LCR that linked fish consumers to their probable energy sources. Carbon and sulfur isotopes ($\delta^{13}C$ and $\delta^{34}S$) have been shown to be good indicators of food source and can be traced through trophic levels (De Niro and Epstein 1978 and Peterson 1999). Nitrogen isotopes ($\delta^{15}N$) are good indicators of trophic level; organisms with higher trophic position show an enrichment of heavy to light isotope compared to food sources (De Niro and Epstein 1981). In addition, we used mixing models of carbon isotopes to show the relative contribution of LCR and Colorado River carbon sources to the isotopic signal of adult humpback chub in the LCR (Whitledge and Rabeni 1997).

The relative contribution of LCR and mainstem Colorado River food resources to the diet of humpback chub was estimated using mixing models

based the $\delta^{13}C$ signals of invertebrates from the LCR and the Colorado River. Mixing models were produced using the minimum and maximum endpoints of the 90% confidence intervals for source $\delta^{13}C$ signals. The minimum value from one source was combined with the maximum value for the other and vice versa to estimate the full range of possible mixtures. Additionally selected samples were analysed for ^{34}S and used to verify patterns established with the ^{13}C analysis. Values reported are ratios of heavy to light isotope (^{13}C /^{12}C, $^{15}N/^{14}N$, or $^{34}S/^{32}S$) relative to international standards in parts per thousand (‰).

Samples of available food items and fish tissues were collected for analysis in conjunction with benthic sampling trips during the summer of 1998. In the case of invertebrates, several whole organisms were combined so that there would be a sufficient amount of tissue to sample. Fish were sampled non-lethally, except for incidental mortalities from monitoring activities carried out by O. T. Gorman, U. S. Fish and Wildlife Service. Tissue from fish < 250 mm were sampled by removing a portion of the pectoral and lower caudal fins. Samples from several individuals of the same size class were combined to create a sample large enough for mass spectrometry. Large fish (> 250 mm) were sampled either by taking fin clips or by using a biopsy instrument to remove a 4 mm diameter muscle plug from the dorsal area of the fish. Wound sites were treated with Betadine™ before the fish were released. Tissue samples were rinsed with distilled water then air dried in the field and further dried in a laboratory dessicator. Each sample was ground to a fine powder with a Wig-L-Bug™ amalgam shaker, weighed and analyzed by mass spectrometer. Mineral carbonate contamination in samples of detritus, algae, invertebrates, and fish tissue was tested by treating samples with dilute HCL (0.01N) and

comparing spectrophotometer results with those from untreated samples. The relationship of fin clips to muscle tissue was also examined by using incidental mortalities to compare isotopic signals of fin clips to muscle tissue from the same individual. Signal differences among food sources and trophic levels were tested using a t-test.

Results

Water Quality

The hydrology of the LCR was characterized by episodic high discharge and extended periods of base flow from springs with no flow from the upper drainage. Base flow was exceeded on 66% of the days between January 1, 1998 and September 30, 1999. There was less winter runoff in the second year of the study due to a dry winter (Fig. 2). Peak flows during the study period were approximately 54 $m^3 \cdot s^{-1}$.

The temperature range of the LCR remained higher than the cool Colorado River. Annual mean water temperature in the LCR was 17.8˚C, and ranged between 9.4 and 24.7˚C. Low temperatures did not persist for long periods and were associated with short intervals of high runoff during winter months (Fig. 2).

At base flow, the LCR showed a downstream longitudinal pattern of increasing pH, turbidity, and conductivity, while dissolved CO_2 decreased (Table 1). Following long periods of base flow, the reach containing our km 10.1 site typically exhibited increased carbonate precipitation (reflected by peak turbidity) and travertine deposition (Strength 1997).

When the LCR exceeded base flow, increased suspended particulates and dilution by increased water volume obliterated the base flow longitudinal pattern of water quality. Suspended particulate concentrations

in the top 30 cm of the water column during a spate in August 1998 were approximately 2.8 $g \cdot l^{-1}$. As suspended particulate load increased with flow, Secchi depth decreased. At the km 14.5 site, Secchi depth decreased from >2.5 m at base flow to < 0.01 m under high discharge. During high discharge summer spates, turbidity measurements exceeded 5100 NTUs, reflecting a high, suspended sediment load.

Benthic composition

The phytobenthic standing mass of the LCR was dominated by the filamentous yellow-green alga Vaucheria sp. (Chrysophyta: Tribophyceae). This alga formed tufted mats attached to travertine dams under a thin film of flowing water, a microhabitat inaccessible to fish. The mats also contained other filamentous algae such as Oscillatoria sp. and Spirogyra sp., as well as diatoms. The branched filamentous green alga (Cladaphora sp.) was also present in small amounts at the km 10.1 and km 0.9 sites.

The benthic invertebrate standing crop on hard substrates was composed mainly of mayflies (Baetis sp.) and caddisflies (Hydropsyche sp.), and some dipterans (mostly Chironomidae). We also found a hemipteran (Rhagovela sp.), Megaloptera (Corydalidae), and annelid worms. Soft substrates contained mainly Chironomidae, oligochaetes, and occasionally a sediment burrowing odonate (Gomphus sp.). Snails were also present in samples that contained large amounts of detritus.

Benthic Standing Mass

Invertebrate standing mass of sites within the LCR was an order of magnitude lower than an adjacent site in the mainstem Colorado River during the same time period (0.250 $g \cdot m^{-2}$, 0.027 SE). Standing mass of

the benthos was not distributed evenly among sites in the LCR but was concentrated at the upstream site (km 14.5), where carbonate precipitation and travertine deposition were relatively low and dissolved CO_2 was relatively high. In addition, standing mass at the km 14.5 site was positively correlated with duration of base flow prior to collection. At the downstream sites (km 10.1, km 0.9), where carbonate precipitation and travertine deposition were relatively high and dissolved CO_2 was reduced, biomass responded negatively to long periods of base flow. Standing mass varied significantly by river kilometer (Wilks' Lambda = 0.27, df = 5,116, $P < 0.001$), sampling period (Wilks' Lambda = 0.14, df = 25,432, $P < 0.001$), and substrate type (Wilks' Lambda = 0.40, df = 5,116, $P < 0.001$). Further analysis of spatial and temporal patterns on hard and soft substrates were conducted separately.

The highest standing mass of algae and macroinvertebrates on hard substrates were found at km 14.5 in June 1999 (Trip 6) after 201 consecutive days of near base flow (Table 2; Fig. 3). In contrast, invertebrate mass decreased at downstream sites during the same period of extended base flow (Table 2). For sampling trips that were not preceded by at least 30 d of base flow (Trips 1 through 4, Fig. 2), there were no significant differences in algal or invertebrate or standing mass among sites or sample periods. During trips 1 through 4 the overall mean standing mass of invertebrates was 0.056 $g \cdot m^{-2}$ (0.011 SE) and algal standing mass was 7.15 $g \cdot m^{-2}$ (2.641).

Standing mass of algae and macroinvertebrates at km 10.1 remained relatively low and stable over the period of study except for a significant increase (Tukey test, $P < 0.05$) in October 1998 (Trip 3) when invertebrate mass increased from an overall mean of of 0.028 $g \cdot m^{-2}$

(0.005) to 0.098 $g \cdot m^{-2}$ (0.027) (Fig. 3), and algal standing mass increased from an overall mean of 0.52 $g \cdot m^{-2}$ (0.271) to 3.54 (1.021)

Benthic standing mass associated with soft sediments was concentrated in shallow areas near stream edges that were protected from higher current velocities compared to deeper midchannel areas. Macroinvertebrate standing mass in soft substrates was highest at km 14.5 following a long period of base flow which allowed accumulations of algal and detrital biomass in protected pools. Macroinvertebrate mass at this site reached 1.17 $g \cdot m^{-2}$ (0.62) in April 1999 while combined algal/detrital mass reached 28.07 $g \cdot m^{-2}$ (17.93). In contrast, macroinvertebrate mass was 0.084 $g \cdot m^{-2}$ (0.079) at the km 10.1 site which had less protected stream edge habitat. Other than the April 1999 sampling period, there were no significant differences in any category of benthic standing mass in pool habitats at the km 10.1 and 14.5 sites. Detrital retention in pools was generally poor because of moderate current velocities. Estimated mean detrital standing mass for all sites and trips other than April 1999 was 7.53 $g \cdot m^{-2}$ (0.1.60, N = 60). Invertebrate standing mass in pool habitats over the same period was 0.17 $g \cdot m^{-2}$ (0.07, N= 60).

Drift

CPOM drift at km 10.1 and 14.5 consisted of detritus, aquatic and terrestrial macroinvertebrates, and algae. Detrital drift was low except during high stream flows in August 1998 (Trip 2). Detrital drift increased from an overall of 0.0119 $g \cdot m^{-3}$ (0.005 SE) to 2.170 $g \cdot m^{-3}$ (0.390) in August 1998. Invertebrate drift was low and constant with no significant increases among sampling periods or sites. Overall invertebrate drift in the LCR 0.0004 $g \cdot m^{-3}$ (0.0002). Algal drift increased at both sites during

April 1999 (Trip 5) from an overall mean of 0.0001 $g \cdot m^{-3}$ (0.0001) to 0.010 $g \cdot m^{-2}$ (0.002).

Composition of FPOM drift varied between sites and consisted of detritus, zooplankton (cyclopoid and harpacticoid copepods, cladocerans, ostracods) and miscellaneous invertebrates (early instars of aquatic and terrestrial insects, Tardigrada, Collembola, Gastropoda, and the protozoa Astrameoba and Centropyxis). Miscellaneous invertebrates made up approximately 75% of the total invertebrate weight of samples from km 14.5 and km 10.1, and miscellaneous invertebrates by weight were dominated by harpacticoid copepods and ostracods.

Biomass estimates for FPOM drift did not differ for the km 14.5 and km 10.1 sites. Trips associated with base flow and low turbidity (Trip 1, Trip 3, Trip 4, and Trip 6) had similar lower levels of invertebrate and detrital drift. Overall means for these periods in the LCR were 0.0003 $g \cdot m^{-3}$ dry mass (0.0001 SE) for combined invertebrates and 0.0037 $g \cdot m^{-3}$ AFDM (0.0006) for detritus.. In response to increased discharge, detritus and combined zooplankton and miscellaneous invertebrate drift increased in August 1998 (Trip 2) and April 1999 (Trip 5) at both sites. The highest invertebrate drift occurred at km 14.5 in April (0.0021 $g \cdot m^{-3}$ dry mass, 0.0008). Detrital drift at this site was 0.0386 $g \cdot m^{-3}$ AFDM (0.0122). The highest FPOM drift detrital mass was at km 14.5 during August 1998 (2.263 $g \cdot m^{-3}$ AFDM, 1.378). However, during this period invertebrate drift was only 0.0009 $g \cdot m^{-3}$ dry mass (0.0003).

Energetic model

We estimated that approximately 58,850,527 $Kcal \cdot yr^{-1}$ in the form of aquatic drift passed through the LCR at the km 10.1 site supplying the

primary energy source for the trophic web. Caloric conversions were made using a value of 5168 cal·g^{-1} AFDM of aquatic detritus (Cummins and Wuycheck, 1971). Drift estimates were made both for base flows (mean discharge = 6.44 m^3·s^{-1} with a mean drift rate of 0.0119 g·m^{-3}) and flows above base discharge (mean discharge = 21.26 m^3·s^{-1} with a mean drift rate of 0.0611 g·m^{-3}). We estimated that 280 days of the one year period were at base flow discharge while 85 days were at >1 m^3·s^{-1} over base flow. Short periods of high discharge supplied approximately 84% of the total annual drift to the site. This estimate does not reflect the very high drift rates; 2.170 g·m^{-3} (0.390) associated with the short duration of peak discharges.

Invertebrates produced between 23,660 and 73,837 Kcal·yr^{-1} in the 1 km reach associated with the km 10.1 site. This estimate combines the calories produced on hard substrate, which was estimated to be 11,821 m^2 and covered 45% of the reach and the soft substrates that covered the remaining 14,448 m^2 of the reach. Hard substrate produced between 0.49 and 3.14 Kcal·yr^{-1}·m^{-2}. Minimum values were based on overall mean standing crop (0.28 g·m^{-2} AFDM) multiplied by a P/B ratio of 2.5. Maximum values were based on the highest mean standing crop measured at the km 10.1 site (0.98 g·m^{-2}) multiplied by a P/B ratio of 5. Soft substrate produced between 1.27 and 2.45 Kcal·yr^{-1}·m^{-2}. Caloric conversions for hard substrates were based on 6409 cal·g^{-1} AFDM estimate for baetid mayflies and conversions for soft substrate organisms were based on 6050 cal·g^{-1} AFDM for chironomid larvae (Cummins and Wuychek, 1971).

We estimated that the benthic standing crop of the LCR at the km 10.1 site would support 13,243 to 41,328 g·km^{-1} of humpback chub at

15˚C during the study. Assuming a mean weight of 140 g for humpback chub, this converts to between 95 and 295 fish·km^{-1}. This estimate is based on a VO_2 of 0.01762 ml O_2·g^{-1}·hr^{-1} (0.002 SE) reported by Shuman (1978). The active caloric requirement of humpback chub at 15˚C was estimated to be 1.43 Kcal·yr^{-1}·g^{-1} (0.16 SE). For the purposes of the model we assumed that the fish population of this reach was 100% humpback chub and humpback chub >150 mm eat only macroinvertebrates.

Stable isotope analysis of trophic links

Stable isotope analysis indicated that CPOM and FPOM were the major carbon sources for invertebrates in the LCR (Fig. 4). Particulate organic matter (CPOM, FPOM and detritus) and aquatic invertebrates had approximately equal isotopic signals for $\delta^{13}C$ (t-test, $P > 0.05$) ranging from -26.7 to -21.9‰. Isotopic signals of $\delta^{15}N$ showed significant trophic enrichment between particulate organic matter and invertebrates (t-test, $P < 0.05$). Mean trophic enrichment between particulate organic matter (POM) and invertebrates was 4.9‰. Stable isotope results indicated that algae and macrophytes contributed very little to the trophic web of the LCR. Algae and macrophytes had depleted $\delta^{13}C$ (-24.8‰, 4.8 SD) compared to organic particulate matter and d 15N (7.6‰, 4.8 SD) was high compared to invertebrates from the LCR (6.5‰, 0.6 SD). Large variances for phytobenthic d 13C and d 15N complicated our analysis. However, the ^{34}S signals of algae were far more positive (5.02‰, 0.23 SD) than drift (1.98‰, 1.06 SD), invertebrates (2.32‰) or humpback chub (-0.83‰). Lack of replication for ^{34}S precluded statistical analysis. However, isotope evidence combined with the very low abundance of algae

indicated that algae were not a key energy source for invertebrates or humpback chub in the LCR.

Smaller humpback chub (<150 mm) had $\delta^{13}C$ and $\delta^{15}N$ signals that indicated aquatic invertebrates within the LCR were a major carbon source: mean $\delta^{13}C$ and $\delta^{15}N$ signals were -23.4 and 11.0‰ respectively, and$d^{15}N$ was enriched over invertebrates by 4.3‰. In contrast, $\delta^{15}N$ of humpback chub >150 mm (12.9‰) was enriched compared to humpback chub < 150 mm (11.0‰).

Humpback chub < 150 mm appear to have used the same food resources as other small fish in the LCR since there was much overlap in the isotopic signals among these fish. Juvenile humpback chub, plains killifish (Fundulus kansae), fathead minnow (Pimephales promelas), juvenile channel catfish (Ictalurus punctatus), and speckled dace (Rhinichthys osculus) all had $\delta^{13}C$ composition between -22.9 and -24.2‰. Isotopic composition of $\delta^{15}N$ for these fish ranged from 9.4 to 11.58‰. The $\delta^{13}C$ signal for humpback chub >150 mm were different from smaller fish and indicated they were obtaining a portion of their food resources from outside the LCR trophic web. Larger humpback chub showed depleted isotopic signals for $\delta^{13}C$ compared to smaller humpback chub (Fig. 4). Invertebratesd ^{13}C in the Colorado River (-26.74, 1.1 SD) were depleted compared to invertebrates from the LCR and were a likely alternative source of energy for these fish. Results from a mixing model based on the range of the 90% C.I. for $\delta^{13}C$ signals for invertebrates from the Colorado River and the LCR showed that adult humpback chub sampled in the lower-most 2 km of the LCR obtained between 0 and 75% of their carbon from LCR sources, indicating a strong reliance on the mainstem Colorado River food base. While adult humpback chub sampled from the

km 10.1 site did not have significantly different $\delta^{13}C$ signals from humpback chub sampled near the confluence (t test, $P > 0.05$), there was a trend towards more reliance on a LCR carbon source and more individual fish showed fidelity to this carbon source. Adult humpback chub from this site obtained from 25 to 100% of their carbon from LCR sources according to our mixing models.

The $\delta^{15}N$ of humpback chub >150 mm (12.9%) was enriched compared to humpback chub <150 mm (Fig. 4). This enrichment was not as great as that of large channel catfish (d 15N = 14.2%), which has been cited as a predator on small fish in the LCR (Marsh and Douglas 1997), but indicates that at least part of the diet of humpback chub >150 mm was comprised of smaller fish within the LCR. Alternatively, this enrichment could be the product of an enriched d 15N value for invertebrates from the mainstem Colorado River, however, that same enrichment was seen in the few individual fish from the km 10.1 site whose $\delta^{13}C$ values indicated minimal use of the mainstem Colorado River food base.

Discussion

We demonstrated through an energetic model and stable isotope analyses that smaller humpback chub (< 150 mm) depended entirely on the food base of the LCR, a warmwater tributary of the Colorado River in Grand Canyon, whereas the larger adult portion of the humpback chub population utilized the neighboring Colorado River for as much as 100% of their dietary needs even though the cold temperatures there were below optimum for growth. These findings are consistent with previous studies that have shown that adult humpback chub move seasonally between the LCR and the mainstem Colorado River, e.g., Gorman and Stone 1999,

Valdez and Hoffnagle 1999. However, the underlying energetic reasons for movement out of the LCR back to the colder mainstem Colorado River has not been addressed until this study. Our findings indicate that the adult humpback chub population of the LCR may be strongly dependent on energy sources from the mainstem Colorado River for achieving spawning condition and subsequent spawning success in the LCR.

Oberlin et al. (1999) found that the abundance and diversity of invertebrates in Grand Canyon tributaries with large drainage areas were limited by frequent spates combined with high sediment concentrations. Kubly and Cole (1979) speculated that benthos within the LCR might be limited because of continual carbonate (travertine) encrustation. Our results indicate that carbonate deposition combined with frequent spates that carry high sediment loads create a very hostile environment for benthic organisms in the LCR and results in a very limited food base for fish populations. The physico-chemical conditions of the LCR support active travertine deposition during base flow downstream of Chute Falls at 14.5 km (Mattes 1993, Strength 1997). Carbonate precipitation in this system has been estimated to be $1.05 \cdot 10^{-5}$ moles$\cdot L^{-1} \cdot s^{-1}$ (Strength, 1997). Our benthic standing mass estimates showed a significant decrease between sites above Chute Falls compared to those below. Moving downstream, we found algae and detritus totally encrusted with solid travertine, restricting both growth and grazing. In addition, we frequently observed caddisfly webs that were totally solidified, forming a travertine tube instead of a capture net. Invertebrates may escape encrustation in travertine by molting carapaces before they encrust or burrowing in soft sediments, however the primary carbon sources and feeding ability are greatly reduced by continual encrustation by travertine.

High discharges carrying high suspended sediment loads scour and dislodge the benthos (Rosenburg and Weins 1978, Grimm and Fisher 1989). The benthic community can recover from these disturbances upstream of km 14.5, which has low travertine deposition rates. However, as a food supply, the benthic community above km 14.5 may not be directly available to humpback chub since they are upstream of their observed range in the LCR (Kaeding and Zimmerman 1983; Douglas and Marsh 1996) and the limitation may be related to high levels of dissolved CO2 (Mattes 1993; Robinson et al. 1996; Strength 1997). Downstream drift does not hold promise as a food supply either; we found invertebrate drift at all sites in the LCR to be orders of magnitude lower than the mainstem Colorado River during base flow conditions (Blinn et al. 1999).

Isotope analysis showed that primary production from algae played a very minor role in the food base and that the major source of carbon (energy) input was in the form of allochthonous detrital drift. The high rate of travertine deposition in the LCR presented a hostile environment for filamentous algae and macrophytes, and only very small amounts of algae were present in drift samples. We found algae to be a conspicuous component of the benthos only in areas where travertine deposition was greatly reduced or absent, e.g., above km 14.5 or in small, spring-fed tributaries, and these areas were not accessible or inhabited by humpback chub.

The energetics model indicated that the relatively low food availability in the LCR limits the carrying capacity for the resident fish population. We recognize that our model could be refined with further research, however we believe that the assumptions we made were both logical and conservative and would lead to higher estimated carrying

capacities than could realistically be expected. First, we assumed that humpback chub was the only fish population in the LCR, but at the time of our study, they represented 38% of fish community (Gorman et al. 2002), and we assumed that all benthic production went towards the maintenance of this population. Secondly, the energetic needs of these fish were calculated solely for maintenance and we did not allow additional caloric intake required for growth. Despite these assumptions, the predictions of our energetic model are similar to base population estimates for humpback chub > 150 mm reported by Douglas and Marsh (1996): our 95-295 fish·km^{-1} vs. their 222 fish·km^{-1}.

Our stable isotope analysis suggests that adult humpback chub in the LCR utilize small fish as a food resource. Humpback chub are known to be opportunistic, generalist feeders (Vanicek 1967, Tyus and Minckley 1988, and Valdez and Hoffnagle 1999). Kaeding and Zimmerman (1983) and Stone (1999) found fish remains in the stomachs of adult humpback chub captured in the LCR and small humpback chub may represent a significant portion of their diet because they are an abundant prey item in the LCR after spawning (Stone 1999). Stone (1999) observed localized movement patterns by humpback chub in the vicinity of our LCR km 10.1 site, which appear to be a response to piscivory by adult humpback chub on younger age classes. Piscivory by adult humpback chub on small fish underscores our argument that food, particularly macroinvertebrates, is a limited resource for the adult humpback chub population in the LCR. Moreover, competition for this limited food resource in the LCR must be exacerbated by the influx of adult humpback chub from the Colorado River during the spring spawning season.

While small fish are completely dependent on food resources within the LCR, our stable isotope mixing model suggests larger fish which can move between the mainstem Colorado River and the LCR, utilize the mainstem food base for a major portion of their energetic requirements. Prior to impoundment of the Colorado River at Glen Canyon Dam, the then warm mainstem habitat may have provided energy for growth of small fishes in excess of the carrying capacity of the LCR. Post-impoundment temperatures and discharge variation limit the growth and survival of immature humpback chub in the mainstem (Converse et al. 1998, Clarkson and Childs 2000). Given the very limited food resources available to adult humpback chub in the LCR, the post-impoundment Colorado River provides critically needed food resources for adult humpback chub that can tolerate the colder temperatures of the mainstem.

We suggest that our stable isotope analysis probably underestimated the amount energy adult humpback chub obtain from the mainstem Colorado River. This is because cold temperatures decrease the metabolism and the amount of food ingested for many fish species (Jobling 1994). Thus, while the isotopic signal provides an indicator of the type and location of the food ingested, it will underestimate the amount of time spent in colder habitats compared to warmer habitats, which increase metabolic demand. For adult humpback chub that spend a large portion of time residing in the cold Colorado River, the isotopic signal represents a minimum indicator of their dependency on food resources of the mainstem river. Thus, we argue that our results underscore the importance of the mainstem food resource for the maintenance of the adult humpback chub population in Grand Canyon. A greater understanding of the energetic budget of adult humpback chub could be acquired by studying the

physiological response of these warmwater fish to cold temperature environments.

The population of humpback chub in this study uses both the mainstem Colorado River and the LCR to meet its energetic demands and fulfill life history requirements for spawning. While the LCR meets the energetic needs of smaller fish, the larger adults in the population are required to move out of the LCR to obtain sufficient food resources. Once in the mainstem, these fish must move back into the LCR in order to find a suitable spawning habitat in warmer water (Gorman and Stone 1999). These movements require that energetic tradeoffs be made by individual fishes and help to explain both the migratory movements of large adults noted by some researchers (Kaeding and Zimmerman 1983; Gorman and Stone 1999), and the apparent resident population of smaller adults (Douglas and Marsh 1996; Gorman and Stone 1999). Gorman and Stone (1999) have noted that nearly all adult humpback chub >300 mm undergo seasonal migration between the LCR and the mainstem Colorado River. Adult humpback chub that return to the mainstem Colorado River following spawning in the LCR show a rapid recovery of condition factor (Meretsky et al. 2000), which suggests that the reduced metabolic demands in cold water coupled with an adequate food base facilitates recovery of weight loss following spawning. However, young fish that move out of the LCR are faced with thermal conditions unfavorable to growth even though food is available (Gorman et al. 2002). Recruitment into the adult population appears to be limited to those fish that remain in the LCR until they have reached a size which can withstand the cooler temperatures and escape predation. The reproductive contribution of adult migratory fish is

substantial and critical to the long-term persistence of the humpback chub population in Grand Canyon.

Conservation efforts need to recognize that maintenance of the humpback chub population in Grand Canyon is energetically dependent on both the LCR and the mainstem Colorado River. Expansion of the humpback chub population in Grand Canyon can only be achieved by restoring environmental conditions in the mainstem Colorado River sufficiently to provide suitable habitat and food resources for reproduction and rearing. At the same time, the environment of the LCR needs to be maintained as spawning and rearing habitat for humpback chub, which has historically been the dominant member of the LCR fish community (Gorman et al. 2002). Recent expansion of non-indigenous fish populations in the food-limited LCR (Gorman et al., 2002) represents a threat to the long-term persistence of humpback chub in Grand Canyon.

Acknowledgments

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samples were analyzed at the Institute of Ecology, University of Georgia, Athens (carbon and nitrogen) and Department of Earth Sciences, University of Waterloo, Ontario (sulfur). Bruce Hungate and Stan Hillyard provided valuable insight into use of stable isotopes and energetic modeling respectively. Dennis Stone, Randy Van Haverbeke, Allison Martinez, and Wendy Hertzog provided collecting assistance and happily carried heavy packs during the course of this study. This manuscript was greatly improved by comments from Dennis Stone.

Table 1. Longitudinal patterns of selected base flow water quality parameters (pH, turbidity, conductivity, and dissolved CO_2) at 3 different sites in the Little Colorado River, AZ during May 1999.

Site	pH	Turbidity (NTU)	Conductivity (mS)	Dissolved CO_2 (mg l^{-1})
Km 14.5	7.39	2	3.3	30.2
Km 10.1	7.61	19	3.5	17.4
Km 0.9	7.91	7	4.1	5.7

Table 2. Longitudinal patterns of benthic standing mass (AFDM g m^{-2} ± SE) on hard substrates for aquatic invertebrates, algae and detritus at 3 different sites in the Little Colorado River, AZ during June 1999 after 201 days of base flow conditions.

Site	Invertebrates	Algae	Detritus
Km 14.5	0.3061 (± 0.074)	13.8568 (± 3.919)	0.4111 (± 0.287)
Km 10.1	0.0024 (± 0.002)	0.0850 (± 0.076)	0.0622 (± 0.029)
Km 0.9	0.0043 (± 0.002)	0.0133 (± 0.013)	1.3228 (± 1.294)

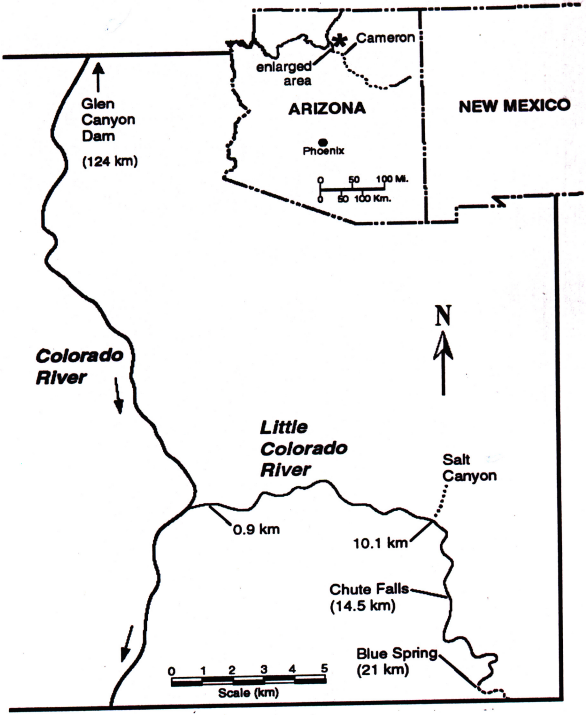

Figure.1. Map of Little Colorado River study area showing collection sites. Ephemeral portions of the channel are indicated by dashed line.

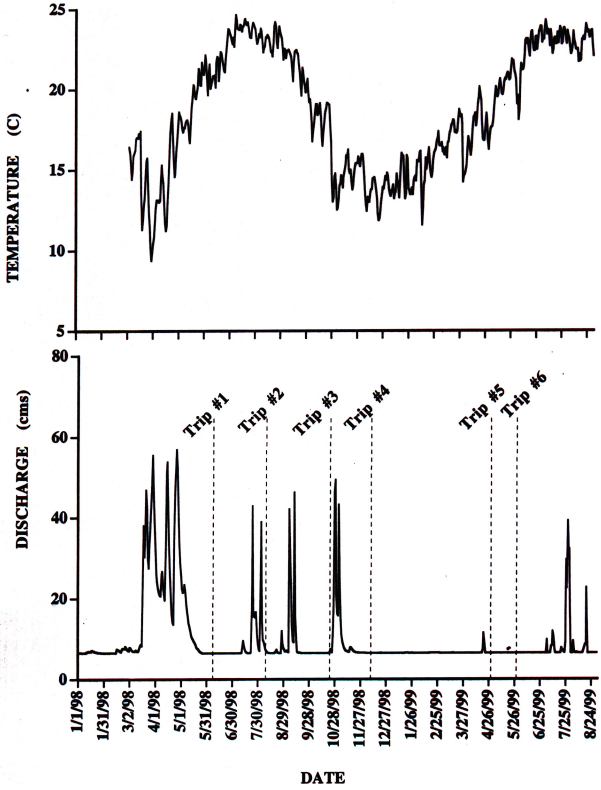

Figure. 2. Temperature and discharge records for the Little Colorado River (LCR) during study period. Discharge (mean daily m3.s-1) was measured at U. S. Geological Survey gage near Cameron, AZ and added to discharge from Blue Springs to estimate discharge at the study site.

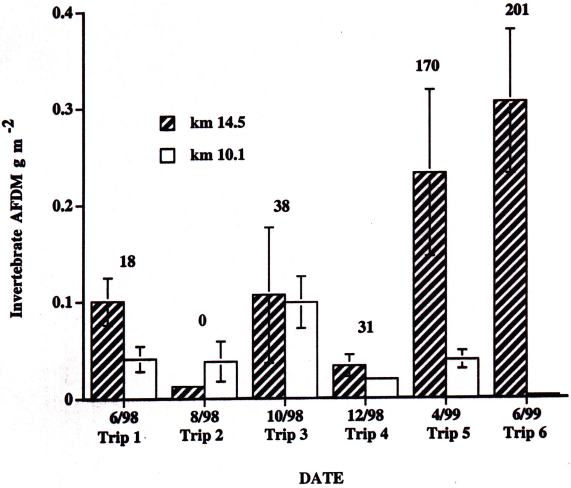

Figure. 3. Temporal changes in standing mass of macroinvertebrates for two contrasting sites in the LCR. Site 14.5 was located upstream of the distribution of humpback chub (humpback chub) in the LCR and where travertine deposition was low. Humpback chub were resident and travertine deposition rates were high at site km 10.1. Sampling trips 1-4 occurred within 30 days following above base flow discharge and trips 5 and 6 were preceded by >170 d of near base flow conditions. Numbers above each column indicate the number of consecutive days of near base flow discharge preceding the sampling trip. Error bars represent standard error.

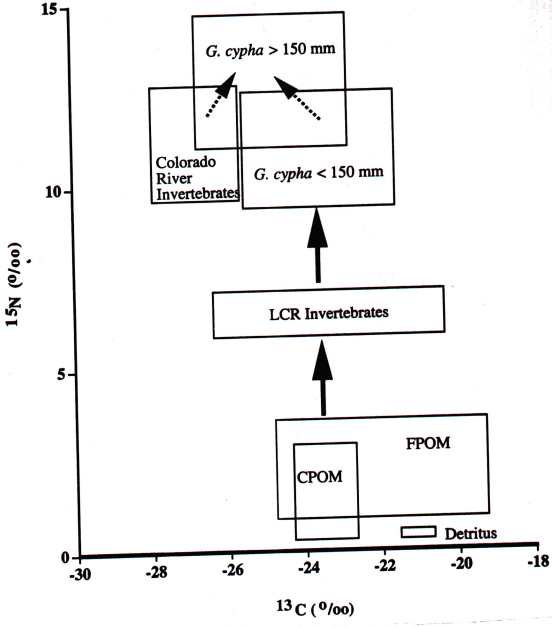

Figure. 4. Trophic linkages for the LCR food web based on enrichment of isotopes of 13C and 15N. Boxes for each group were generated from mean and standard deviations for d13C and d15N for each group. Arrows show trophic links between groups in the food web.

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Chapter 4: Sustained effect of a wildfire on stream benthos: Kanab Creek, Grand Canyon National Park.

INTRODUCTION

Recent intense wildfire seasons in western North America and the use of perscribed burns to reduce the intensity of wildfires has focused attention on their impacts to the landscape[1]. However, the effects of wildfires and perscribed burns on stream communities is poorly understood[2]. In the summer of 1996 the Bridger-Complex Fire occured within the Kanab Creek drainage on Kaibab National Forest, Arizona. Kanab Creek is a tributary of the Colorado River in Grand Canyon in which we have a long term benthic monitoring station. Seven collections between 1991 and 2001 within Kanab Creek revealed a protracted recovery period with macroinvertebrate biomass estimates remaining < 15% through 2001 compared to pre-fire estimates. Tapeats Creek, an adjacent tributary that served as an unburned control, did not vary significantly in macroinvertebrate biomass during the same period. We suspect ash deposition in pools and re-suspension during spates was the mechanism preventing benthic recovery. The size of arid land fires may have a disproportional impact on stream communities because of reduced or absent riparian zones to filter ash and sediment during storms within the burned areas.

METHODS

Benthic collections were taken in 1991, 1993, 1994, 1996, 1997, 1999 and 2001 in Kanab Creek (response site) and Tapeats Creek (control site). Macroinvertebrate samples were randomly collected with a Hess substrate sampler along three transects located 1 km up stream from the Colorado River (n=6). Samples were placed on ice and sorted within 24 h. Multiple analysis of

variance (MANOVA) was used to determine if there was difference bewteen collection date and macroinvertebrate density for both creeks. For more details concerning methods see Oberlin et al.[9].

The Bridger-complex fire vegetation types were in order of occurance; ponderosa pine, grass,oak, sage-brush and pinon-juniper. See the Kaibab National Forest Service web-site for more information[11].

RESULTS AND DISCUSSION

Fire effects on terrestrial ecosystems are well studied[1], while the reaction of stream ecosystems to fires within drainages is a realitively new science[2]. Most stream studies investigating the effects of fire analyzed water quality[3] and only recently has the lotic community been examined[4,5]. The 1988 catastrophic fire season in Yellowstone National Park spurred several long term studies[2,5,6] that have begun to reveal the complexities of fire and lotic ecosystem interactions[6]. These complexities include fire intensity, fuel loads, vegetation types, catchment size, and climate both pre-and post fire. During the past several years western North America has experienced acute wildfirefire seasons[7], which have focused interest on the use of prescribed burns to reduce fuel loads and extreme fires[8].

One reason for the scarcity of wildfire-stream interaction studies is logistical; fire needs to occur within a drainage that already has a long-term stream study in place to have an established reference condition. This coincidence occured in our Kanab Creek study site in Grand Canyon. Kanab Creek empties into the Colorado River 231.2 river kilometers (rkm) downstream of Lees Ferry, Arizona, the only access site for river trips. Tapeats Creek is located at rkm 214.8 and served as the un-burned control site. Both of these tributaries are part of the long-term monitoring of the Colorado River ecosystem and impacts of the operations of Glen Canyon Dam[9]. During the summer of

1996 wildfires occurred 24 km upstream of the collection site on the North Rim of Grand Canyon and covered 21 sq km. on the west slope of the Kaibab Plateau. On 9 September 1996 the Colorado River turned black with ash from a flash flood in Kanab Creek, indicating that large amounts of ash had washed downstream from the fire (Michael Kearsley, per.comm. NAU Dept. Biological Sciences, Flagstaff, AZ). Typically, recovery from disturbances within streams occurs in about 30 days[10], however, continued benthic macroinvertebrate monitoring five years post-fire reveals a slow recovery to pre-fire conditions (Fig. 1). In contrast, Tapeats Creek macroinvertebrate biomass remained consistent with the variance attributed to annual disharge regimes, e.g. spring run-off and monsoon storms[9] (Fig. 1). Kanab Creek benthic aquatic insect biodiversity was also reduced five years post-fire. Simuliid blackflies and Chironomid midges increased from 60% of the taxa present pre-fire to 90% post-fire, while Trichoptera, Ephemoroptera, and Megaloptera nymphs represented <10% of the benthic biomass post-fire. Tapeats Creek macroinvertebrate biodiversity remained consistent with Trichoptera, Ephemoroptera, Diptera and Plecoptera representing 90% of the density.

Prolonged benthic recovery in Kanab Creek study site can be attributed to the deposition of ash in pools and periodic resuspension during spates which would negatively impact the benthos (Fig. 2). These ash-laden pools were temporarily “sealed” with gravel and stones from small flash floods. Ash would remain in the stream bottom during base flow conditions, then would be re-suspended, washed downstream, and be re-deposited in pools on the decending limb of spates. We observed six pools with ash between 30 and 60 cm deep in 1998 and pools still had between 10 and 20 cm of ash five years post-fire in 2001. Ash was also observed in the interstitial areas between cobbles and

covering cobbles, which could hinder macroinvertebrate movement, breathing ability, and food quality[5].

Arid land wildfires may have a disproportionate impact on stream ecosystems because of reduced riparian zones that buffer fire effects in comparison to temperate watersheds. Minshall et al.[2] argued that fire intensity and catchment size are the two most influential components of wildfires affecting stream ecosystems. However, the Bridger Complex fire burned <1% of the Kanab Creek catchment and fire intensity was rated 25% light and 75% moderate-severe[11]. Prior to European settlement ponderosa pine (Pinus - ponderosa) forests burned every 2-15 years primarily in the grassy undergrowth which maintained an open forest and reduced fire intensity[12] . During the past 100 hundred years of fire suppression ponderosa pine fuel loads have increased, while riparian zones have been reduced because of river regulation and ground water mining[13]. These human impacts on forests result in a complex interaction between aquatic and terrestrial ecosystems that implies prudence and aquatic research be conducted during perscribed burns.

Native fish in the arid-southwest are the most threatened with extinction in the United States, 22 out of 26 native fish in Arizona are listed as imperiled[14], and wildfires maybe another source of risk. Kanab Creek is home to several native fishes; five species of Cyprinid minnows, and two species of Catostomid suckers, with three of the minnows extirpated since the 1960's. Large tributaries of the Colorado River through Grand Canyon are commonly used as refugia for native fishes from the stenothermic cool and food limited mainstem[9]. Therefore, more research on the impacts of wildfires and perscribed burns on aquatic ecosystems, with particular attention to arid biomes and native fish populations is needed. In 2000 the United States Federal Government spent

$1.4 billion on perscribed burns and wildfires, but not one aquatic ecologist was hired to monitor stream and river biota[7].

ACKNOWLEDGEMENTS

We would like to thank Dave Wegner for initiating this long-term study with funding from the Bureau of Reclamation in cooperation with the National Park Service. Expedition style collecting, which is required while studying the Colorado River through Grand Canyon, requires dedicated field hands and we thank the following staff members and volunteers for their efforts; Kevin Wilson, Allen Haden, Kristin Straka, Mike Yard, Mark Wetzel and Barry Gold. Constructive comments improving this mauscript were made by Stev Earl and Thomas Whitham.

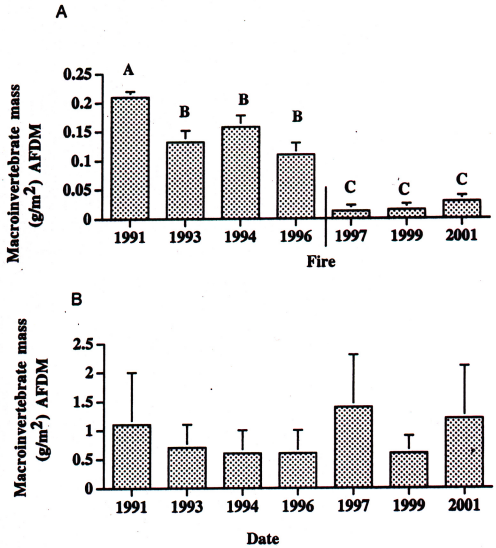

Figure 1 . Comparison of macroinvertebrate biomass in drainage that sustained a wilfire (A-Kanab Creek) and a nearby control stream (B-Tapeats Creek) over a ten year period. Letters indicate significant differences in biomass ($p<0.05$) in Kanab Creek and no differences in biomass were detected in Tapeats Creek

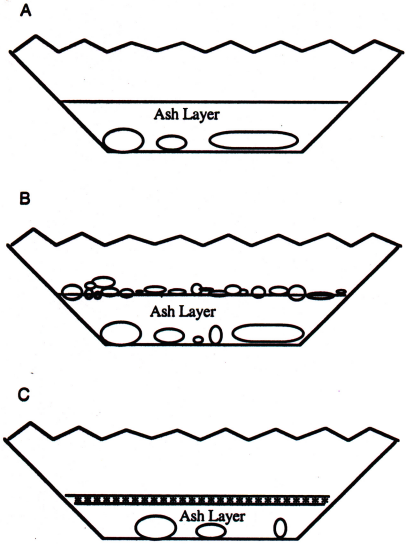

Figure 2. Probable mechanism for retaining ash in Kanab Creek. A) Deposition of fire ash.B) Ash layer sealed by gravel from small spate.C) Ash layer washed down stream by large spate, ** indicates new deposition of ash from upstream.

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Chapter 5: VERTICAL DISTRIBUTION OF THE AQUATIC FOOD BASE IN THE COLORADO RIVER BELOW GLEN CANYON DAM

INTRODUCTION

The food base community of phyto- and zoo-benthic organisms in the Colorado River below Glen Canyon Dam (GCD) is integral to the health of higher trophic levels in this riverine ecosystem and also supports linkages to terrestrial components including water fowl, riparian insectivores, and birds of prey (Carothers and Brown 1991, Shannon et al. 1994, Blinn et al. 1998, Benenati et al. 2000). Long-term research and monitoring of benthic communities of large rivers are important; however, they are often limited by logistical concerns such as river access and depth, current velocity, and safety of investigators. As a result benthic sampling frequently occurs at the river's edge in shallower and slower velocities relative to the rest of the river. Very little has been reported on phytobenthic sampling and distribution, specifically vertical distribution and sampling reliability in large regulated rivers (Hardwick et al. 1991, Morin and Cattaneo 1992). This is largely due to the dominance of benthic macroinvertebrate studies (Brown et al. 1987, Haag and Thorp 1991, Palmer et al. 1995, Panis et al. 1995, Rempel 2000) and the dangers of deep sampling using SCUBA equipment under unstable flow conditions.

During the summer of 2000 the Grand Canyon Adaptive Management Program recommended an unprecedented discharge regime of steady flows for three months (227 m^3/s from 1 June - 1 September 2000). The purpose of these ecological flows was an attempt to temporarily reduce the impact of GCD operations (fluctuating water

levels, flow patterns, volume, turbidity, and temperature) and stabilize riverine conditions in an effort to promote the health of the aquatic community, specifically the humpback chub. During these steady eco-flows of 2000 we had an opportunity to sample the deep benthic community under relatively safe conditions. In addition, the controlled flows allowed for analogous phytobenthic growth habitats throughout the river corridor for two months prior to collection which would allow for comparisons based solely on river depth and distance downstream.

Our investigation objectives concerning the benthic community in the Colorado River below GCD were: 1) compare biomass and composition of the phyto- and zoo-benthic community between different depths in the riverbed to determine the reliability of our monitoring sampling protocol to represent the river channel in general. 2) compare benthic composition and/or biomass longitudinally between two sites 365 kilometers apart to determine if distance downstream from GCD continues to be a factor during relatively stable conditions created by artificial eco-flows, and 3) determine if overall vertical and longitudinal diatom community composition has significantly changed since a related investigation occurred 15 years prior (Hardwick et al. 1992).

METHODS

Phytobenthic samples were collected in Glen Canyon at river kilometer (rkm) -4.8 and in Grand Canyon at rkm 360 during a summer steady flow regime of 226 $m^3 \cdot sec^{-1}$ on 29 and 30 July 2000. Collection dates two months after the onset of steady flows were selected in order to allow sufficient time for the phytobenthic community response and equilibrium to stable conditions (Round 1981, Lowe 1979, Peterson 1986). Collection

sites were selected as representatives of longitudinal upstream (GCD tailwaters) and downstream (lower Grand Canyon) river habitat and for vehicle accessibility. Samples were taken from rock substrate on vertical cliff walls using SCUBA equipment at various depth intervals between 0 and 7 m below the river surface. Depth intervals varied slightly due to changes in river channel topography between sites. Each phytobenthic depth interval sample was 20 cm^2 area and taken in triplicate using a modified slurp gun (Fig. 1). Glen Canyon depth collections were at 0.0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, and 5.0 m. Grand Canyon depth collections were at 0.0, 0.5, 1.0, 1.5, 2.0, 4.5, 5.0, and 7.0 m.

Benthic samples were sorted to categories of Cladophora glomerata, crustose Oscillatoria, detritus, diatom epiphyton, MAMB (miscellaneous algae, macrophytes, and bryophytes), and grouped macroinvertebrates. MAMB was dominated by Fontinalis spp. and diatom mucilage matrix. The grouped invertebrate category was dominated by gastropods (Physella spp., Pisidium spp.) and Gammarus lacustris; however, various Chironomidae (e.g. Cricotopus annulator, C. globistylus), megadrile worms (Lumbricidae and Lumbricullidae), and oligochaetes (Naididae and Tubificidae) were also present. All categories were oven-dried at 60°C to a constant weight and ashed (500°C) for 1 h to obtain ash-free dry mass (AFDM).

Diatom epiphyton was extracted from the phytobenthos after invertebrates were removed but before sorting into separate categories. The phytobenthic material was placed in a Whirl-pak™ containing 100 ml of filtered (0.45 µm) Colorado River water and shaken for 60 seconds to remove epiphyton. This procedure removed at least 80% of diatoms, based on microscopic analysis, and was found to be the most effective

technique for separating intact epiphytic diatoms from phytobenthos (Blinn et al. 1995). The epiphyton suspension was filtered onto Whatman (GF/C) 4.7 µm glass microfiber filters. The filters were oven-dried for at 60°C to a constant weight and ignited at 500°C for 1 hr to obtain ash-free dry mass per area (AFDM/20 cm^2).

Ashed periphyton was scraped from microfiber filters and mounted onto microscope slides using Hyrax® medium. A minimum of 200 diatoms per slide were counted and identified to determine relative percent composition of cells per sample.

Data Analyses

Multivariate analysis of variance (MANOVA) was performed to determine relationships between biomass of benthic categories within each site and between sites. Relationships of diatom taxa relative percent was also tested by depth within each site and overall between sites.

Biomass of benthic categories was Log_{10} transformed and diatom relative percentages were arcsine square root transformed to insure constancy of variance (Zar, 1984). Overall patterns were determined using Wilks' lambda statistic and individual responses were detected with post hoc univariate tests. Pearson correlations with the Bonferroni adjustment were used to measure associations of benthic variables within and between sites. All calculations were performed using SYSTAT® (Statistics, version 5.2 edition, SYSTAT, Inc., Evanston, Illinois).

RESULTS AND DISCUSSION

Glen Canyon

Biomass of the benthic categories of macroinvertebrates, detritus, Oscillatoria, MAMB, and epiphyton in Glen Canyon did not vary significantly by depth (0 - 5m), however some taxa showed distinct patterns. Cladophora was the only benthic category to significantly change between depths ($p < 0.01$), although depth appeared to have little relationship with Cladophora as biomass sporadically ranged between 0.000 and 0.005 (± 0.002 SE) g AFDM over the depth intervals (Fig. 2).

Detritus and Oscillatoria also showed sporadic patterns of appearing and disappearing with no apparent relation to depth levels averaging 0.0003 (±0.0003) and 0.0001 g (±0.0001) AFDM, respectively (Figs. 3 and 4). This is not unusual as detritus and Oscillatoria usually have low biomass in the clear, tailwater reach of the Colorado River just below GCD. The remaining categories of MAMB, epiphyton, and macroinvertebrates showed consistent biomass throughout the depth levels (Figs 5, 6, and 7). In fact, both macroinvertebrate and epiphyton/host biomass levels were significantly correlated with MAMB ($p < 0.001$ and 0.05 respectively). This is in contrast to our documented benthic patterns of the past decade where Cladophora, regardless of its biomass level, would consistently show significant positive associations with epiphyton and invertebrates with the reverse being true for MAMB. More investigation is recommended to study this potential change in benthic trophic patterns. Benthic biomass differences may be related to decreased light at increased depths which may have allowed MAMB to outcompete Cladophora.

MAMB was the overall dominant taxa at Glen Canyon comprising over 95% of the total host phytobenthic biomass (Figs. 5 and 8). MAMB also dominated significantly ($p < 0.01$) over Cladophora with

an average of 40-fold greater biomass at all depths sampled (0.042; ±0.011 g AFDM). MAMB has been a strong component in the Colorado River benthos since 1995 which was found to be related to changes in the upstream reservoir water volume and quality, as well as, discharge regimes from GCD (see Benenati et al. 2000).

Grand Canyon

Multivariate analysis revealed no significant changes in phytobenthic biomass across depths. Univariate analysis showed no changes in the categories of Cladophora, detritus, Oscillatoria, and macroinvertebrates across depths; however, both MAMB and epiphyton varied significantly ($p < 0.001$ and 0.05, respectively). Dramatic decreases in MAMB and epiphyton/host biomass occurred in the deeper sampling sites below 2 m (Figs. 9 and 10). Cladophora and Oscillatoria also dropped off in biomass at or below 2 m depth (Figs. 11 and 12). This is probably related to light extinction in the water column due to increased sediment loads in the lower reaches of Grand Canyon (Blinn et al. 1995, Shaver et al. 1998). Greater amounts of fine suspended sediment trapped during the filtering process likely accounted for increased epiphyton biomass in Grand Canyon over Glen Canyon (0.45; ±0.01 and 0.12; 0.001, respectively).

Presence was sporadic across depths for Oscillatoria and detritus which also occurred at the Glen Canyon site; however, each had significantly ($p < 0.01$) 7-fold greater biomass at the Grand Canyon site with overall averages of 0.002 (±0.0015) and 0.001 (±0.0004), respectively (Figs. 12 and 13). This is likely related to greater amounts of sediment and debris in the river channel that occurs with increasing distance downstream and cumulative tributary input.

Cladophora had a significant ($p < 0.01$) 10-fold overall increase in biomass as compared to the Glen Canyon site with an average of 0.017 (±0.005) g AFDM (Fig. 11). However, MAMB was again dominant over Cladophora at this site with an overall biomass average very similar to Glen Canyon at 0.046 (±0.011) g AFDM (Fig. 12). Both MAMB and Cladophora were significantly ($p < 0.05$) correlated with epiphyton biomass; however, neither were correlated with invertebrates.

Macroinvertebrate biomass averaged 0.0005 (±0.0002) g AFDM (Fig. 14). Compared to the Glen Canyon site this is a significant ($p < 0.001$) 50-fold decrease while total supporting phytobenthic biomass actually doubled in biomass (Figs. 15, 16, 17). This dramatic decrease in macroinvertebrate biomass is likely related to the deteriorating condition of the food base in lower Grand Canyon due to decreased light conditions and increased scour disturbance on phytobenthos.

Diatoms

Twelve dominant diatom taxa groups were identified out of 49 diatom species (Table 1). Diatoms of the same genera with corresponding ecological factors (e.g. conductivity and sediment tolerance levels) were grouped together e.g. Cocconeis pediculus and C. placentula var. lineata were grouped as Cocconeis spp. Diatom composition of Glen Canyon and Grand Canyon was similar although relative percent values for dominant taxa differed significantly ($p < 0.001$) between these two sites as also reported by Hardwick et al. (1992). Another similarity with the Hardwick et al. study (1992), was that under steady flow conditions most diatom taxa within each site did not change significantly between depths. An exception occurred with three out of twelve taxa at Glen Canyon ($p < 0.05$;

Cocconeis spp., Diatoma vulgare, and Fragilaria ulna; Fig. 18) and two out of twelve at Grand Canyon ($p < 0.05$; Amphora perpusilla, and Navicula spp.; Fig. 19).

Overall, diatom relative percent patterns corresponded with ecological changes in river conditions. Large or upright diatoms found in flowing water of moderate conductivity e.g. Cocconeis spp, Diatoma vulgare, Rhoicosphenia curvata, and Ellerbeckia arenaria dominated in the Glen Canyon reach. In the Grand Canyon, smaller, sediment and higher conductivity tolerant diatoms increased in relative percent e.g. Cymbella spp, Navicula spp, Diatoma moniliformis, and Nitzschia spp. (Czarnecki and Blinn 1978).

Some of the patterns of dominant taxa in this study follow those of 15 years previous as reported by Hardwick et al. (1992). Cocconeis pediculus, Diatoma vulgare, and Rhoicosphenia curvata remained in the dominant group in Glen Canyon for this study, although the former dominant, Achnanthes affinis, has been replaced with a mixed group of Achnanthes taxa (Table 1). Some compositional changes have occurred with a few taxa now matching or exceeding the former dominants in relative percent values in Glen Canyon, notably Ellerbeckia arenaria and Amphora perpusilla (Fig. 18). Similar patterns that occurred 15 years ago are also present downstream with the above Glen Canyon dominant taxa dropping out and a substantial increase in Cymbella and Nitzschia species. Diatoma vulgare and Rhoicosphenia curvata are large, upright epiphytes that thrive in sediment-free water and are easily scoured by increased sediment that frequently occurs in the lower Grand Canyon. In contrast, Cymbella and Nitzschia species are bi-raphid, thus able to attach and move easily in sediment conditions, and are also associated with

a higher conductivity environment that also develops due to accumulated tributary sediment, detritus, and nutrient input in the Grand Canyon reach.

CONCLUSION

Long-term research and monitoring are necessary to detect patterns and changes in the Colorado River components and ecosystem as a whole. Periodic evaluation of sampling methods are advised to ensure all food base components are detected and included in long-term studies. This study confirms no bias occurs in channel collections related to sampling depth. Sampling at multiple depths may be advisable in future collections to obtain a better picture of trophic responses to the continued management policy of load-following discharge regimes resulting in fluctuating river (and food base) depths.

Table 1. List of epiphytic diatoms in the Colorado River in Glen Canyon and Grand Canyon sites. Diatom taxa were collected from Cladophora, MAMB (miscelaneous algae, macrophytes, and bryophytes), and Oscillatoria. Taxa are marked (X) to indicate dominance at the Glen Canyon site, Grand Canyon site, or both sites.

Taxon	Glen	Grand	Both
Achnanthaceae			
Achnanthes spp.			X
Achnanthes affinis Grun.			
Achnanthes clevei Grun.			
Achnanthes clevei var. *rostrata* Hust.			
Achnanthes lanceolata (Breb.) Grun.			
Achnanthes lanceolata var. *dubia* Grun.			
Achnanthes linearis (W. Sm.) Grun.			
Achnanthes minutissima (Kütz.)			
Cocconeis spp.		X	
Cocconeis pediculus Ehr.			
Cocconeis placentula var. *lineata* (Ehr.)			
Rhoicosphenia curvata (Kütz.) Grun. *ex* Rabh.		X	
Coscinodiscaceae			
* *Cyclotella bodanica* Skv.		X	
* *Melosira varians* Ag.			X
Ellerbeckia arenaria Moore ex Ralfs	X		
Cymbellaceae			
* *Amphora coffeiformis* (Ag.) Kutz.*		X	
* *Amphora ovalis* (Kütz.)*		X	
Amphora perpusilla (Grun.) Grun.	X		
* *Cymbella mexicana* (Ehr.) Cl.*			X
* *Cymbella minuta* Hilse *ex* Rabh.		X	
* *Cymbella sinuata* Greg.		X	
Cymbella spp.			X
Cymbella microcephala var. *crassa* Reim.			
Cymbella prostrata (Berk.) Cl.			
Cymbella prostrata var. *auerswaldii* (Rabh.) Reim. comb. nov.			
Fragilariaceae			
* *Diatoma mesodon* (Ehr.) Grun.		X	
Diatoma moniliformis Kütz.			X
Diatoma vulgare Bory	X		

Taxon	Glen	Grand	Both
Fragilaria spp.			X
Fragilaria brevistrata Grun.			
Fragilaria capucina Desm.			
Fragilaria constricta Ehr.			
Fragilaria construens (Ehr.) Grun.			
Fragilaria leptostauron (Ehr.) Hust.			
Fragilaria pinnata Ehr.			
Fragilaria ulna (Nitz.) Ehr.		X	
* *Opephora ansata* Hohn et Hellerm.	X		
Gomphonemaceae			
* *Gomphonema clevei* Fricke			X
* *Gomphonema olivaceum* Lyngb.		X	
* *Gomphonema sphaerophorum* Ehr.		X	
* *Gomphonema truncatum* Ehr.			X
Naviculaceae			
* *Anomoeoneis vitrea* (Grun.) Ross		X	
* *Caloneis bacillum* (Grun.) Cl.		X	
* *Frustulia vulgaris* (Thwaites) DeT.		X	
* *Gyrosigma attenuatum* (Kütz.) Rabh.			X
* *Navicula tuscula* Ehr.		X	
Navicula spp.			X
Navicula tripunctata var. *Schizonemoides* (V.H.) Patr.			
Navicula venata Kütz., Bacill.			
Nitzschiaceae			
Nitzschia spp.		X	
Nitzschia communis Rabh.			
Nitzschia denticula Grun.			
Nitzschia dissipata (Kütz.) Grun.			
Nitzschia frustulum (Kütz.)			
Nitzschia sublinearis Hust.			

Taxa sporadically present were placed into miscellaneous category and indicated with a (*) notation. Genera of similar ecology are grouped together under spp. (e.g. *Nitzschia* spp.).

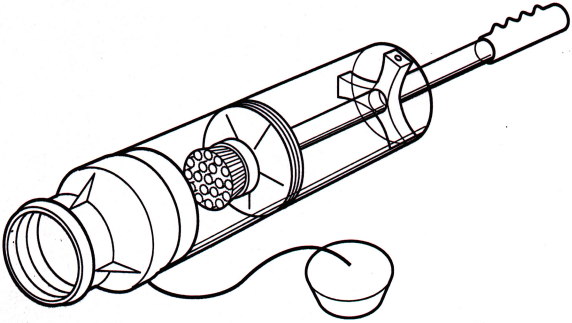

Figure 1. Illustration of modified benthic slurp gun used to collect phytobenthic samples of 20 cm^2 area from rock substrate at river depths from 0.0 to 7.0 m in July 2000.

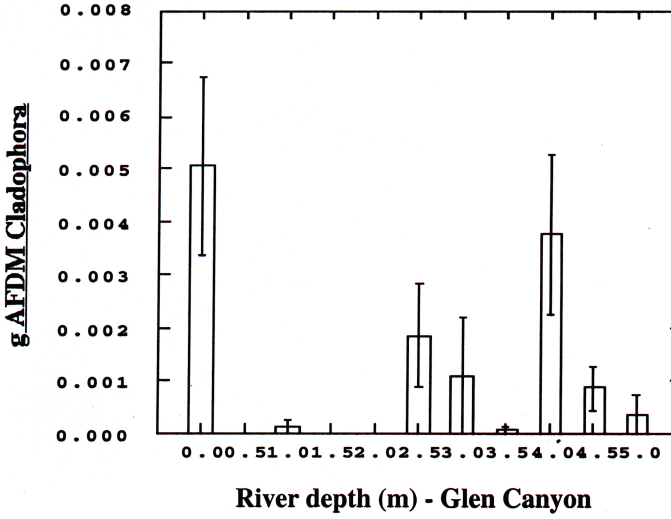

Figure 2. Mean Cladophora glomerata biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 5.0 m in Glen Canyon in July 2000.

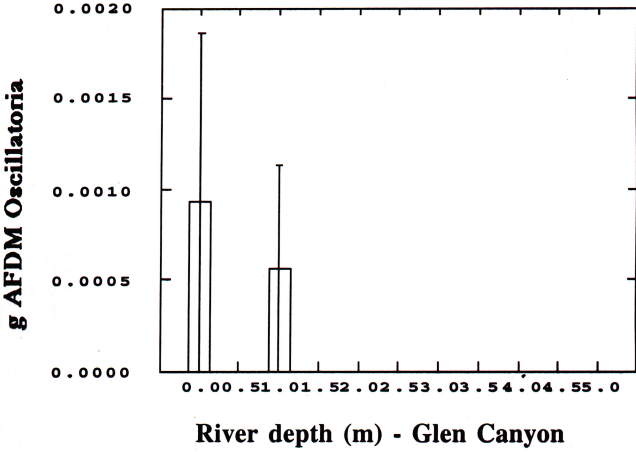

Figure 3. Mean Oscillatoria biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 5.0 m in Glen Canyon in July 2000.

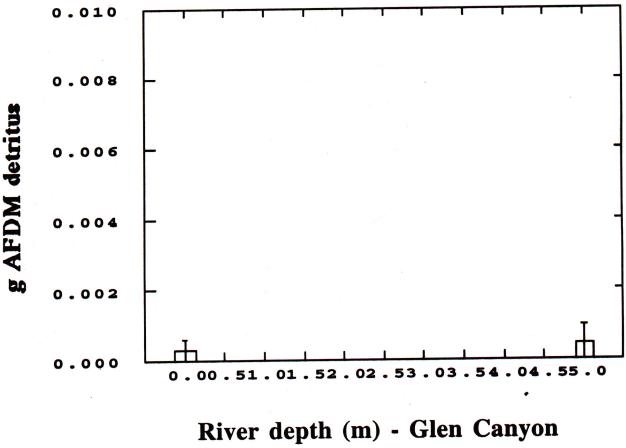

Figure 4. Mean detritus biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 5.0 m in Glen Canyon in July 2000.

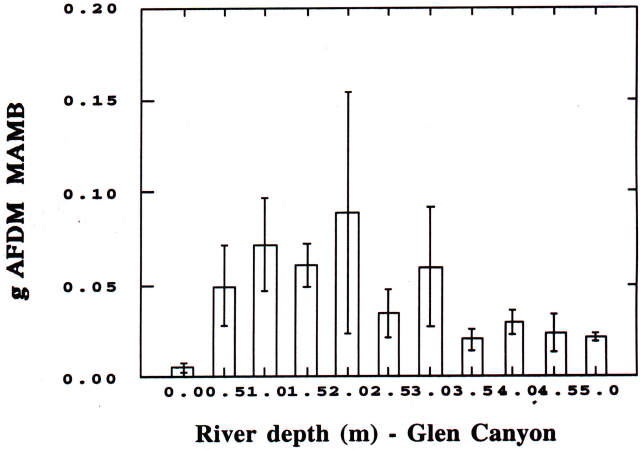

Figure 5. Mean MAMB biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 5.0 m in Glen Canyon in July 2000.

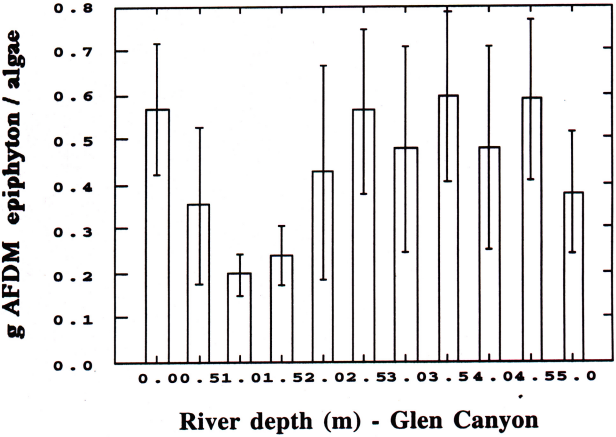

Figure 6. Mean biomass of epiphyton per g host (g AFDM) collected at depths of 0.0 to 5.0 m in Glen Canyon. Host collectively includes Cladophora glomerata, Oscillatoria, MAMB in July 2000.

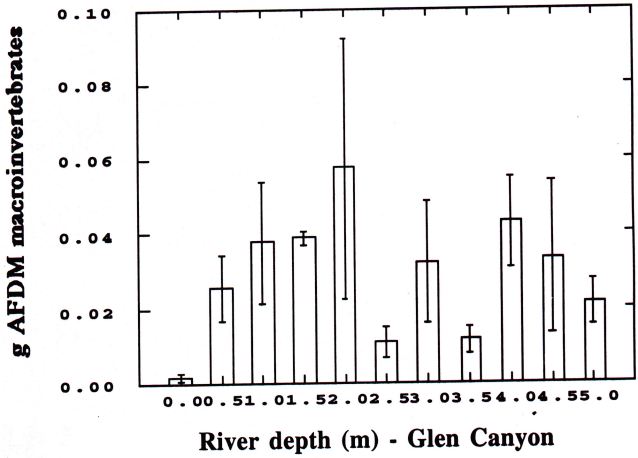

Figure 7. Mean macroinvertebrate biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 5.0 m in Glen Canyon in July 2000.

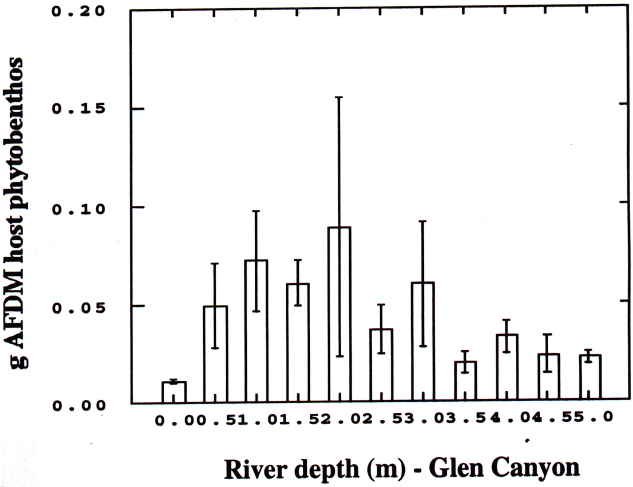

Figure 8. Mean host phytobenthos biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 5.0 m in Glen Canyon. Host phytobenthos collectively includes Cladophora glomerata, Oscillatoria, MAMB in July 2000.

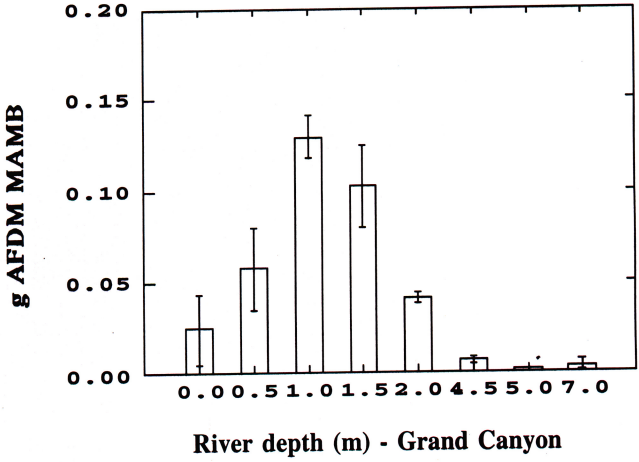

Figure 9. Mean MAMB biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 7.0 m in Grand Canyon in July 2000.

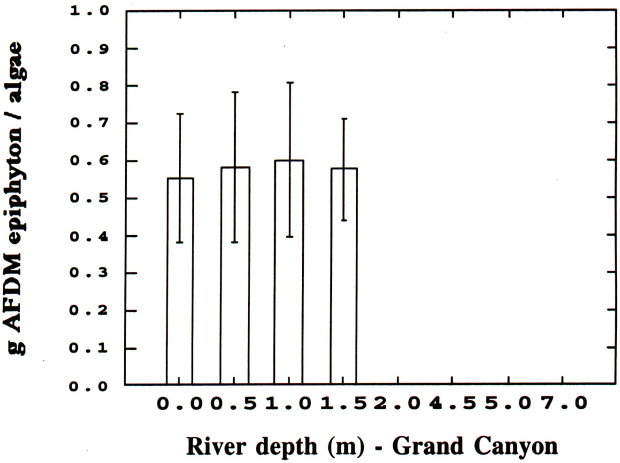

Figure 10. Mean biomass of epiphyton per g host (g AFDM) collected at depths of 0.0 to 7.0 m in Grand Canyon. Host collectively includes Cladophora glomerata, Oscillatoria, MAMB in July 2000.

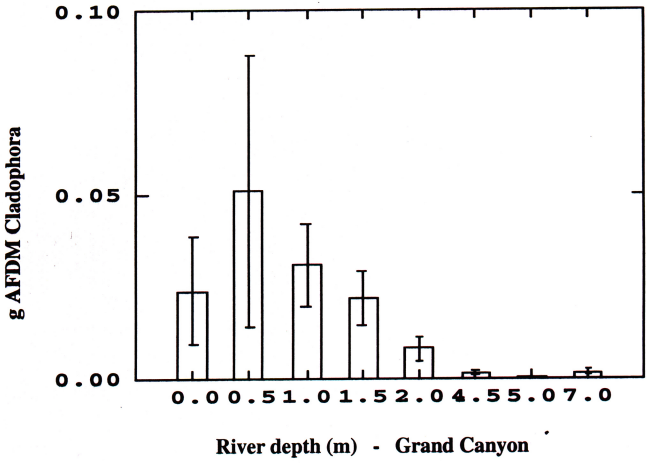

Figure 11. Mean Cladophora glomerata biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 7.0 m in Grand Canyon in July 2000.

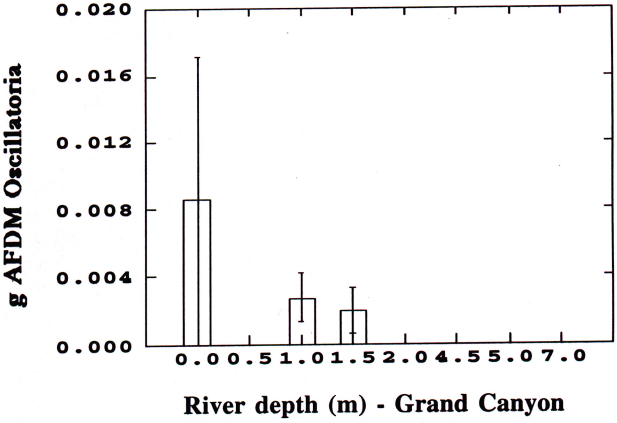

Figure 12. Mean Oscillatoria biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 7.0 m in Grand Canyon in July 2000.

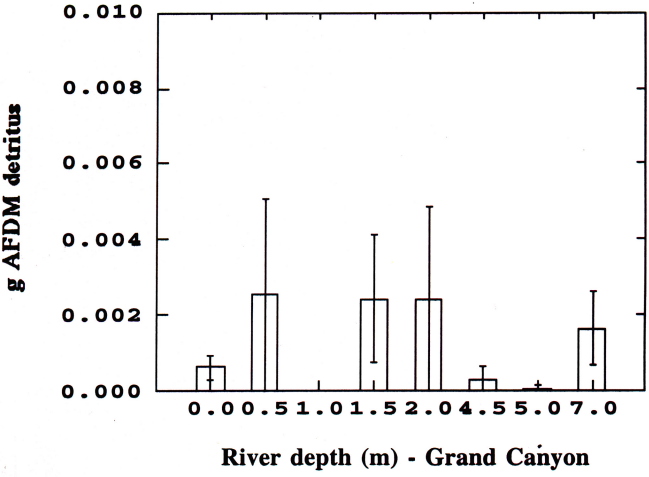

Figure 13. Mean detritus biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 7.0 m in Grand Canyon in July 2000.

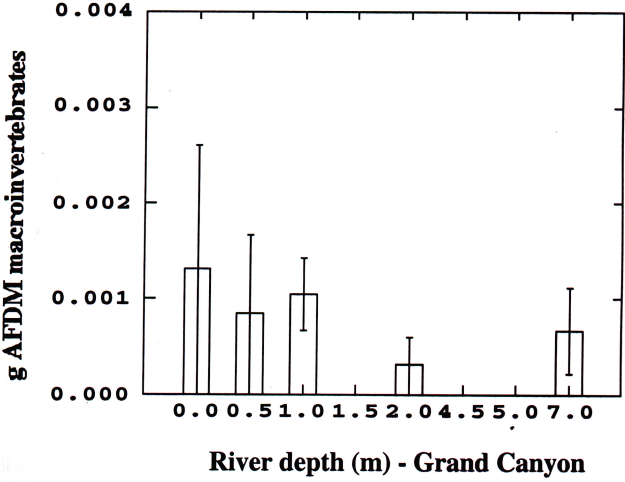

Figure 14. Mean macroinvertebrate biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 7.0 m in Grand Canyon in July 2000.

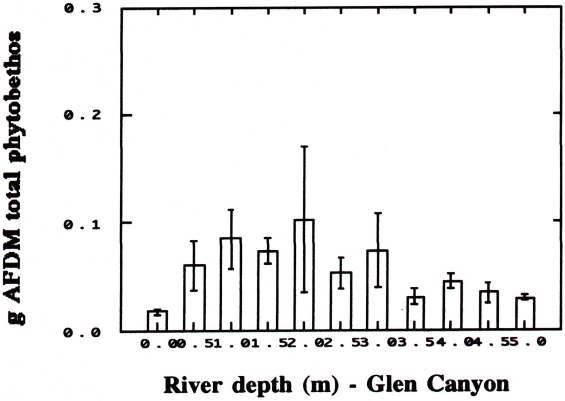

Figure 15. Mean total phytobenthos biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 5.0 m in Glen Canyon. Total phytobenthos includes epiphyton plus other phytobenthic categories of Cladophora glomerata, Oscillatoria, MAMB in July 2000.

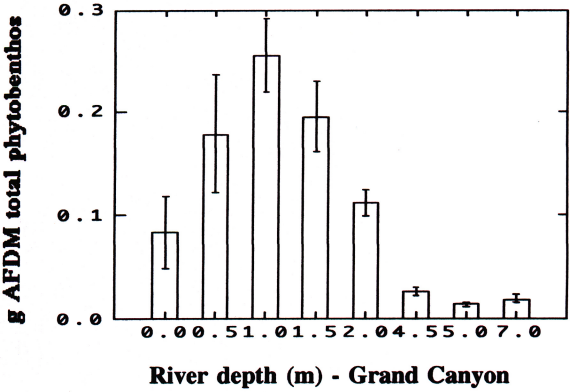

Figure 16. Mean total phytobenthos biomass (g AFDM / 20 cm^2 ± 1 SE) collected at depths of 0.0 to 7.0 m in Grand Canyon. Total phytobenthos includes epiphyton plus other phytobenthic categories of Cladophora glomerata, Oscillatoria, MAMB in July 2000.

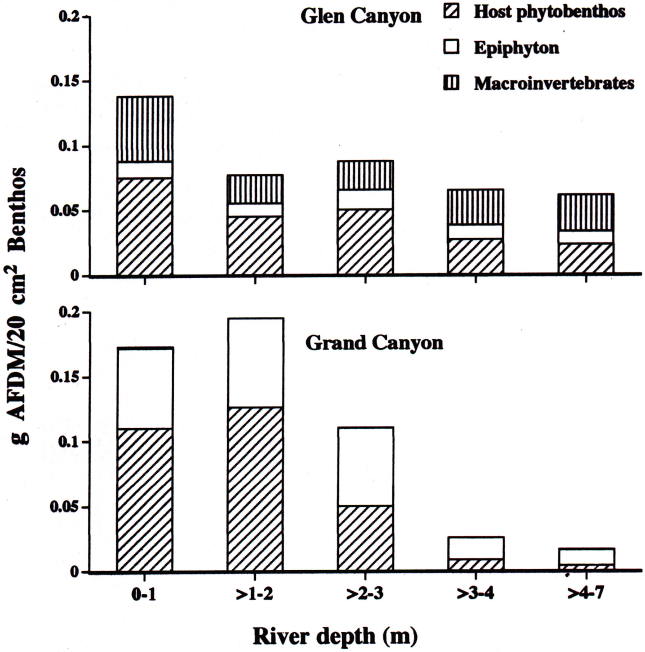

Figure 17. Macroinvertebrate, host phytobenthos, and epiphyton relative biomass averages (g AFDM / 20 cm^2) at grouped depths of 0-1m, >1-2m, >2-3m, >3-4m, and >4-7m at Glen and Grand Canyon sites.

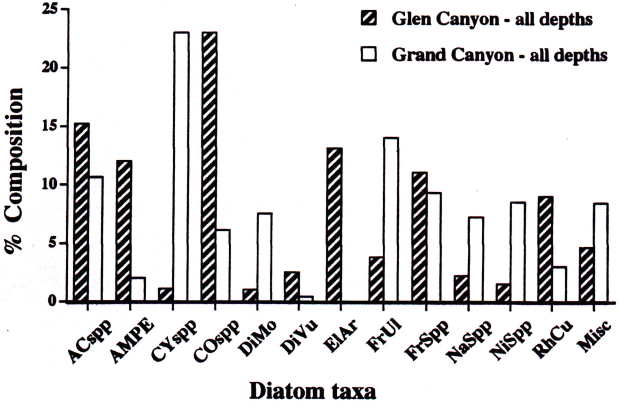

Figure 18. Relative percent composition of epiphytic diatom taxa collected from phytobenthos in Glen Canyon (0.0 to 5.0 m depths) and Grand Canyon (0.0 to 7.0 m depths) in July 2000.

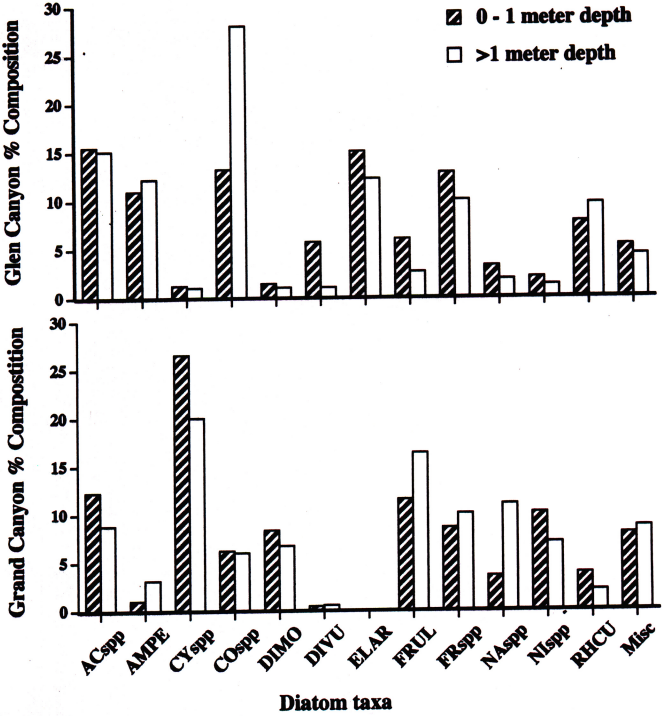

Figure 19. Relative percent composition of epiphytic diatom taxa collected from phytobenthos in Glen Canyon (0.0 - 1.0 vs. 1.5 - 5.0 m) and Grand Canyon (0.0 - 1.0 vs. 1.5 - 7.0 m) in July 2000.

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Chapter 6: Initial evaluation of dual stable isotope analysis as a monitoring tool of rainbow trout (Oncorhynchus mykiss) health: Colorado River below Glen Canyon Dam, Arizona.

INTRODUCTION

Rapid environmental changes have the potential to affect the health of aquatic organisms and the habitat on which they depend. While some effects (removal and death) are relatively simple to quantify, others (growth and reproductive success) may be more difficult to measure and relate to specific environmental changes. This is especially true in environments that are subject to multiple environmental changes within the life span of the organism. Correlating specific environmental disturbances with sub-lethal effects, which may not immediately manifest on target organisms, is a difficult task. However, such information would identify potentially cumulative environmental effects that shape community development and ecosystem function.

The use of physiological responses at the organismal level has potential as a tool in this situation. Physiological responses have the benefit of showing rapid responses to environmental stress and can be related to overall fitness of the organism in question. Several authors have called for increased use of these metrics (Adams et al. 1993, Marshall et al. 1999).

The objective of this study is to test the use of stable isotopes in specific tissues as a metric of river regulation induced environmental stress in rainbow trout below Glen Canyon Dam, AZ. Pinnegar and Pulunin (1999) found that the $\delta^{13}C$ of liver tissue was depleted compared to white muscle tissue in laboratory raised rainbow trout by as much as 2‰. They attributed this difference to the concentration of lipids in liver tissue

compared to white muscle tissue. In addition, liver and analogous tissues have been shown to have higher tissue turnover rates than muscle or bones in birds and invertebrates (Parker and Anderson 1991, Hobson and Clarke 1992), indicating that liver tissue may reflect changes in diet sooner than muscle tissue.

We hypothesize that changes in the relative difference between fish liver and muscle $\delta^{15}N$ and $\delta^{13}C$ could indicate changes in diet or health due to the consumption of stored lipids. While a full understanding of temporal variation in isotope signals of fish tissue is beyond the scope of this limited study, our purpose is to illustrate the feasibility of measuring change in a field setting against a background of low seasonal and high spatial variation of isotopic signals in the Colorado River (Shannon et al. 2001). If change is detectable in a field situation, further studies on the specific effects are warranted.

Glen Canyon Dam regulates flows in the Colorado River in response to demand for hydroelectric power and the need for water supplies downstream. Rainbow trout are abundant in the Colorado River below Glen Canyon Dam for 380 km to the head of Lake Mead, AZ. These fish are dependent on locally produced, autochthonous benthic food resources (Angradi 1994, Shannon et al. 2001). There is a significant enrichment of $\delta^{13}C$ of primary producers as well as consumers with increasing distance from the dam (Shannon et al. 2001). The hydrologic regime of releases from Glen Canyon Dam exerts a strong influence on the standing mass and composition of the benthic community as well as the health and reproductive capacity of the fish community (Shannon et al 1994, Persons et al. 1985).

During the summer of 2000, the Bureau of Reclamation in cooperation with other agencies, released a steady 227 m^3/s from Glen Canyon Dam from June through August (Fig. 1; Fritzinger et al. 2000). This experimental flow was designed to benefit the health and reproductive success of the endangered native fish, humpback chub (Gila cypha) as well as, disadvantage alien fish taxa such as rainbow trout through spike flows of 935 m^3/s in May and September. These experimental flows are a departure from the previous pattern of daily fluctuations and were expected to have a substantial impact on both fish and their food supply. In fact, water temperatures increased by 2˚C 25 km below the dam and by as much as 10˚C at sites farthest downstream of the dam. Benthic community composition changed and standing mass was reduced at sites downstream of Glen Canyon Dam (Shannon et al, unpublished data). This management action provided the treatment or disturbance to evaluate environmentally induced changes in muscle and liver tissue $\delta^{15}N$ and $\delta^{13}C$.

We hypothesized that trout displaced downstream would show increased difference between $\delta^{13}C$ of muscle and liver tissue as fish were displaced into areas with enriched $\delta^{13}C$ signals. Alternatively fish that were unable to find food and utilized internal lipid resources should show decreased difference between liver and muscle $\delta^{13}C$ signal. Additionally, we expect to see $\delta^{15}N$ enrichment in tissues of fish under nutritional stress. Linking non-lethal, physiological changes in fish would provide a valuable tool for understanding how rapid changes in environment affect the fish community.

METHODS

We collected rainbow trout during 2 sampling periods: June 2000 at the beginning of the low flow experiment and September 2000 near the end of the 3-month experiment. During both periods, fish were collected by angling, as river trips moved downstream from Lees Ferry, AZ (rkm 0) to Diamond Creek (rkm 360). Fish in the 26-km reach above Lees Ferry were collected by Arizona Game and Fish Department electro-fishing during the same time as the downstream river trips. The location of capture, weight, total length, fork length, and standard length were recorded. All samples were taken from adult fish (total length ≥ 220 mm). Shannon et al. (2001) has shown that $\delta^{15}N$ increases with fish size and we wanted to hold size as a constant so that changes in $\delta^{15}N$ would reflect changes in condition only.

Rainbow trout tissue samples were taken from the white dorsal muscle and the liver of each fish (n = 106). Tissues were dried at 60˚C to a constant weight. Isotopic ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ were ascertained by mass spectrometry at Louisiana State University Center for Coastal Ecology. Isotopic ratios are expressed as δ values, relative to international standards.

Isotopic signals of muscle and liver ($\delta^{15}N$ and $\delta^{13}C$) as well as the difference between the two tissues were tested against river km and fish condition (kn) using regression methods. We also used ANCOVA tests for different response of isotope values with river mile by sample date. Analysis of variance (ANOVA) was used to test for differences in fish condition and tissue isotope signals before and after the flow treatment. Fish condition was estimated from a relative condition factor equation developed specifically for the Lees Ferry trout fishery,where [$Kn = W/10^{(-4.6 + 2.856 Log10(L))}$], and W = weight (g) and L = total length (mm)

(McKinney et al. 1999). All statistical analysis was carried out in JMP IN ver. 3.2.1 for McIntosh (SAS Institute 1996).

RESULTS

The carbon isotope signals of rainbow trout muscle and liver were significantly correlated with each other. Liver tissue was depleted compared to muscle (mean difference = 0.66‰) and the $\delta^{13}C$ of liver could be predicted from muscle tissue with the regression equation: Liver $\delta^{13}C = 7.46105 + 1.29936$ (Muscle $\delta^{13}C$), $n = 103$, $r^2 = 0.78$, $p < 0.0001$. The $\delta^{13}C$ of liver and muscle tissues enriched with increasing distance downstream from Glen Canyon Dam (Fig. 2) however, there was no significant effect of either sample date or distance downstream in the relative difference of $\delta^{13}C$ between the two tissues.

The nitrogen isotope signals of trout muscle and liver were also significantly correlated. While there was no significant change of $\delta^{15}N$ in muscle tissue with increasing distance downstream from Glen Canyon Dam, the difference between $\delta^{15}N$ of muscle and liver tissue increased with distance from the dam: Muscle - Liver $\delta^{15}N = -0.041 + 0.00376$ (river mile), $n = 103$, $r^2 = 0.049$, $p = 0.024$. In addition, $\delta^{15}N$ of liver tissue became significantly enriched from the June sample date to the September sample date (ANOVA, $F = 7.86$, $df = 103$, $p = 0.006$) (Fig 3A). The difference between liver mean $\delta^{15}N$ for June and September was 0.49‰.

Trout condition (kn) declined significantly from June to September from 76.5 ± 1.6 SE to 71.7 ± 1.5 (ANOVA, $F = 4.66$, $df = 100$, $p = 0.033$; Fig. 3B). Overall, the condition of rainbow trout was negatively correlated with liver $\delta^{15}N$: Liver $\delta^{15}N = 15.5244 - 0.2576$ (kn), $n = 100$,

$r^2 = 0.09$, $p = 0.0021$. Similarly the condition of trout was positively correlated with the difference between muscle and liver $\delta^{15}N$: Muscle - Liver $\delta^{15}N = -1.3706 + 0.2118$ (kn), $n = 100$, $r^2 = 0.08$, $p = 0.006$ (Fig. 4).

DISCUSSION

We could not trace changes in diet as fish moved downstream or used stored lipids using $\delta^{13}C$ of muscle or liver. In light of the fact that natural enrichment of food base $\delta^{13}C$ occurs with increasing distance downstream (Shannon et al. 2001), fish under nutritional stress could show enrichment of $\delta^{13}C$ due to of loss of lipids, to their movement downstream in search of additional food resources, or a combination of both. Additionally, the use of $\delta^{13}C$ as an indicator of lipid content in wild fish populations may be limited by the relative fat content of the fish compared to those used in laboratory experiments. Pinnegar and Polunin (1999) found nearly 2‰ difference between liver and muscle with a corresponding lipid concentration of over 40%. The fat content of fish in the wild may be less than those raised under controlled laboratory conditions. Our data showed that the difference between the two tissues was much less than the Pinnegar and Polunin results (0.66‰). However, our data show that $\delta^{15}N$ may be a potential, sensitive indicator of nutritional stress in rainbow trout. The liver has been linked to production of non-essential amino acids such as taurine, which is found in fish organs (Pinnegar and Polunin 1999). Under periods of environmental stress, these amino acids may be produced from stored compounds producing enrichment of liver tissues as nitrogen compounds are metabolized (Hobson and Clarke 1994). Liver tissue (and blood) are likely sites to monitor the initial changes in body chemistry

since these organs are storage sites for stored lipids and have high metabolic activity compared to other body organs (Robinson and Mead 1973).

Due to potentially high tissue turnover rates we expect that liver $\delta^{15}N$ will respond to nutritional stress much sooner than body condition (kn). While specific rates of tissue turnover are not generally known (Gannes et al. 1998), Tieszen et al. (1983) found that the half life of carbon in gerbil livers (Meriones unguienlatus) was 6.4 days compared to 47.5 days in slow turnover tissues such as hair. Additionally, Parker and Anderson (1991) found that the digestive gland of shrimp (Penaeus vannamei and P. setiferus) responded to changes in diet in less than 5 days. These results indicate that changes in trout liver could be detected within days of environmental disturbance rather than the 3 month period of this study. Consequently, isotopes may provide a tool to measure response to nutritional stress which leads to decreases in condition well before changes in condition can be detected.

Stable isotopes have potential as an indicator of physiological stress in wild populations of fish. We have shown that change in isotopic ratios of specific tissues is correlated with changes in condition and environmentally induced stress over a period of three mo. This was accomplished with a relatively small sample size (106 total fish were sacrificed) and a very limited logistical effort. Moreover, isotopic analysis can easily be accomplished by non-lethal methods such as fin clips, muscle plugs and blood extraction. These methods would open up new avenues of research on threatened fish populations and make experiments using repeated measures analysis possible. Although the specific causes of the isotopic changes are still unclear, the mechanisms of these changes can be

identified through experimental trials. Specifically, assays of lipid content in relation to diet, environmental stress, and isotopic composition are needed. There is also a need to understand tissue turnover rates in juvenile and adult fish as well as the effect of gonad production on isotope signals in specific organs. We reccommend that specific experiments be designed and funded which can verify the stressed status of the fish and the specific isotopic response. Once these issues have been resolved, we will possess a powerful tool to monitor the health of wild fish stocks that can be applied in situations where relatively rapid environmental changes produce a variety of potential stresses on organisms.

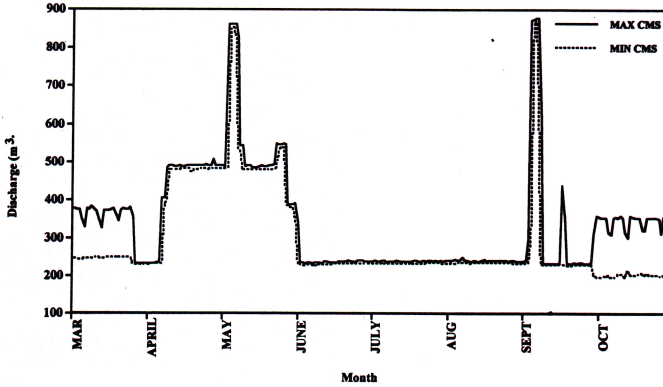

Figure. 1. Daily minimum and maximum discharge ($m^3 \cdot s^{-1}$) in the Colorado River at Lees Ferry, AZ from March 2000 to October 2000. Data obtained from U.S. Geological Survey ADAPS program.

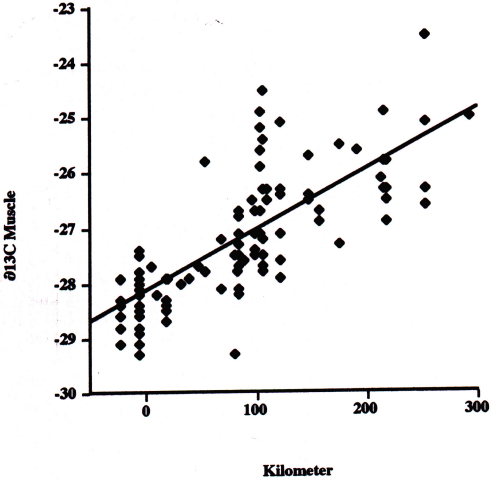

Figure. 2. Enrichment of $\delta^{13}C$ from muscle tissue of rainbow trout in the Colorado River with increasing distance from Glen Canyon Dam, AZ. Data were collected during June and September 2000. The pattern of enrichment is similar to that for fish, invertebrates and algae reported by Shannon et al. (2001).

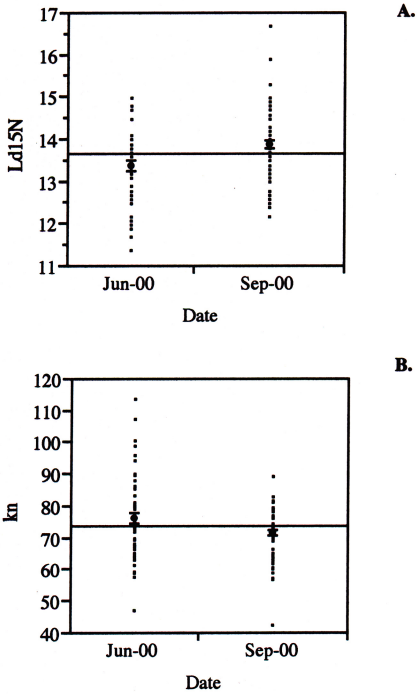

Figure. 3. Differences in Liver $\delta^{15}N$ (A.) and condition (kn) (B.) for rainbow trout in the Colorado River during June and September 2000. Data are represented as points while the diamonds represent the mean and 95% confidence interval for the mean. Both comparisons show significant differences (ANOVA, $p < 0.05$).

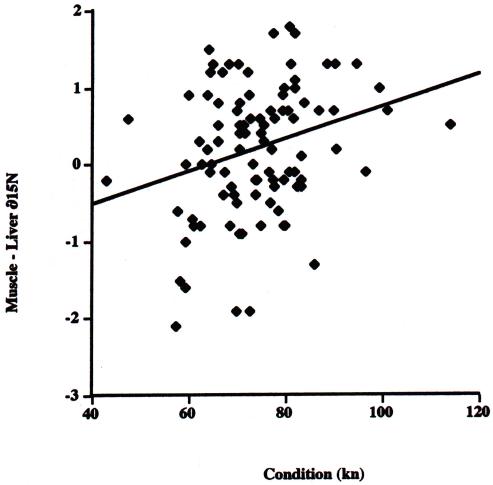

Figure. 4. Condition (kn) of rainbow trout is positively correlated with the difference between $\delta^{15}N$ values of muscle and liver in rainbow trout from the Colorado River.

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Chapter 7: Aquatic community structure response to the 2000 experimental flows from Glen Canyon Dam; Colorado River through Grand Canyon National Park.

INTRODUCTION

Ecologically based flows from river regulation structures have recently been discussed as a method to minimize the impact of hydro-power dams (Freeman et al. 2001). Flow regimes based on pre-dam discharge patterns provide the physical habitat in which native organisms evolved and require to maintain healthy populations (Humphries and Lake 2000). Design of these eco-flows need to consider flow magnitude, frequency, duration, timing, and ramping rates to be comparable with pre-dam flow regimes (Poff et al. 1997). Delineating these hydraulic variables allows decision making stakeholders and researchers to plan experimental eco-flows within the range of natural variability thereby increasing the probability of attaining management goals (Richter et al. 1997; Stanford et al. 1996).

Recovery of native fish habitats and populations has been the primary management goal for several eco-flow experiments (Valdez et al. 1999) and analysis (Sheldon et al. 2000, Freeman et al. 2001). Justifiably so, Ricciardi and Rasmussen (1999) reported extinction rates for native fish in North America alone were 1000 times greater this century (40 out of 1061 fishes) than the historical background rate. River modification (eg. dams, inter-basin transfers, reservoir storage capacity and evaporation) is the leading cause of fish extinction. The Colorado River basin was defined as the most “strongly affected” river through modification in North America by Dynesius and Nilsson (1994).

In the Colorado River through Grand Canyon, Glen Canyon Dam (GCD) operations have created an artificial cool-clear stenothermic

and autocthonous carbon based river dominated by alien taxa (Shannon et al. 2001). This contrived aquatic ecosystem has replaced a thermally variable, turbid, and allocthonous carbon base river that supported eight native fish in Grand Canyon at the turn of the century; today four species remain including the endangered humpback chub (Gila cypha; Haden et al. 1999). Included in the 1995 Environmental Impact Statement on the operation of Glen Canyon Dam was the recommendation for further study on warming the Colorado River through penstock modification and releasing surface water from Lake Powell (USDI BOR 1995). Low summer steady flows were also recommended by the United States Fish and Wildlife Service in their biological opinion to benefit native (USDI BOR 1995). From these two mandates a series of eco-flows, including low-steady summer flows, were released from GCD from spring to fall 2000 in an effort to foster the aquatic community and the humpback chub, in particular (Fig 1).

Our study examined the effects of these 2000 eco-flows on the water quality, benthos, organic drift, near-shore vegetation growth and small fish habitat selection in the Colorado River through Grand Canyon. We wanted to know if the river would warm with distance downriver from GCD and if there was any additional channel margin warming. This is first time since 1963 and that low summer steady flows were released from GCD and we wanted to determine what effect this novel flow regime (steady 227 m^3/s for 3 mo.) would have on the aquatic community. Because small fish prefer vegetated habitats because of cover from predation and food availability (Grenouillet and Pont, 2001), we assessed nearshore vegetative growth and experimentally examined the role of vegetative structure as fish habitat.

STUDY AREA

Our collection stations were located in the Colorado River below Glen Canyon Dam through Glen Canyon National Recreation Area and Grand Canyon National Park, Arizona (Fig. 2). These sites were selected to bracket the Paria River and Little Colorado River (LCR), two of the largest tributaries, and include the two largest populations of humpback chub. These populations were located near the confluence of the LCR between river kilometer (rkm) 98.6-109.6 and in middle granite gorge (rkm 202.9). The aquatic community is controlled by three factors: 1) stenothermic cool (~ 9˚C) hypoliminitic releases from Lake Powell which limit macroinvertebrate composition (Pomeroy et al. 2000), 2) typically clear water (Secchi depths >3m) in the first 24km tailwaters, while downriver of the Paria River seasonally turbid water occurs from tributary input of suspended sediments (Secchi depths < 2m) which reduces biomass and energy availability (Blinn et al. 1998), and 3) hydro-electric peaking power (or load-following) discharges ranging from 142-708 m^3/s that change on an annual, seasonal, monthly, weekly, daily, and hourly basis which creates flow reversals during up-ramping that limits benthic biomass and increases organic drift (Shannon 2001; Shannon et al. 1996).

The combination of these factors has created a functioning but variable artificial benthic community. Up to 1995 grazing macroinvertebrates were dependent on Cladophora glomerata and its epiphytic diatom assemblage (Blinn et al. 1998), but from 1996 through 2000 Cladophora was replaced by a mixed assemblage of rooted macrophytes, filamentous green, red and blue-green algae taxa (Benenati et al., 2000). Also since 1995 the dominate grazers and detritivores

consisting of nearctic-chironomids, Gammarus lacustris and oligocheates has been surpassed by various Physa spp., Physella spp. And the New Zealand Mudsnail (Hydrobiidae: Potamopyrgus antipodarum). These changes in primary and secondary producer composition probably resulted from the filling of Lake Powell diluting nutrient concentrations, highly variable flow regimes, and possibly complex trophic interactions (Benenati et al. 2000).

The fish community in Grand Canyon is dominated by alien fish including rainbow trout (Oncorhychus mykiss), fathead minnow (Pimephales promelas), common carp (Cyprinus carpio) and channel catfish (Ictalurus punctatus), listed in order of dominance (Valdez et al. 2001). Native fish include speckled dace (Rhinichthys osculus), humpback chub (Gila cypha), flannelmouth sucker (Catostomus latipinnis), and blue head sucker (Catostomus discobolus) listed in order of dominance. The humpback chub is listed as an endangered species by the US Fish and Wildlife Service; flannel mouth suckers are being considered for listing while bluehead suckers and speckled dace are common in Grand Canyon (USDI BOR 1995). The Grand Canyon humpback chub population is the largest in the Colorado Basin and spawns primarily in the LCR tributary (Robinson and Childs 2001). The CGD 2000 eco-flows were designed primarily to improve humpback chub larval growth and annual recruitment by impounding the mouth of the Little Colorado River and warming of the main stem Colorado River.

METHODS

Eco-Flow Hydrograph

Through the adaptive management process implemented in 1996 regarding the operation of Glen Canyon Dam a hydrograph was designed to benefit the humpback chub and other native fish, while considering other natural and human resources (Fig. 2; Walters et al. 2000).

The kingpin of the 2000 eco-flow design was the steady flow (227 m^3/s) period from 1 June through 3 September. The rationale was a low and steady discharge volume released from the metalimnion of Lake Powell would increase in temperature as it moved downstream and enhance native fish recruitment. This was the first time since 1963 that low steady summer flows were released from GCD for more than three days. Normally June through September are medium to high flow months with maximum daily fluctuations for hydro-power. In 1999 during these four months the flows ranged from 319 to 645 m^3/s and averaged 492 m^3/s. Prior to GCD flows in Grand Canyon peaked in June at an annual average of 2420 m^3/s with a maximum estimated peak at 8500 m^3/s in 1884 and then dropped through the summer averaging <200 m^3/s (Webb et al. 2000). We collected during 14 day sampling trips in June and August to determine the effect of 227 m^3/s flows, again in September to determine the effect of the 835 m^3/s, and in October to determine any if any of the responses recorded continued into the fall and return to peaking-power flows.

Water Quality

We collected conductivity (mS), pH, temperature (˚C), and dissolved oxygen concentration (mg/L) data with a Hydrolab® Scout II H20 at the time of

collection at each site (Fig. 2). River and channel temperature (˚C) data was also collected at rkm 4.0, 82.9, 109.6, and 199.2 at five locations: 1) in the river channel 2 m below the 227 m^3/s water level, 2) 10 cm from shore and10 cm below the water surface, 3) 50 cm from shore and 10 cm below the water surface, 4) shaded terrestrial, above 935 m^3/s, and 5) direct sunshine terrestrial, above 935 m^3/s. Data was collected and stored every 12 minutes with On-Set® tid-bit data loggers from June through October except during the September spike flow (Fig. 1). Turbidity data (NTU) was collected at station during each sampling trip with a VWR Scientific turbidity meter. Water transparency was measured with a Secchi disk.

Benthic Biomass Estimates

Benthic sampling was conducted along three transect 30 m apart on each cobble bar/riffle habitat with a modified Hess substrate sampler (lid added for greater sampling depth). Two samples were taken along each transect (n=6) along with water depth (cm), current velocity (m/s), and substrate type (% sand or cobble). Samples were processed live within 24 h and sorted into five biotic categories: *Cladophora glomerata*, *Oscillatoria* spp., detritus, miscellaneous algae, macrophytes, and bryophytes (MAMB), and macroinvertebrates. Macroinvertebrates were numerated into *Gammarus lacustris*, chironomid larvae, simuliid larvae, and miscellaneous invertebrates. Miscellaneous invertebrates included lumbriculids, tubificids, physids, trichopterans, terrestrial insects and unidentifiable animals. Detritus was composed of both autochthonous (algal/bryophyte/macrophyte fragments) and allochthonous (tributary upland and riparian vegetation) flotsam. Each biotic category was oven-

dried at 60°C and weighed to determine dry weight biomass. Samples were then ashed (500°C, 1 h), and reweighed for ash free dry mass estimates.

Organic Drift Biomass Estimates

Near-shore surface drift samples (0-0.5 m deep) were collected at each site for coarse particulate organic matter during each collection trip. Samples were taken in triplicate between 1000 h and 1500 h at each site with a circular tow net (48 cm diameter opening with 500 µm mesh) held in place behind a moored raft or secured to the river bank. Samples were sorted and processed live for biota as outlined for benthic biomass estimates Current velocity was measured at the mouth of the net with a Marsh-McBirney electronic flow meter and collection duration was recorded for volumetric calculations (mass/m^3/s).

Nearshore Vegetation Patterns

Three transects, 15 m apart and 3 m long, perpendicular to the river's edge were established at each site adjacent to the thermal monitoring stations. Density and composition of plants were recorded in 0.5 m^2 plots on the upstream side of the transect at 1 m intervals.

Small Fish Habitat Selection

Six minnow traps (0.48 m x 0.22 m) were set in cobble/riffle habitats, sand, and within an artificial emergent vegetation habitat. Minnow traps set in sand were to evaluate the effect of the minnow traps serving as a habitat themselves and biasing the results. Artificial habitat was constructed of plastic carpet (1.2 m x 2.5 m) with plastic coated wire plants, that mimic horsetail, fastened to reinforcement bar spread 20 cm

about across the carpet. Density of the plastic stems (60/m^2) was similar to horsetail density found within the study area. Traps were set for about 12 h between 1800 and 0600 h near the thermal monitoring stations. Water depth and current velocity was recorded at the time of deployment at each end and in the middle of each trap to characterize the physical habitat. Size, weight, total length, and standard length of each fish species caught was recorded.

Statistical Analysis

Multiple analysis of variance (MANOVA) was used to determine overall patterns in benthic and organic drift biomass estimates determined during the 2000 eco-flows. Predictor variables were collection station and date. Response variables included: *Cladaphora*, MAMB, *Oscillatoria*, detritus, macroinvertebrate (g AFDM/m^2), and macroinvertebrate density (#/m^2). More refined analysis to examine patterns within the 2000 eco-flows were done with the Kruskal-Wallis test (September spike flow). Kruskal-Wallis tests were used to compare changes between June and August to access the impact of the steady flows.

During the summer of 1997 a period of relatively steady-high flows (560-790 m^3/s) were released from GCD because of higher than average snow pack (Pulwarty and Melis 2001). Data collected from June and August 1997 with same protocols as described above were compared to the 2000 eco-flow data with MANOVA tests. All calculations were performed with SYSTAT ™ Ver. 5.2 computer software (SYSTAT, Inc., 1992) on ln+1 transformed data.

RESULTS

Water Quality

Conductivity, pH and dissolved oxygen concentrations did not vary from previous years collection trips (Benenati et al. 2000) however, the Colorado River did warm during the three months of steady low flows (Table 1). Conductivity averaged 0.826 mS (± 0.15 sd) , pH averaged 7.9 (± 0.24 sd) and dissolved oxygen concentration averaged 12.1 mg/L (± 0.19 sd) with all of these parameters within the range normally reported within the study site. River temperatures in the channel ranged from 9.4 ˚C at Lees Ferry in September during the spike flow to 19.1 ˚C at Diamond Creek (rkm 361.6) in June during steady flows. We did detect slight shoreline warming of ~ 1 ˚C in the first 110 rkm and ~ 2 ˚C 200 rkm between the channel and shoreline data. Terrestrial temperatures varied with season and ranged from 8.4 to 60.5 ˚C. The Colorado River temperature usually does not warm more than 7˚C from GCD to Diamond Creek (rkm 361.6) and only during May or June because the flow volume increases in July and August.

During the September spike flow the river cooled as the hydrostatic wave passed each sensor in the channel and recovered to nearly the same temperature before the spike flow (Figure 3). We calculated a thermal recovery rate at each station: rkm 4.0 = 0.36 ˚C/d; rkm 82.9 = 0.56 ˚C/d; rkm 109.6 = 0.64 ˚C/d; rkm 199.2 = 0.66 ˚C/d. These data show that in September most of the warming occurs in the first 100 km.

The Colorado River was primarily clear because of a dry spring and summer, but was very muddy in the fall. Secchi depths, measure of light penetration, ranged from > 4m at rkm 0.8 to 2.1 m at rkm 202.9 in June to 0.1 m at rkm 199.2 in October. Turbidity followed the same pattern of NTU ranging from 1 to 6 in June at rkm 0.8 and 202.9

respectively, while in October the river was very turbid with NTUs measured at 10,000 at rkm 202.9.

Benthic Biomass Estimates

The summer 2000 eco-flows had a significant influence on benthic biomass between both sampling dates and location (Table 2). Cladophora biomass averaged 4.0 g AFDM/m^2 (± 2.1 se) across the study site in June and increased to 8.2 g AFDM/m^2 (± 7.5) in September however, patchiness was high as indicated by the error term. Average MAMB biomass decreased through the study site from 47 g AFDM/m^2 (± 30.9) in June to 11.5 g AFDM/m^2 (±5.1) in October. The MAMB assemablage consisited primarily of filamentous Chlorophyta (Ulothrix, Spirogyra, Mougeotia, Stigeoclonium spp.) and Osillatoria spp., with a small perscentage of Potamogeton pectintus, Elodea spp., Chara contraria and Fontinalis spp. Study site wide macroinvertebrate biomass increased from 3.2 g AFDM/m^2 (±1.8) in June to 7.8 g AFDM/m^2 (± 5.1) by August. However, this increase was comprised of snails which increased compositionally from 41% to 93% of the total density. Additionally, miscellaneous macroinvertebrate density peaked in August at the end of the steady low flows at 3437/m^2 (± 1627 se) and was lowest in October at 702/m^2 (± 503) study site wide. Miscellaneous macroinvertebrate category was comprised of planaria flat worms, ostracods, nematodes, water mites, and hydroptilid nymphs.

Three months of steady 227 m^3/s flows also had a variable but significant influence on the benthos (Table 3). At Lees Ferry lumbriculid, miscellaneous macroinvertebrate densities increased 92%, 95%, respectively, while macroinvertebrate biomass increased an order of

magnitude. Simuliid larvae density decreased 92%. Detritus was the only biotic category to change significantly at Two-Mile Wash during the steady flows and it decreased 95%. In the LCR detritus, macroinvertebrate biomass, tubificid density and miscellaneous macroinvertebrate density all decreased an order of magnitude during the steady flows. Tanner Cobble responded with Cladophora and MAMB biomass decreasing 100% and 47%, respectively, while simuliid density decreased 70%. However, snail density increased from 0 to 175/m^2 (± 107) during the steady flows.

Only MAMB biomass responded at the Middle Granite Gorge site to the three months of steady flows by increasing from 0 to 4.8 (± 1.9) g AFDM/m^2.

Although multivariate tests showed significant overall differences in biomass between June 1997 and summer 2000 for the entire study site biomass estimates (Wilks' Lamda 0.7; $p<0.001$), univariate tests indicated only Cladophora varied signficantly ($p<0.001$). June 1997 Cladophora biomass estimates were 10.0 g AFDM/m^2 (± 6.5) while June 2000 estimates were 4.0 g AFDM/m^2 (± 2.1). August 1997 biomass estimates were significantly different after a summer of high steady flows compared to August 2000 low steady flows (Wilks' Lamda 0.5; $p<0.001$). August 1997 estimates for Cladophora, detritus, MAMB and macroinvertebrates were 23.7 (± 14.6), 6.2 (± 4.0), 5.3 (± 1.8), and 3.1 (± 2.5) g AFDM/m^2, respectively. Cladophora and detritus biomass was 83% and 40% higher in August 1997 than in 2000 ($p<0.02$). However, MAMB biomass was 4.7 times greater in 2000 and there was 60% more macroinvertebrate biomass ($p<0.01$), although primarily composed of snails.

Benthic response to the four day spike flow of 835 m^3/s in September was more intense downriver and significant respones varied by biotic category (Table 4). August and October collections bracketed the spike flow and at Lees Ferry miscellaneous macroinvertebrate density decreased by 20%, while at Two-Mile Wash the spike flow had no significant effect on the benthos. The LCR benthos responsed with chironomid larvae, miscellaneous macroinvertebrate, and snail densities all decreasing by an order of magnitude. At Tanner Cobble the spike flow eliminated Gammarus, and reduced miscellaneous macroinvertebrate density and macroinvertebrate biomass also by an order of magnitude. Middle Granite Gorge benthos was negatively impacted by the spike flow as indicated by a significant reductions macroinvertebrate and MAMB biomass, with a 98% loss of chironomid larvae, and 40% of miscellaneous macroinvertebrate density.

Organic Drift Biomass Estimates

Organic drift biomass and density did not vary sigificantly between collection trips, however there were signifcant differences between collections sites for some biotic categories (Wilks' Lamda 0.3; $p<0.001$). Miscellaneous macroinvertebrate biomass increased ($p<0.001$) from an average of 0.19 (±0.1) to 0.35 (±0.2) $mg/m^3/s$ AFDM between Lees Ferry and Middle Granite Gorge during the collection period. Detritus also increased between these two sites from an average of of 6.41 (±3.0) to 445.6 (±411.1) $mg/m^3/s$ AFDM. Contrary to these patterns MAMB decreased between Lees Ferry and Middle Granite Gorge from an average of of 5.7 (±1.9) to 2.3 (±1.0) $mg/m^3/s$ AFDM. Overall particulate organic carbon transported during the collection period averaged 14.0 (±0.91)

mg/m^3/s AFDM at Lees Ferry and 447.0 (± 156) mg/m^3/s AFDM at Middle Granite Gorge.

The 2000 eco-flow coarse organic drift estimates were not signficantly different than the 1997 relatively steady high flow drift data from the same sites and collection periods (Wilks' Lamda 0.9; p=0.14). Overall particulate organic carbon transported during the 1997 collection period averaged 518.0 (±0.470) mg/m^3/s AFDM at Lees Ferry and 309.5 (± 169) mg/m^3/s AFDM at Middle Granite Gorge.

Nearshore Vegetation Patterns

Density of riparian vegetation within 3m of the river varied significantly by collection date and location during the 2000 eco-flows ($p<0.001$; $R^2=0.58$). During the three months of steady flows vegetation average density increased near the rivers edge from 0 to 48 plants/m^2 (±12) and decreased to 2 plants/m^2 (± 1) by October, probably in response to scour from the spike flow and return to peaking-power flows. Plants 3m up the bank from the rivers edge decreased from 59 plants/m^2 (±47) to 25 plants/m^2 (±13) during between June and August during the steady flows and remained near that level into October 21 plants/m^2 (±11). These plots were located above the varial zone so were not directly affected by the return to peaking-power flows at the end of September. *Juncus balticus*, *Tamarix chinensis* and *Juncus torreyi* represented 80% of the plant taxa identified within the study plots (Table 5).

Small Fish Habitat Selection

Small fish preferred vegetation and artifical vegetation over cobble or sand habitats ($p<0.02$). We minnow trapped a total 26 small fish in the

following distribution: 12 vegetation, 10 artifical vegetation, 4 cobbles, and 0 sand. The lack of fish in the sand minnow traps indicates that the traps themselves were not attracting fish. These data were similar to the pattern reported by Shannon et al. (1998) from collections during the 1997 high flows using the same protocols, in ratio of 3:2:0 for vegetation, cobble and sand habitats. Native fish comprised 90% of the fish caught prior to the September spike-flow, but 90% of the fish caught after the spike-flow were alien rainbow trout. Minnow trap depth averaged 0.4 m (±0.01 se), and current velocity averaged 5.8 cm/s (± 0.07 se) with neither varying significantly between habitats. Trap sets averaged 11.5 h (± 0.4 se) and did vary significantly between collection trips.

Nearshore vegetation did respond to steady low flow period by colonizing the rivers edge, but three months was not long enough for abundant growth in the channel. Converse et al. (2001) reported the importance of the vegetated near shore habitat for humpback chub, primarily hanging tamarix branches. This type of cover provides protection from predators, low velocity habitat for growth (Grenouillet and Pont 2000), and food. Benenati et al. (2001) reported 11 times more zooplankton in the vegetated shoreline compared to the channel of the Colorado River in Grand Canyon. This is an example of a habitat that was not present in Grand Canyon before GCD, but is now used by native fish for development (Converse et al. 2001). Pre-GCD backwater habitats probably provide a stable environment for fish development, but now many alien fish also frequent these habitat areas (Walters et al. 2000). Small fish selected the artifical vegetation nearly as often as vegetated shoreline within 12 h after deployment, which indicates the importance of cover to small fish in this aquatic community.

DISCUSSION

The hydrograph design of the 2000 eco-flows from GCD was too short and overly complicated to be of signifcant benefit to the aquatic community (Fig. 1). Flows between April and May were meant to pond tributary mouths, particuarly the LCR, so humpback chub larvae would remain in the warm tributaries long enough to develop and to mimic pre-GCD spring flows. The three months of steady 227 m3/s were designed to allow the young of the year fish to further develop in the main stem, while the September spike flow was supposed to flush alien fish that may have taken advantage of the low summer flows. Therefore, aiding humpback chub development hinged on a good spawning season in the LCR, which is in-turn dependent on at least an average spring run-off to trigger the spawn. This did not occur due to a below normal snow-pack in 2000 for Arizona. As a result, the primary management goal to enhance a cohort of humpback chub did not occur. This underlines the importance of multi-year eco-flows so natural variation in environmental conditions is captured.

Macroinvertebrate biomass, other than snails, did not significantly increase at sites with warmer summer temperatures as may have been initially expected. However, the organisms that have colonized the Colorado River below GCD have been selected over the past 38 years by the cool stenothermic thermal regime. Therefore three months of above normal river temperature was not enough time for any significant changes in biomass or composition. Kanab Creek (rkm 231.2) has water chemistry most similar to the main stem and is a likely source of colonization by aquatic insects if the river is warmed for any substantial

period either through low flows or modification of GCD (Oberlin et al. 1999).

It may be possible that the aquatic community in the Colorado River through Grand Canyon is so contrived that it will not responsed positively to a natural flow regime as several researchers suggest (Poff et al. 1999). Given the complete change in hydrograph, thermal regime, and carbon sources restoration is probably not a realistic goal with GCD in place. However, preventing the extinction of the humpback chub is mandated by the endangered species act and given the decline in health of these fishes (Meretsky et al. 2000) multi-year experimental flows need to be tried and placed in the adaptive management process. It does seem clear that reduction in flow variation from peaking power production would benefit the aquatic community and therefore, native fish including humpback chub.

Ten years of seasonally adjusted steady flows, with unlimited ramping for hydropower within 10% of the seasonal mean discharge would be a logical starting point. Two experimental flows have occured from GCD, the 1996 spike flow (Valdez et al. 2001) designed primarily to conserve sand and the 2000 eco-flows designed primarily to conserve native fish. Neither obtained management goals for any duration because of natural processes overriding the intented results, high Colorado River basin snow-pack in 1996 and low LCR snow-pack in 2000.(Shannon et al. 2001). Nevertheless, data gathered from these experimental flows is extremely valuable and should aid the design of future eco-flows in the Grand Canyon and other regulated rivers world-wide.

Summer of 2000 eco-flows from Glen Canyon through Grand Canyon had variable-short term impacts on the aquatic community. River

temperature did warm with distance down river and across the channel as would be expected during the three summer months of steady 227 m^3/s flow (Table 1). This information is important because it demonstrates that dishcarge from GCD can be used as a warming tool to benefit native fish. Currently the mainstem Colorado River is too cool (8-12 ˚C) for development of native fish larvae so native fish survival is limited to tributary spawning (Robinson and Childs 2001). The September spike flow provided data on the rate of river warming after a return to steady flows and showed that the rate of warming stabilized to ~0.7 ˚C/d after 220 km down river from GCD.

Primary producer biomass patterns were dominated by an increase in MAMB and decrease in Cladophora biomass. The exact mechanism for this shift is not known, but disharge and nutrient delivery rates are probable causes (Benenati et al. 2001). An explosion of snails throughout the study site may be in response to the change in primary producer composition and cannot be considered a positive change for the aquatic community (Hawkins and Furnish 1987). These grazers obtained densities >80,00/m^2, but are a trophic dead end, because they are not found in the drift and do not have an aerial stage to benefit insectivores. Fish in the study site also lack the secondary jaws required to crush the shell to aid in digestion.

Coarse particulate organic drift was similar during the 2000 eco-flows and during the 1997 relatively high steady flow period, although three times more carbon was transported in 1997 because of the higher dishcarges. This pattern supports the idea reported by Shannon et al. (1996) that flucuating flows from GCD has selected for benthic organisms that are tolerant to variable flows and therefore do not exhibit behavioral

drift. Steady low flows then should not limit food availabilty to higher trophic levels.

Table 1. Summary of temperature data (˚C) collected in the Colorado River corridor through Grand Canyon at three sites from June through October 2000. Statistics are from daily data sets.

Site	Sensor Location	Range	Average	±sd	n
Rkm 4.0	Channel	9.4 - 10.1	9.8	0.3	84
	Waters edge	10.7-16.6	11.1	0.6	82
	50 cm from water edge	7.5-17.9	11.0	0.4	91
	Un-shaded terrestrial	10.2-60.2	27.6	3.9	118
	Shaded Terrestrial	8.9 -50.9	26.3	3.4	118
Rkm 109.6	Channel	10.3 - 14.6	12.6	0.2	82
	Waters edge	10.4-16.9	13.44	1.3	96
	Un-shaded terrestrial	8.6-51.5	28.4	5.4	122
	Shaded Terrestrial	6.9-46.7	25.7	5.3	122
Rkm 199.2	Channel	11.2-16.1	13.5	1.2	63
	Waters edge	11.2-18.2	15.1	1.2	96
	50 cm from water edge	11.1-17.4	14.9	1.8	96
	Un-shaded terrestrial	8.7-60.5	31.1	6.4	124
	Shaded Terrestrial	8.4-53.6	28.4	7.2	124

Table 2. Results of multiple analysis of variance comparing benthic biomass in Colorado River through Grand Canyon during the summer of 2000 experimental flows at four sites: rkm 0.8, 3.1, 98.7,109.6 and 202.9. Predictor variables were collection trip and site while response variables (g/AFDM/m^2) were as follows: Cladophora (C), MAMB (A), detritus (D), and macroinvertebrates (M). Only biotic categories with significant ($p<0.05$) univariate responses are listed. Overall Wilks' lambda, trip and site, was significant ($p<0.001$).

Source	Wilks' lambda	Approximate F statistic	df	p	Response variable
Trip	0.5	5.4	16,397	<0.0001	C,A,D,M
Site	0.3	15.3	24,447	<0.0001	C,A,D,M

Table 3. Results of Kruskal-Wallis tests comparing June and August 2000 benthic biomass (g/AFDM/m^2 ± se) and density (#/m^2 ± se) estimates in the Colorado River through Grand Canyon to determine the effect of three months of steady 227 m^3/s flows. Response variables were as follows: biomass; Cladophora (C), miscellaneous algae/macrophytes (A), detritus (D), macroinvertebrates (M) - density; lumbriculids(L), tubificids (T), chironomids (CH), simuliids (B), Gammarus (G), snails (S) and miscellaneous macroinvertebrates (MM). Only biotic categories with significant ($p<0.05$) responses are listed (n=12; df=1)

Site	Biotic category	June		September		p
Lees Ferry (Rkm 0.8)	L	31	(±15)	381	(±156)	0.02
	B	108	(±47)	5	(±5)	0.04
	MM	431	(±220)	8,366	(±2810)	<0.01
	M	5.9	(±4)	26.5	(±5)	0.01
Two-Mile Wash (Rkm 3.1)	D	40.1	(±2.2)	381	(±156)	0.04
Little Colorado (Rkm 98.7)	D	7	(±1.4)	1.1	(±0.8)	0.04
	A	198.9	(±29.6)	32.1	(±10.1)	<0.01
	T	175	(±64)	15	(±9)	0.02
	M	11,798	(±1373)	1,365	(±217)	0.03
Tanner Cobble (Rkm 109.6)	C	0.1	(±0.04)	0.02	(±0.02)	0.03
	A	38.2	(±36.7)	20.6	(±3.5)	0.04
	B	133	(±74	53	(±23)	0.04
	S	0	(±0)	175	(±107)	<0.01
Middle Granite Gorge(Rkm 202.9)	A	0	(±0)	4.8	(±1.9)	<0.01

Table 4. Results of Kruskal-Wallis tests comparing August and September 2000 benthic biomass (g/AFDM/m^2 ± se) and density (#/m^2 ± se) estimates in the Colorado River through Grand Canyon to determine the effect of a four day steady 792 m^3/s flow. Response variables were as follows: biomass; Cladophora (C), miscellaneous algae/macrophytes (A), detritus (D), macroinvertebrates (M) - density; lumbriculids(L), tubificids (T), chironomids (CH), simuliids (B), Gammarus (G), snails (S) and miscellaneous macroinvertebrates (MM). Only biotic categories with significant ($p<0.05$) responses are listed (n=12; df=1)

Site	Biotic category	Rank Sum June		September		p
Lees Ferry (Rkm 0.8)	MM	53	(±12)	4	(±2)	<0.01
Two-Mile Wash (Rkm 3.1)						
Little Colorado (Rkm 98.7)	CH	1,135	(±484)	115	(±63)	0.02
	MM	6,265	(±1365)	411	(±291)	<0.01
	S	217	(±53)	30	(±14)	0.04
Tanner Cobble (Rkm 109.6)	G	26	(±9.8)	0	(±0)	0.02
	MM	1,133	(±535)	112	(±74)	0.01
	M	0.25	(±0.09)	0.07	(±0.03)	0.01
Middle Granite Gorge (Rkm 202.9)	A	4.7	(±1.9)	1.4	(±1.1)	0.02
	CH	127	(±3)	3	(±3)	0.04
	MM	218	(±10)	131	(±4)	<0.01
	M	0.05	(±0.002)	0.002	(±0.0001)	<0.01

Table 5. Riparian vegetation taxa quantified in the Colorado River corridor through Grand Canyon at four study sites from June to October 2000. Taxa are listed in order of most to least commonly occuring.

	Plant Taxa	Rkm 4.0	Rkm 82.9	Rkm 104.0	Rkm 199.2
1	Juncus balticus	6, 9, 10	6	6	
2	Tamarix chinensis	8, 9, 10	6 ,8, 9, 10	6, 8, 9, 10	6
3	Juncus torreyi	8, 9			
4	Equisetum laevigatum	6, 8, 9, 10	6, 8, 9, 10	6, 8, 9,10	6, 8, 9, 10
5	Gnapthalium spp.	8, 9, 10	6, 8, 10	6, 8, 9, 10	
6	Carex spp.		10	6, 8, 9, 10	
7	Equisetum arvensis	6, 8, 9,10	6		
8	Salix exigua	6, 8, 9, 10	6, 8, 9, 10	6, 8, 9, 10	
9	Bacharis spp.	9	6, 8	6, 8, 9, 10	
10	Plantago spp.	8, 9, 10	8		
11	Solidago canadensis	6, 10			8
12	Apocynum cannabinum	6, 8, 9, 10			

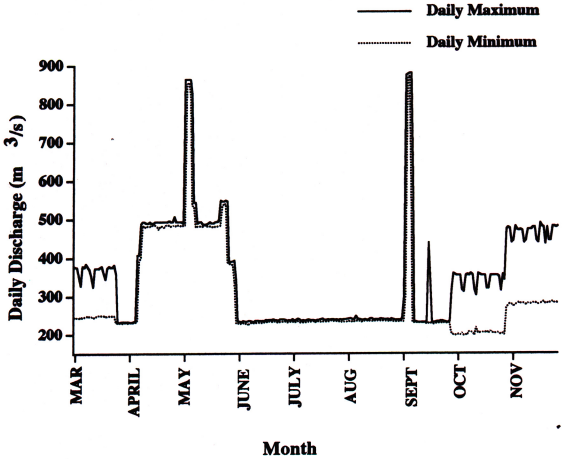
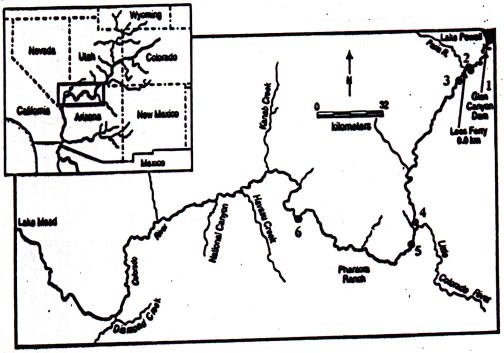


Figure 1. Daily maxiumum and minimum discharge recorded at the Lees Ferry, Arizona USGS gaging station 09380000 on the Colorado River from March through November 2000. Experimental eco-flow started 26 March and ended 30 September. Spike on 18 September was an emergency response for hydro-power.



Legend

	Site	rkm	Elevation (msl)	Orientation	Habitat
1	Glen Canyon Gauge	-23.2	953	Southwest	Drift
2	Lees Ferry Lees Ferry Cobble	0 0.8	947	Southwest	Drift Cobble
3	Two-mile Wash Two-mile Cobble	2.9 3.1	876	South	Drift Cobble
4	Gauge above LCR LCR Island	98.4 98.6	826	South	Drift Cobble
5	Tanner Cobble	109.6	808	Southwest	Cobble/Drift
6	127 Mile Rapid	202.9	616	Northeast	Cobble/Drift

Figure 2. Collection sites in the Colorado River through Grand Canyon, AZ. Elevation is in meters above sea level.

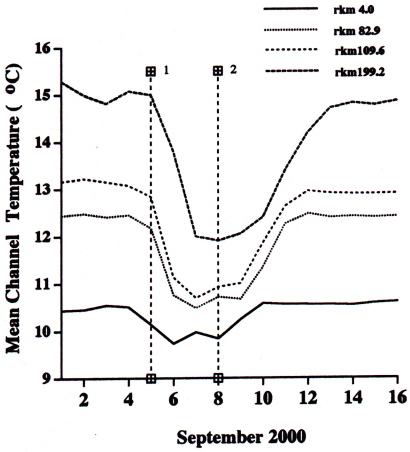


Figure 3. Effect of the September 4 - 8 2000 spike flow of 835 m^3/s on the temperature of the Colorado River at four stations through Grand Canyon. Spike flow duration is indicated by the 1 and 2.

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Chapter 8: Increases in Colorado River gastropod populations below Glen Canyon Dam

INTRODUCTION

The introduction of new taxa to aquatic communities often has profound effects on community composition, energy transfer among trophic levels, and water quality (Spencer et al.1991, Strayer et al.1999). These effects may have cascading implications for higher trophic levels which are of economic concern (Spencer et al. 1991). Introduced taxa often exhibit marked population increases due to release from predation or other environmental limitations found in their native habitat. Predation, direct competition for resources, or indirect competition (Spencer et al. 1991, Haden et al. 1999) may lead to suppression of densities of previously established fauna. Similarly, changes in environmental conditions may allow taxa which existed in low numbers to become dominant members of the community. In such a case, the implications for community composition and energy transfer are the same as an introduction.

Aquatic ecosystems below dams are especially susceptible to introductions of new taxa. In many cases the native taxa may have been eliminated due to changes in water quality, temperature, and discharge regimes (Haden 1997) creating new, open niches. Large magnitude disturbances have been shown to de-stabilize community structure for decades afterwards (Cottingham et al. 1999). Subsequent disturbances caused by management actions after initial flow alteration can further de-stabilize community structure allowing for windows of opportunity for new taxa to take hold (Benenati et al. 1998).

This study documents the changes in the benthic community of the Colorado River below Glen Canyon Dam, AZ from 1992 - 2001. We

focus on increases in snail densities and changes in the composition of the benthic snail community. We discuss implications for trophic transfer of energy and hypotheses for the cause of the changing community structure.

METHODS

Quantitative benthic samples were collected as part of the Northern Arizona University Aquatic Food Base monitoring program. Hess samples (n = 6) were collected at cobble bars at each monitoring site (Fig. 1, Chapter 1) and Petite Ponar samples (n = 12) were collected in pool habitats at each site. Abundances of snails were either counted directly from the sample or estimated using regressions on the dry weight of the sample. Abundance estimates are for the total snail community since no attempt was made to identify various taxa of snails in each sample. This study examines data from 22 collecting trips carried out from 1992 to 2001.

Separate, qualitative taxonomic samples for each site were collected by hand at the time of each benthic collection. Invertebrates were stored in 70% ETOH for later identification. Material for this report were examined by Jerry Landye, U. S. Fish and Wildlife Service, James Mead, Northern Arizona University, and David Richards, Montana State. Taxonomic material is stored at Northern Arizona University.

RESULTS

We identified 8 taxa of aquatic gastropods and 2 taxa of bivalves in the Colorado River below Glen Canyon Dam, AZ between 1992 and 2001 (Table 1). The bivalves are in the family Sphaeriidae and the gastropods

are composed of 4 families: Physidae, Lymaeidae, Pomatiopsidae, and Hydrobiidae.

The composition of the mollusc community has not remained static over the last decade (Table 2). Bivalves have remained in very low numbers and are only found at sites above the Paria River. Physella spp. were common organisms through the decade, however other species have become abundant for short periods. Physa integra and Pomatiopsis lapidaria were found during specific years but do not seem to have had a continuous presence in the river. Fossaria spp. were first noted in the river during 1995 and has had a continuous presence in the river since 1998. In March 2002, the New Zealand Mudsnail (Hydrobiidae: Potamopyrgus antipodarum) was identified from collections at Lees Ferry. No taxonomic keys are readily available for this taxa and it is not known when it colonized the river. Examination of collection snail specimens show that the New Zealand Mudsnail was first collect on 5 August 1995. The abundance of snails has increased by 3 orders of magnitude in the last six years. Previous to 1996, snail abundance was generally less than 100 snails·m $^{-2}$ at Lees Ferry (Fig. 1). Snail abundance at Lees Ferry began to rise in 1996 and since 1997 abundance has been maintained at over 2500 snails·m $^{-2}$ with peak abundances of over 40,000 snails·m $^{-2}$ during the year 2000 (Fig. 1). Snail biomass has become a significant portion of the invertebrates standing mass of the river. At Lees Ferry, snail biomass has increased from less than 6% of the total invertebrate ash-free dry mass in 1992 to over 66% in 2001.

Snail abundance decreases dramatically at sites downstream of the Paria River. Physella spp. has been found during most years, in low densities (<100 snails·m $^{-2}$), at sites as far downstream as 205 mile rapid

(Rkm 328). However, Fossaria spp. which is associated with high snail densities in our samples, was only found as far downstream as Tanner Rapids (Rkm 108) during the low summer steady flow experiment in 2000. Mean snail densities at Tanner Rapids from June through October 2000 were 66 snails·m^{-2} ± 31 SE.

DISCUSSION

While members of the genus Fossaria have been reported from within Grand Canyon tributaries (Spamer and Bogen 1991) they have not been recorded in the mainstem Colorado River below Glen Canyon Dam previous to 1995. Once this group became established in the river it quickly became the dominant taxa of the benthic community representing more than half of the benthic standing mass at Lees Ferry, AZ with densities over 2500 snails·m^{-2}. Although Fossaria's distribution is not as widespread as that of Physella spp., it has become a dominant benthic organism in sites upstream of the Paria River.

Potamopyrgus has also been shown to be a invasive species capable of reaching high densities and dominating the benthic community where it becomes established (Hall and Dybdahl 2001). Other snail species have been recorded in the river in the last decade (Pomatiopsis and Physa) however, our study indicates these taxa have not been able to sustain a measurable population in the river.

We feel it is likely that molluscs were introduced into the Colorado River by waterfowl since it has been shown that waterfowl are capable of transporting aquatic invertebrates between habitats and they feed on aquatic snails (Swanson 1984, Gallagher 1993, Levri and Lively 1996). Over-wintering waterfowl have increased in abundance in the Lees Ferry area in

the last decade (Stevens et al. 1997) and may provide a good vector for importation of invertebrates. However, it is also possible that fishing and boating gear may act as vectors since some species (especially Potamopyrgus) can withstand periods of desiccation and their distribution matches the locations of popular recreational trout fisheries. The U.S. Fish and Wildlife Sevice lists the New Zealand Mudsnail as a nuisance exotic species (http://www.esg.montana.edu/aim/mollusca/nzms/).

Biotic interactions of snails with other invertebrates often result in domination of the aquatic community. Aquatic snails have been shown to be strong competitors with other aquatic invertebrates (Hawkins and Furnish 1987). Hawkins and Furnish (1987) reported that competition with other invertebrates was indirect and caused by the 'bulldozing' of periphyton as snails grazed. However, competition may be direct as well. In another study with the caddisfly Glossoma, which has scraping mouthparts similar to snails, McAuliffe (1984) showed that this feeding strategy can reduce periphyton resources to the point where other invertebrates cannot feed effectively. Both studies showed the effect of snails as the dominant grazer reduced the abundance of other grazers in the stream.

It is also likely that changes in discharge patterns and the phytobenthic community may have contributed to the takeover of the benthic community by snails. Changes in water quality, phytobenthic composition, and discharge patterns from Glen Canyon Dam all occurred in the mid 1990's (Benenati et al. 2000). Also, highest abundances of snails are associated with very steady flows during the 2000 low summer steady flow experiment. However, without further analysis and experimentation, we will not know what changes in environmental conditions allowed for the

domination of the benthic community in the Colorado River at Lees Ferry by Potamopyrgus spp.

Snails have been reported to exert control over the phytobenthic community through selective grazing. Tuchman and Stevenson (1991) showed that diatoms were enhanced compared to filamentous forms by removal of the attached filamentous overstory. In addition, Holomuzki and Hemphill (1996) showed that the snail Physella integra limited the growth of the filamentous algae Cladophora and promoted the growth of diatoms in grazing experiments. Hall and Dybdahl (2001) found that high biomass (> 25 $g \cdot m^{-2}$ AFDM) of Potamogyrus may be reducing total algal production in the Firehole River Wyoming. These effects may have severe implications for the Colorado River since the filamentous algae Cladophora glomerata is considered a keystone species of the phytobenthic community (Blinn et al. 1998).

It has been hypothesized that high densities of snails may alter the structure of lotic food webs (Hawkins and Furnish 1987). Since snails have become the dominant form of invertebrate standing mass there is the potential for disruption of energy flow from invertebrates to fish and riparian insectivores in the Colorado River. Snails do not often occur in the drift of the Colorado River nor do they have aerial stages. For fish like, rainbow trout (Onchorynchus mykiss) and humpback chub (Gila cypha) which feed on drifting invertebrates or riparian birds this means a reduction in the amount of available food. It is apparent that snails are not a preferred food of rainbow trout. Snails represented 10 fold less relative gut volume of rainbow trout from Lees Ferry compared to the amphipod Gammarus lacustris during 1997 (McKinney et al. 1999). Snails may only be available to fish which feed directly from benthic surfaces. Further

evidence that snails may not provide a good food source for fish is that even though trout densities in the Colorado River above Lees Ferry are extremely high (>200,000 fish, McKinney et al. 1999), snail populations remain high indicating that predation on snails has little effect on population densities.

Another possible effect of increased snail densities and changes in species composition is the spread of parasites. Aquatic snails are known to be hosts to Trematodes or liver flukes (Pennak 1989). Trematodes have complex life histories, requiring secondary hosts. While we could find no specific information on the parasites or secondary hosts associated with the Fossaria obrussa group of snail taxa, trematodes of snails are known to infect ruminant, avian, and fish hosts (Kaplan et al 1995, Levri and Lively 1996, Mitchell et al. 2000).

The increase in snail abundance and the consequent changes in the benthic community are likely to have far reaching effects on the Grand Canyon ecosystem. Subtle, non-lethal changes in the environment such as changes to temperature regimes and food resources have been implicated in the ability of organisms to maintain viable populations over the long-term (Vinson 2001). Because of this community shift we recommended that fish and avian monitoring programs pay specific attention to possible effects of decreased food availability and increased parasites in a variety of hosts. The rapid changes in the benthic community also emphasize the importance of continued monitoring of the benthic community composition since future species introductions coupled with unsteady environmental conditions will lead to further variability in community structure and function. We also reccomend that research aimed at determining the

availability of snails as a food resource for higher trophic levels and the effects on the benthic community be implemented.

Table 1. Taxa of Mollusca collected in the Colorado River between 1992 and 2002. Identifications were made by James Mead (JM) Laboratory of Quaternary Paleontology, Northern Arizona University, Jerry Landye (JL) U. S. Fish and Wildlife Service, New Mexico or David Richards (DR) Montana State

Bivalvia		
	Sphaeriidae	
	Pisidium casertanum	(JM)
	Pisidium walkeri	(JM)
Gastropoda		
	Physidae	
	Physella virgata	(JM)
	Physella heterostropha	(JM)
	Physella gyrina	(JM)
	Physa integra	(JL)
	Lymaeidae	
	Fossaria parva	(JM)
	Fossaria obrussa	(JM)
	Pomatiopsidae	
	Pomatiopsis lapidaria	(JM)
	Hydrobiidae	
	Potamopyrgus antipodarum	(DR)

Table 2. Presence of gastropod taxa in the Colorado River between Glen Canyon Dam and Diamond Creek from 1992 through 2001. * indicates that the taxa was present.

	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Physella spp.		*	*	*	*	*	*			*	
Physa integra	*		*								
Fossaria spp.				*			*	*	*	*	*
Pomatiopsis lapidaria				*							
Potamopyrgus antipodarum				*	*	*	*	*	*	*	*

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Chapter 9: Flow and benthic variability in the colorado river through Grand Canyon, Arizona, U.S.A.

ABSTRACT

Nonscouring flow increases have a significant impact on the benthic community structure in the Colorado River through Grand Canyon. Data logging velocity meters recorded flow reversals during the up-ramp of the daily fluctuation in flow for hydropower production. We developed a hydraulic metric, the discharge fluctuation factor (DFF), which was calculated from the maximum range in daily discharge for each month prior to collection. The DFF was evaluated with a 1997-1998 benthic data set, which was a period of contrasting flow regimes, and negatively correlated with biomass of Cladophora glomerata, other phytobenthic taxa, and macroinvertebrate biomass. Oscillatoria spp. and detritus were more related to velocity and slightly to depth. The DFF was also examined as a predictor of benthic biomass for the collection period of 1991-1999 (510 samples at four sites) and was determined to be correlated with C. glomerata and other phytobenthic taxa, but not macroinvertebrates. Sources of flow reversals and applicability to non-regulated rivers are discussed.

INTRODUCTION

Flow is the unifying abiotic factor in lotic ecology and has been identified as the single most influential structuring mechanism within aquatic communities (Statzner & Higler 1986). Filamentous periphyton biomass, composition, and morphology are affected by changes in flow (Grimm & Fisher 1989, Power 1992, Biggs & Close 1989). Biggs & Thomsen (1995) developed an experimental approach to better understand the relationship

between flow, sheer stress, filamentous algae, and diatom communities and concluded that some diatom taxa (adnate forms) are very resistant to high flows, while some filamentous algae are not. Macroinvertebrate composition, distribution, and abundance are also strongly influenced by hydraulic conditions (Statzner, Gore & Resh 1988;,Cobb, Galloway & Flannagan 1992), which in particular affect flow refugia (Lancaster & Hildew 1993).

Benthic response from spates has been the focus of many field investigations involving extreme flow affects and substrate movement (Power & Stewart 1987, Rempel et al. 1999). However, non-scouring changes in flow can also effect the behavior e.g. drift rates, feeding, case, and net building ability (Statzner et al. 1986) and distribution of aquatic animals (Imbert & Perry 2000). Impounded rivers regulated for hydropower production generally follow a predictable daily release pattern, and therefore provide an avenue to examine non-scour flow changes on benthic communities (Irvine & Henriques 1984, Gore et al. 1994).

Flow variability has been used by many investigators as a means of stream classification (Puckridge et al. 1998) or predictive modeling (Hawkins et al. 2000). Usually hydraulic metrics are developed from data collected while sampling the benthos or from long-term river gaging data sets. Hydraulic metrics that have been used in past investigations include discharge, water velocity, depth, and wetted perimeter data that were determined at the time of benthic collection and were used directly as a predictor treatment or in the calculation of flow types, including Reynolds number, Froude number, etc. (Rempel et al. 2000, Imbert & Perry 2000). A myriad of discharge metrics have been developed depending on the

hypothesis tested but they are usually calculated around flood-frequency, flow mean, flow maximum, flow minimum, and several estimates of variance of these statistics based on a chosen temporal scale. Puckridge et al. (1998) developed 23 such flow criteria ranging from multi-year mean annual flows to the variability of flow pulses and zero flows for 52 rivers throughout the world from arid, temperate, tropical, and polar climate regions.

In this investigation we analyzed a decade of typically non-scouring flow variability effects on the aquatic benthic community in the Colorado River below Glen Canyon Dam, Arizona. We wanted to evaluate the impact of daily flow fluctuations from hydropower production on the benthos and determine a hydraulic mechanism created by these variable flow patterns that may control the benthic structure. This information is discussed in terms of how non-scouring flow increases could affect both regulated and natural river benthic community structure.

METHODS

Study area

The benthic community in Colorado River below Glen Canyon Dam is governed by three abiotic factors: 1) fluctuating flows, 2) cool stenothermic river temperatures, and 3) turbid water (Shannon et al. 2001). These three elements have shaped an artificial aquatic community dominated by alien taxa. Glen Canyon Dam (GCD) is mandated to release a minimum of 142 $m^3 s^{-1}$ and a maximum of 708 $m^3 s^{-1}$, with allowable daily fluctuations of 142, 170, or 227 $m^3 s^{-1}$ depending on monthly water allotments and peaking power electrical demands. Hourly ramping rates can not exceed 112 $m^3 s^{-1}$ up and 43 $m^3 s^{-1}$ down. The daily hydrostatic

wave released from GCD is maintained through the entire 400 km reach to Lake Mead; the trough attenuates < 25% while the peak attenuates < 5%, because the narrow canyon walls of Glen, Marble, and Grand Canyon contain the wave (Webb et al. 1999).

Hypolimnetic releases from GCD average 10 ˚C year-round with a summer warming rate of 0.023˚C km^{-1} even when air temperatures exceed 35 ˚C (Benenati et al. 2000). This lack of thermal variability has selected for macroinvertebrates that do not need thermal cues to complete their development, and therefore common Ephemeroptera, Plecoptera, and Trichoptera taxa are not found within the study site, even though they do occupy side streams (Oberlin, Shannon & Blinn 1999).

Spates from tributaries increase the suspended sediment load within the river reducing overall benthic biomass due to abrasion and light attenuation with distance from GCD (Shaver et al. 1998, Wilson, Shannon and Blinn 1999). The arid Grand Canyon region retains many sedimentary strata that erode easily during late winter storms or summer monsoons. The Paria River (Fig. 1) can carry 780 g of sediment L^{-1} and release 2.75 10^6 tones of sediment annually (Andrews 1991) which is remarkable for a stream with a base flow of 0.08 m^3 s^{-1} (Oberlin et al. 1999).

Therefore the cool, fluctuating and occasionally turbid Colorado River has selected for benthic taxa that can tolerate these conditions. The phytobenthic assemblage has been dominated by Cladophora glomerata, but in recent years has been replaced by a mixed assemblage of macrophytes (Potamogeton pectinatus L., Elodea spp.), the bryophyte Fontinalis spp., the macro-alga Chara contraria and several taxa of filamentous algae (Rhodochorton spp., Batrachospermum spp., Ulothrix zonata, Mougeotia spp., Stigeoclonium spp., Oscillatoria spp, Tolypothrix spp.and

Enteromorpha intestinalis (Benenati et al. 2000). This phytobenthic assemblage is named MAMB (miscellaneous algae, macrophytes and bryophytes) for simplicity. Chromophyta are the most important constituents of the phytobenthic community and are sometimes dominated by aggregates of Cymbella spp. and Gomphonema spp. These epiphytic diatoms provide food for grazing macroinvertebrates (Blinn et al. 1998, Benenati et al. 2000).

Cladophora glomerata, MAMB, and associated diatoms support a macroinvertebrate assemblage consisting of Gammarus lacustris, various chironomid (Sublette, Stevens & Shannon 1998), Simuliium arcticum, gastropods (Physella spp., Fossaria obrussa), megadrile worms (Lumbricidae and Lumbricullidae), and oligochaetes (Naididae and Tubificidae) (Shannon et al. 2001). The chironomids, simuliids, and G. lacustris are nearctic in origin and demonstrate how the macroinvertebrates are selected for by the artificial conditions created by GCD (Sublette et al. 1998). Snails, G. lacustris and the chironomids comprise the largest percentage of the benthic biomass and they graze epilithic and epiphytic diatoms.

Benthic Collections

Phytobenthic and macroinvertebrate samples were collected from four sites in the Colorado River with a covered Hess substrate sampler so collections could be made at depths > 45 cm (Fig. 1). These sites bracketed the two largest tributaries, the Paria River at river kilometer (rkm) 2.8 and Little Colorado River (rkm 99.0). Duplicate samples were randomly taken along three transects set 30 m apart on each cobble bar (n=6) at the greatest depth possible. Collections were taken in February, March, June, August,

October of 1997, and January and March of 1998. Samples were placed on ice and processed live within 24 h of collection into the following biotic categories; macroinvertebrates, C. glomerata, detritus, and MAMB. These samples were oven-dried, weighed to the nearest µg and converted to ash-free dry mass (AFDM) estimates from regression analysis for each category ($p<0.001$; $R^2>0.85$; $n=325$). Macroinvertebrates were also numerated for G. lacustris, chironomids, simuliids, tubificids, lumbriculids, gastropods, and any other taxa encountered.

Physical data measured at the time of collection include depth, water velocity taken with a Marsh-McBirney electronic flow meter, and Secchi depth. During the June 1999 collection trip we deployed a Marsh McBirney Flo-Tote II™ data logging flow and depth meter at each camp site for a 10 - 12 h collection period at 5 min-intervals. This information gave us a range of water velocity, depth and discharge values at various cobble bars throughout the study site. The Flo-Tote II was also deployed in September 2000 at Lees Ferry for 5 days to evaluate steady 227 $m^3 s^{-1}$ flows from GCD.

Light intensity (Lumens/0.1 m^2) was continuously monitored during the collection period with HOBO™ data loggers adjacent to the collection sites. Three light sensors were is used to quantify light intensity as a surrogate for turbidity. One sensor was secured on land as a control for ambient light and two were attached to a weighted chain, one 50 cm above and the other 50 cm below the 227 $m^3 s^{-1}$ stage. These arrangements allowed for data collection within all ranges of dam operations. These light intensity data were reduced to ranked data by calculating the mean for each 55-60-d period prior to benthic collections. This was done by averaging the daily peak light intensity from all three sensors and

determining the percentage of light intensity at each depth for that day, which were in turn was averaged for a depth integrated value to the nearest 10%.

Flow Metric

Discharge values from the Untied States Geological Survey gauging station (09380000) at Lees Ferry, Arizona were used for a direct value at the time of collection and for calculating a flow metric (Fig. 2). A discharge fluctuation factor (DFF) was calculated from the maximum range in daily discharge for each month prior to collection. For example, if the daily flows during a month were fluctuating between 300 and 500 $m^3 s^{-1}$ but on the second Sunday of the month the minimum flow went to 200 $m^3 s^{-1}$ then the DFF would be 300. Low Sunday flows are routine because of reduced electrical demand.

Phytobenthic Observer

We constructed a heavy submersible sled referred to as the Phytobenthic Observer (PBO), that could withstand large flow and stage changes that commonly occur within the study site in order to delineate the physical changes caused by fluctuating flows (Fig 3). The PBO was made of plate steel 2.5 cm thick and 30 cm wide, in a U-shaped configuration (50 cm x 100 cm) and weighed 110 kg. Attached to it was a McBirney Flo-Tote II™ data logging flow and depth meter, light intensity (Lumens/0.1 m^2), and water temperature (˚C) HOBO™ data loggers.

The PBO was deployed from 15 January to 15 February 2000 on a cobble bar near Lees Ferry and benthic collections were made at the time of deployment and retrieval. January was a peak volume month and

February flows were reduced by 30%, which allowed us to experimently test the DFF metric. Benthic collections (n=12) for comparison between monthly flow regimes were made by scraping the phytobenthos within a circular template (20 cm^2) placed on cobbles which were randomly collected at the same depth as the PBO. Samples were placed on ice and processed as described above within 24 h. Maximum phytobenthic filament length was also measured to the nearest cm during each collection. Turbulence was calculated with Reynolds Numbers (R_e), as defined by $R_e = U L' / \underline{v}$, where U is the velocity, L´ is water depth and $\underline{v}$ is kinematic water viscosity (1.31×10^{-5} Ns/m^2) at 10˚C (Smith, 1992)

Decade evaluation of DFF metric

We wanted to evaluate if the DFF would be a good predictor of the following months benthic collection, so we merged benthic and DFF data from 1991 through June 2000 from the four sites already discussed (n=85; Fig. 1). Operations of GCD have gone through several phases during the 1990's with daily flows ranging from 142 - 935 $m^3 s^{-1}$ to essentially steady flows of 560 $m^3 s^{-1}$ in response to the run-off into Lake Powell and management policy changes (Benenati et al. 2000). Benthic collection and processing protocols were the same for this DFF evaluation and those described above, expect that light intensity data were not collected.

Statistical Analysis

Principal Components Analysis (PCA) of physical and biotic variables were used to evaluate correlations during the 1997 - 1998 collection period. All data were logarithmically transformed [ln (x+1)]. Differences in biotic

components between PBO deployment and retrieval was examined with an Independent Student-T Test.

The ability of the DFF metric to predict the biomass of biotic variables in the following months benthic collection was assessed with step-wise multiple regression analysis. Mean biotic data, n=1 instead of n=6 for each site, were not transformed so the results would be conservative. Biotic variables included C. glomerata, MAMB, and macroinvertebrate biomass estimates because the PCA indicated these three variables were related to the DFF while detritus and Oscillatoria spp. were not. All analyses were performed with SYSTAT ver. 5.2.1 software (SYSTAT Inc., 1992).

RESULTS AND DISCUSSION

1997-1998 DFF Evaluation

Cladophora glomerata, MAMB, and macroinvertebrate biomass are correlated with DFF and light intensity while Oscillatoria spp. and detritus biomass are more related to velocity and slightly to depth (Fig. 4). PCA factor 1 explains 25% of the variance and depicts the lack of relationship between DFF, associated biotic estimates, and site as indicated by kilometer. PCA factor 2 explains 16% of the variance and primarily illustrates that collection trip and discharge at the time of collection are negatively related. These results provide evidence that the DFF is a good predictor of benthic biomass and of similar magnitude as light intensity, which has been proven to a strong factor structuring the aquatic community within the study site (Blinn et al. 1998).

Rempel et al. (2000) evaluated seven hydraulic measures on the Fraser River in Canada, a large gravel-bed river (mean annual flow 2900

$m^3 s^{-1}$), and determined that hydraulic conditions represent a major gradient for benthic structuring along with substratum type and organic matter distribution. These data further support the pattern of reduced DFF resulting in an increase in C. glomerata, MAMB, and macroinvertebrate biomass in the Colorado River (Fig. 5).

Peak phytobenthic biomass occurred in June and August 1997 following the lowest DFF during the collection period, indicating an inverse relationship (Table 1; Fig. 5). This biomass pattern occurred at the end of a period of high flows with relatively little daily fluctuations, followed by a 3-d period of 227 $m^3 s^{-1}$ flows for assessment of beach size via aerial photography, which in turn was followed by high flows with daily fluctuations. Three days of 792 $m^3 s^{-1}$ in early November, in an effort to store sand in the channel margins, added more complexity to the hydrograph (Fig. 2). Cladophora glomerata responded positively to high flows and low DFF, increasing by 11.2 g AFDM m^{-2} between February and August 1997 (Fig. 4). Conversely, MAMB dropped 33.4 g AFDM m^{-2} biomass during the same period. Benenati et al. (2000) reported that MAMB is less tolerant than C. glomerata to extreme releases (1275 $m^3 s^{-1}$), and MAMB was still the dominate phytobenthic assemblage for this collection period. Neither phytobenthic component recovered to June 1997 levels by June 1998. Macroinvertebrate biomass estimates followed a similar pattern as the C. glomerata biomass, peaking at ~ 4.3 g AFDM m^{-2} in June and August, probably because C. glomerata provides both flow refugia and epiphytic diatoms for food (Shannon et al, 1994).

DFF Mechanism

Velocity information gathered in June 1999 with the data logger indicated that the mechanism for the DFF as a predictor of biomass could be flow reversals during up-ramp or rising limb of the daily flow fluctuation. At sites where the flow increased during the night, the flow data were negative or reversed 62% of the time while data collected during the down ramp of the daily fluctuation were reversed 18% of the time. This mechanism was further tested in September of 2000 during steady 227 $m^3 s^{-1}$ flows for 6-d where the flows never reversed and averaged 0.21 $m^3 s^{-1}$ (±0.03 SD). Gore et al. (1994) reported that up-ramping for hydro-power on the Caney Fork River in Tennessee had greater hydraulic instability and maximum shear stress than the steady peak flows. Imbert & Perry (2000) also reported that abrupt increases in flows within experimental flumes increased drift and that repeated increases would negatively impact the benthos.

Through the use of the PBO we found that a significant decrease in MAMB biomass occurred, while C. glomerata increased with a lower DFF (Table 2). Reduced discharge from GCD between January and February 2000 resulted in a 16% reduction in daily maximum flow, with the minimum depth (1.17 m) at PBO location, the maximum depth in February. This flow reduction also resulted in an 81% reduction in maximum water velocity, a 40% decrease in the DFF and R_e 75% lower in February than January (Table 2). Cladophora glomerata biomass increased significantly, 10-fold within 30 d, while light intensity remained similar between months. Reducing flow and depth variability results in a steady light regime thereby stimulating C. glomerata growth. However, MAMB biomass decreased significantly, 33% between collections (Table 2).

Filament length did not change between collections. Macroinvertebrate biomass increased 28% but was not statistically different between deployment and retrieval estimates. The addition of underwater video-photography, and computer assisted measurements of the benthos will greatly improve the utility of the PBO while allowing for "event" based or long-term monitoring

The Colorado River through Grand Canyon is a medium-large size river that is canyon bound with highly variable geomorphology and numerous debris fans, which result in a highly complex river channel (Webb et al 1999). This type of river channel coupled with mercurial flows result in turbulent conditions with high Reynolds numbers (Table 3). Rubin and McDonald (1995) investigated eddy pulsations within Grand Canyon in an effort to better understand sand transport and reported mid-channel flow reversals associated with periodic vortex shedding associated with debris fan. This information supports our concept of flow reversals occurring within the study site particularly on cobble bars where channel complexity is high.

Decade evaluation of DFF metric

Discharge fluctuation factor was significantly and negatively correlated with the benthic biomass of *Cladophora glomerata* and MAMB biomass, but not with macroinvertebrate biomass, for 85 collections between 1991 and 1999 (Table 3). These results further support that the DFF metric is a good predictor of phytobenthic biomass in the Colorado River below GCD over a wide range of flows (141 - 935 $m^3 s^{-1}$) and ramping rates. This investigation also illustrates the important role that non-scouring increases in flow can have in structuring benthic communities.

Macroinvertebrate biomass did not exhibit a predictable relationship with DFF when examined over the 1991 - 1999 collection period (Table 3). This may be a result of combining macroinvertebrate feeding guilds and niche types. Grazers such as G. lacustris and many taxa of chironomids, are closely associated with the phytobenthos while simuliids, oligochaetes and gastropods are not. Additionally, detrital biomass is more related to depth and water velocity at the time of collection than the DFF (Fig. 4), which could also be related to macroinvertebrate biomass.

CONCLUSIONS

We determined that non-scouring increases in flow can have an adverse effect on the benthic community in the Colorado River below Glen Canyon Dam. The Phytobenthic Observer (PBO) allowed us to determine that the probable mechanisms were flow reversals occurring during the daily up-ramp for production of hydro-power. The Discharge Fluctuation Factor (DFF) and subsequent flow reversals in the Colorado River through Grand Canyon suggest that increases in flow in unregulated streams may be an important factor in stream organization. Nonscouring increases in flow, from small tributary spates or localized storms could have disproportionate effects especially on streams with complex channels.

Table 1. Summary of daily flow variables and discharge fluctuation factor (DFF) for the month preceding benthic collections during 1997-1998. Statistics include; m=mean, sd=standard deviation, and coefficient of variance=cv.

Collection Month and Year		Discharge Maximum ($m^3 s^{-1}$)	Discharge Minimum ($m^3 s^{-1}$)	DFF Metric ($m^3 s^{-1}$)
January 1997		570	441	215
	m	551	328	
	sd	22	34	
	cv	0.04	0.08	
February 1997		764	464	198
	m	644	612	
	sd	98	111	
	cv	0.15	0.18	
June 1997		617	543	51
	m	603	580	
	sd	6.8	11	
	cv	0.01	0.02	
August 1997		632	563	62
	m	603	599	
	sd	7	42	
	cv	0.01	0.07	
October 1997		677	228	383
	m	609	469	
	sd	81	66	
	cv	0.13	0.14	
January 1997		639	450	152
	m	619	517	
	sd	19	23	
	cv	0.03	0.04	
March 1998		600	430	182
	m	600	472	
	sd	28	18	
	cv	0.05	0.04	
May 1998		540	200	274
	m	479	317	
	sd	64	31	
	cv	0.13	0.10	

Table 2. Physical and benthic data from Phytobenthic Observer deployment during January and February 2000. Benthic data, light intensity and river temperature data are means (± SE).

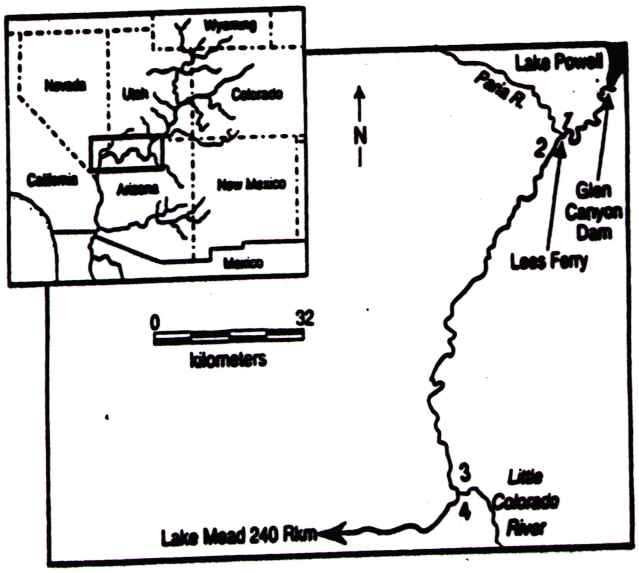
Physical Data	January 15-31	February 1-16
Discharge ($m^3 s^{-1}$)		
Maximum	467	392
Minimum	281	234
Depth (m)		
Maximum	1.28	1.17
Minimum	1.17	1.05
Velocity ($m s^{-1}$)		
Maximum	+0.47	+0.09
Minimum	-0.84	-0.23
DFF Metric ($m^3 s^{-1}$)	186	113
R_e		
Maximum	750,229	184,351
Minimum	459,237	80,381
Light intensity (Lumens/0.1 m^2)		
Underwater	193.5 (16.6)	273.0 (40.0)
Terrestrial	625.4 (55.5)	607.6 (70.4)
Temperature (˚C)	10.1 (0.09)	9.6 (0.05)

Benthic Data	Deployment 15 January	Retrieval 16 February	Probability
C. glomerata (mg AFDM m^{-2})	17.0 (2.1)	200.0 (42.5)	$p < 0.01$
MAMB (mg AFDM m^{-2})	370.0 (35.0)	250.0 (80.2)	$p < 0.01$
Macroinvertebrates (mg AFDM m^{-2})	10.1 (2.7)	14.0 (1.9)	$p = 0.06$
Filament length (cm)	11.0 (1.5)	11.2 (5.8)	$p = 0.18$

Table 3. Results of step-wise multiple regression between benthic collections (g AFDM m^{-2}) and the discharge fluctuation factor (DFF) metric at four sites in the Colorado River below Glen Canyon Dam between 1991 and 1999. Miscellaneous algae, macrophytes, and bryophytes are abbreviated by MAMB.

Source	Variable	Coefficient	Probability	Standard error of estimate
DFF	Macroinvertebrates	0.94	0.78	
	Cladophora glomerata	-1.13	0.02	0.51
	MAMB	-1.42	0.01	0.56
	Constant	210.31		

Analysis of variance: $F_{(2,75)} = 6.0$; $p = 0.004$; multiple $R^2 = 18.5$



Legend

Site	Name	rkm
1	Lees Ferry	0.8
2	Two-Mile Wash	3.1
3	Little Colorado River Island	98.6
4	Tanner Canyon	109.6

Figure 1. Collection sites in the Colorado River below the Glen Canyon Dam through Grand Canyon National Park, Arizona. Lees Ferry is designated river kilometer 0.0 (rkm) and Glen Canyon dam is located 23.2 km up-river.

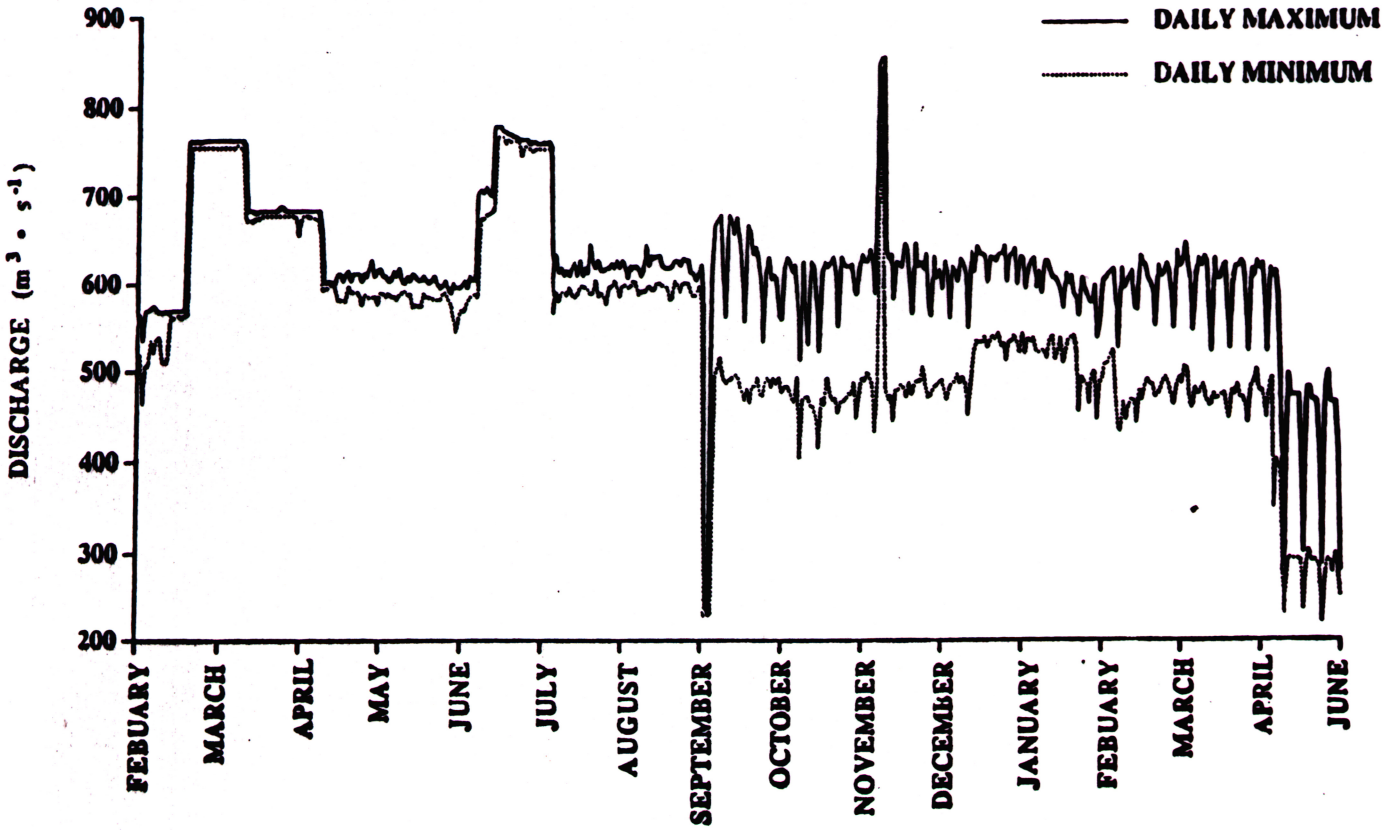


Figure 2. Daily maximum and daily minimum discharge (m^3 s^{-1}) from the Lees Ferry gaging station on the Colorado River, Arizona.

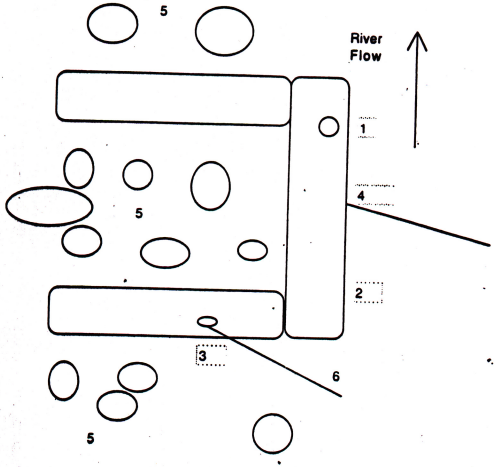


Figure 3. Diagram of Phytobenthic Observer. The PBO was made of plate steel, 2.5 cm thick and 30 cm wide, with an overall dimension of 50 cm x 100 cm and it weighed 110 kg. Legend: thermistor (1), light intensity meter (2), velocity/depth sensor (3), chain to shore (4), river cobbles (5), cable to data logger on shore (6).

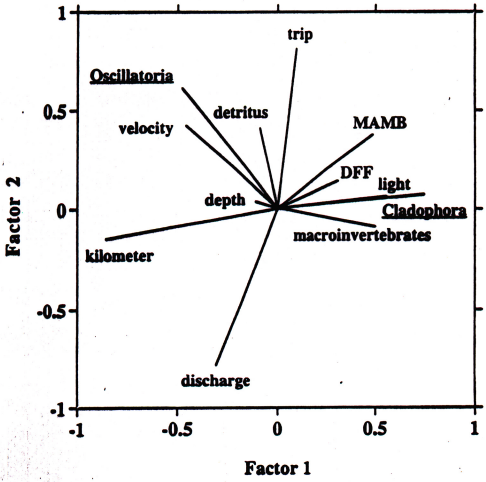


Figure 4. Results of Principal Components Analysis (PCA) of physical and biotic variables that were used to evaluate correlations during the 1997 - 1998 collection period.

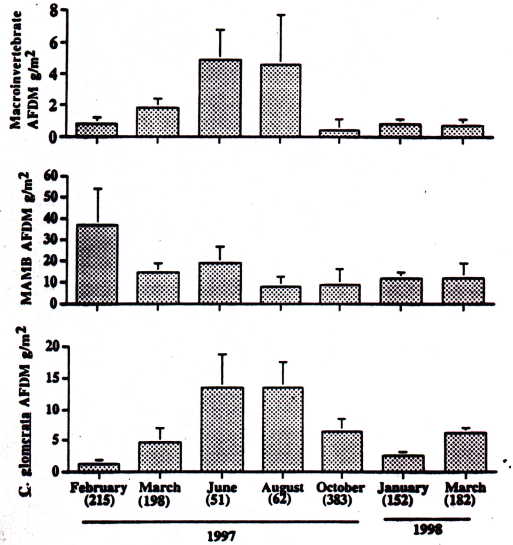


Figure 5. Average benthic biomass estimates from four sites in the Colorado River through Grand Canyon from February 1997 through June 1998. See Figure 1 for site locations. MAMB stands for miscellaneous algae, macrophytes and bryophytes. Numbers under each month are the discharge fluctuation factors for the preceding month.

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Chapter 10 Gammarus survivorship on Cladophora vs. Oscillatoria habitats; an in-situ experiment

INTRODUCTION

Riverine ecosystems below hydroelectric dams experience profound changes due to the effects of flow regulation which include varying discharge patterns and impounded sediment and organic matter. Downstream biota are often subject to the detrimental effects of flow regulation for the purpose of electricity production. Fluctuating discharge regimes result in periodic short- and long-term exposure and desiccation of both zoo- and phytobenthos due to the effects of dewatering and ultraviolet light (Stanford and Hauer 1992, Ward and Stanford 1979). Benthic communities below dams often show depleted species diversity, density, or biomass in varial zones subject to periodic stranding and desiccation (Fisher and La Voy 1972, Hardwick et al. 1992, Blinn et al. 1995, Humphries et al. 1996, Benenati et al. 1998).

The carbon source of the aquatic food web in the Colorado River below Glen Canyon Dam (GCD) has changed from an allochthonous-based (upland wood and detritus) source prior to the construction of Glen Canyon Dam to an autochthonous (benthic algae) source due to river impoundment and sunlight penetration (Flowers 1959, Blinn and Cole 1991, Haden 1997). Because the upland carbon source is trapped behind GCD, the Colorado River ecosystem must rely on the growth of benthic algae to support higher trophic levels including invertebrates, waterfowl, riparian insectivores, and birds of prey (Brown et al. 1987, Blinn and Cole 1991, Stevens et al. 1997).

The filamentous green alga, Cladophora glomerata, has dominated the phytobenthos in the Colorado River below GCD since its completion in 1963 (Czarnecki et al. 1976, Mullan et al. 1976, Blinn et al. 1989) and is also common in other tailwater communities within and outside the Colorado River basin (Ward 1976, Lowe 1979, Skulberg 1984). Cladophora is considered a keystone algal species in the Colorado River below GCD due to its role in supporting higher trophic levels. The multibranched, mucilage-free filaments of Cladophora have a large surface area to serve as a structural host for epiphytic diatoms, a primary food source for invertebrates, dominated by the amphipod Gammarus lacustris and various chironomid species (e.g. Cricotopus annulator, C. globistylus; Sublette et al. 1998). Cladophora also serves as a refugium from river currents and predation for both macroinvertebrates and fishes and as an important food host for fish due to high associated macroinvertebrate density (Dodds 1990, Hardwick et al. 1992, Shannon et al. 1994, Blinn et al. 1995, Blinn et al. 1998, Benenati et al. 2000).

Cladophora is successful in flowing environments due to characteristics that include a branching habit, thick cell walls, and strong rhizoidal holdfasts which also help survival in tailwater conditions of changing water volume and velocity (Dodds 1991, Dodds and Gudder 1992). Although Cladophora has adaptations that can support survival under occasional submergence and emersion cycles, large quantities are removed and washed downstream from the varial zone due to daily fluctuating water levels associated with GCD operations (Blinn et al. 1995, Benenati et al. 1998). Atmospheric exposures of only 10 h can result in a 43% decrease in the chlorophyll a of Cladophora (Angradi and Kubly 1993). Blinn et al. (1995) reported a >60% reduction in Cladophora and

epiphyton biomass in the varial zone after 5 consecutive days of 12-h exposures and a 4-fold reduction in invertebrate biomass than that in the permanently submerged channel of the Colorado River.

Replacement of Cladophora is restricted due to suppressed zoospore reproduction in the cold (9-11°C) Colorado River and slow recolonization processes which are dependent on drifting fragments or re-growth of basal holdfast cells and adversely affected by discharge patterns (Blinn et al. 1995, Shaver et al. 1997, Benenati et al. 2000). Therefore, continuous losses of Cladophora biomass with limited replacement may have serious consequences in the Colorado River ecosystem for higher trophic levels. In contrast to the submerged channel with principal constituents of Cladophora and other green filamentous algae, the cobbles in the intermittently dry varial zone are covered by the crustose cyanobacteria, Oscillatoria. The silt-filament matrix characteristic of Oscillatoria can trap and hold moisture allowing survival and growth in marginal conditions that may not be tolerated by Cladophora or other algal types. While Oscillatoria is highly adapted and successful under varial zone conditions, we have found productivity to be significantly decreased in this zone (Hardwick et al. 1992, Shaver et al. 1997, Benenati et al. 1998). The replacement of Cladophora with Oscillatoria due to variable discharge regimes would result in a dramatic loss of algal and macroinvertebrate food base. Oscillatoria provides a poor substrate for diatoms and macroinvertebrates due to its reduced surace area and exposed location. Moreover, Oscillatoria spp. contributes less potential energy (4405 kcal · g AFDM; ± 340) than Cladophora (5170 kcal · g AFDM; ± 580) or diatoms (5470 kcal · g AFDM; ± 160) (Cummins and Wuycheck, 1971). Stevens et al. (1997) found only 34 total organisms on cobble bars within the Oscillatoria

dominated varial zone in 396 bi-monthly Hess samples throughout 363 km of the Colorado River in 1991 as compared to 3,860 total organisms collected on cobble bars in the Cladophora dominated submerged zone below baseflow (≤ 142 m^3/s). Although there were >100-fold more animals found in Cladophora, these numbers are substantially reduced from subsequent samples (Shannon et al. 1996, Shaver et al. 1998) due to highly variable flows (± 750 m^3/s) that occurred during 1991. Therefore, Oscillatoria spp. has little trophic significance in the Colorado River compared to Cladophora, even though it is the dominant alga in the varial zone.

Previous studies have repeatedly shown that Cladophora provides a superior habitat for both epiphyton and invertebrates over Oscillatoria and other filamentous algae (Blinn and Cole 1991, Blinn et al. 1992, Angradi 1994, Shannon 1994, Ayers and McKinney 1998, Benenati et al. 1998, Shannon et al. 1998, Benenati et al. 2000). In light of these findings our objective for this study was to test the suitability of the Cladophora versus the Oscillatoria habitat by comparing survivorship of Gammarus lacustris between these two habitats after a period of one month in-situ incubation in enclosures.

METHODS

This study was conducted in the Colorado River below Glen Canyon Dam at a site 4.8 km upstream of Lees Ferry on river right that was undisturbed by fishing and boating activities (Figure 1). The site was chosen for its low disturbance level, nearness to shore, and moderate current velocity (0.18 - 0.40 m/s) to facilitate experiment monitoring.

Thirty enclosures were constructed using plastic crates (20 x 17 x15 cm) with a base area of 340 cm^2. The crates were lined with 600 µm mesh nylon nitex which was attached with waterproof aquarium silicone sealant and zip ties. The enclosures were divided into two treatments of 15: one treatment to contain Cladophora-covered cobbles lining the bottom of the crates and the other treatment to contain Oscillatoria-covered cobbles. Enclosures were bolted to boards (183 cm length; 5 enclosures / board) leaving a 16 cm space between each one to facilitate current flow and drift removal during the incubation period. A 'V' shaped deflecter was attached to the upstream end of each board for the purpose of moving the flow of drift material away from the enclosures. A length of chicken wire was nailed to the bottom of each board upon which to place rocks to secure the boards on the river bottom.

Gammarus lacustris were collected from the Colorado River, measured, and counted in order to have 600 Gammarus of the same length (5.8 mm; SE 0.06) with 20 / enclosure. The selection of 20 Gammarus / 340 cm^2 enclosure area was based on means of the Aquatic Food Base Project Colorado River collections from 1990 - 1999 (19 / 340 cm^2; SE 0.3). Treatment enclosures of Cladophora or Oscillatoria were randomly placed on the boards.

The boards with enclosures were placed on the river bottom using SCUBA 40 cm apart in a lengthwise direction that was parallel to downstream flow. Twice weekly enclosures were monitored and drifting material was brushed off the outsides during the incubation period. At the end of one month the enclosures were pulled out of the river, Gammarus were collected from each enclosure noting dead versus live amphipods, then deposited into separate corresponding containers which were placed

on ice for transport to Northern Arizona University Aquatics Lab for immediate processing.

Lab processing included sacrificing Gammarus with sodium bicarbonate tablets, measuring body length, drying (60°C for 48 h), and ashing (500°C for 1 h) to obtain ash-free dry mass (AFDM).

RESULTS

Gammarus significantly ($p < 0.001$) increased in overall length during the one- month incubation in both treatments. However, Gammarus in the Cladophora treatment had a greater increase over those in Oscillatoria (+1.94 mm; SE 0.18 vs +1.68 ; SE 0.20, respectively).

The difference in AFDM and length increases between the treatments was non-significant ($p > 0.30$). However, survivorship of Gammarus was significantly ($p < 0.001$) higher in the Cladophora enclosures compared to the Oscillatoria enclosures (55% vs 40%) (Figure 2). Also, at the end of the incubation period Gammarus were physically missing or decomposed from the Cladophora and Oscillatoria enclosures (113 vs 130, respectively).

DISCUSSION

Based on survivorship, this study showed Cladophora to be a better habitat for Gammarus than Oscillatoria. Although data analyses from 10 years of study have repeatedly demonstrated Cladophora to be a superior habitat for macroinvertebrates, this experiment design failed to provide us with more definitive data.

Studies attempting to duplicate specific habitats and conditions in the channel of the Colorado River tend to be risky and problematic due to the

dynamic conditions of the substrate in the riverbed. We found substantial algal drift and sediment accumulation over time in the study site and in the enclosures. This may be related to selection of the study site with moderate water velocity to facilitate access to enclosures. Regular cleaning helped mitigate the drift, but could not remove the sediment build-up inside the enclosures. Gammarus lacustris and other macroinvertebrates have been found to be significantly reduced in the benthos when associated with sediments in river systems (Rosenberg and Weins 1978, Shaver et al. 1997).

Improvements in experimental design should allow longer incubation time, prevent problems with substrate changes, and provide more definitive results. We recommend future experiments of this type to employ enclosures that are suspended in the water column, attached to a floating frame, and anchored to shore or a buoy. This method has been used in past experiments with success (Blinn et al. 1995).

Without placing value judgements on pre-versus post-dam food webs (Schmidt et al. 1998), the authors point out continued study and conservation of the existing downstream aquatic food base is linked to higher trophic levels and ultimately tied to native fish and other endangered vertebrates that frequent Grand Canyon.

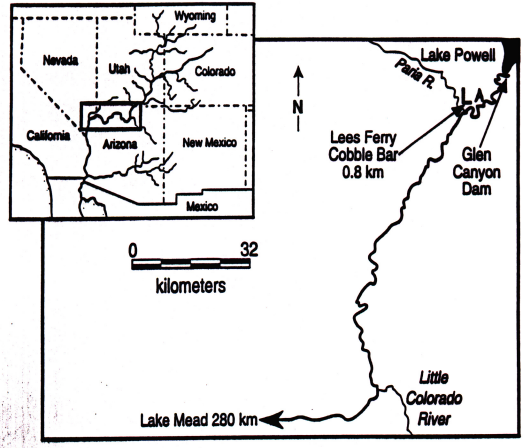

Figure 1. Map showing the region of the Colorado River, Glen Canyon Dam, and Lake Powell. The study site in Glen Canyon Dam tailwaters is 4.8 km upstream of Lees Ferry on river right and designated on the map with the letter "A".

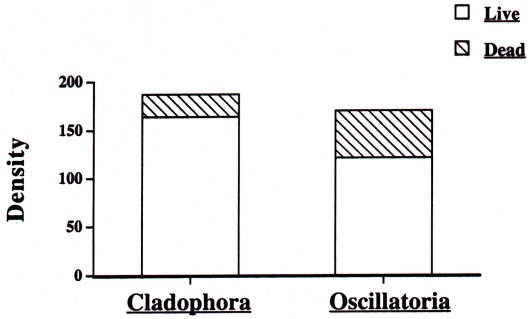

Figure 2. Densities of live and dead Gammarus lacustris in the Cladophora and Oscillatoria habitats from the experimental enclosures at the end of one month incubation. Initial start-up densities of Gammarus lacustris were 300 in each habitat.

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Chapter 11: Food Web Construction and Variability in Colorado River Through Grand Canyon - Management Considerations.

This technical reports described the magnitude of variability within the aquatic community of the Colorado River below Glen Canyon Dam (GCD). Variability ranged from large scale changes such as daily-doubling of discharge to the micro-habitat distribution of epiphytic diatoms and their chemical exudates.

Dual stable isotope analysis revealed an aquatic food web that varied in carbon signal with distance from GCD (see Shannon et al. 2002 for methods). We split the study site into two sections, above and below the Little Colorado River, to illustrate this carbon variance (Fig. 1). Although the energy flow from algae to macroinvertebrates to fish follows the same pathway the carbon source is more enriched relative to the up-stream $\delta^{13}C$ measurements. These data indicate that the Glen Canyon tailwaters reach does not "feed" the down river community that managers often like to discuss so they can manage for the profitable tailwater fishery.

This food web defines the importance of the post-GCD aquatic food base in order to sustain the fish community. Several investigations of native fish stomach contents have indicated that terrestrial arthropods comprise between 0 and 40% of the food items (Hoffnagle et al., 1999). This is contrary to the stable isotope data gathered in this investigation (Fig. 1). The mean-standard error box for terrestrial invertebrates indicates that these organisms could contribute to the carbon source for fish due to their relative vertical position, but the $\delta^{15}N$ measurements are too low. Usually a trophic level is defined by an increase of 1-3 $\delta^{15}N$ between trophic levels (Petersen 1999). In this study we measured a trophic

difference of between 6.3 and 8.8 $\delta^{15}N$. This range in $\delta^{15}N$ would mean that the fish in the study site have very different ^{15}N discrimination processes from all other $\delta^{15}N$ studies or that the fish do not assimilate ingested terrestrial arthropods. Fish in the Colorado River below GCD probably obtain an insignificant amount of sustenance from terrestrial arthropods.

Benthic variability translates into an uncertain energy source for fish (Fig. 2). Comparing the amount of benthic energy available on the Little Colorado River island sampling site (98.6 rkm) between June 1991 and 1996 with varying discharge fluctuation factors (DFF) resulted in 82% more potential fish biomass in 1996 than 1991. This collection site is located within the critical habitat of the humpback chub (Gila cypha) as designated by the United States Fish and Wildlife Service (USDI 1995) and illustrates the need for a more stable food base. Wetted perimeter and therefore area of benthic colonization also varied between collection years due to GCD operations from 5,165 m^2 in 1991 to 39,456 m^2 in 1996 or an seven-fold increase in 1996. Area estimates were made from 1:2400 scaled aerial photographs (Pers. Comm., Mr. Steve Meitz, Grand Canyon Monitoring and Research Center, Flagstaff, AZ). Energy calculations were based on caloric estimates from Blinn et al. (1995) with a 70% assimilation efficiency (Philips and Brockway 1959) and 15 MJ of digestible energy for each kg of fish biomass (Cho 1992). Both of these collections were during periods of low turbidity which is typical for spring in northern Arizona due to stationary high pressure located over the “four-corners” region resulting in little precipitation.

It is evident from these benthic energy to fish biomass estimates (Fig. 2) that the operation of GCD has a strong negative influence on the aquatic

community. The DFF is good predictor of benthic biomass on a monthly scale which results in high spatial (m^2) variability and high temporal variability on a seasonal, yearly and decadal scale (See chapter 10). Although the Environmental Impact Statement of Glen Canyon Dam (USDI 1995) mandated reduced fluctuations these flows remain too radical for a healthy river ecosystem. Freeman et al. (2001) compared an unregulated reach of the Tallapoosa River to a reach subjected to peaking-hydropower regulation similar to GCD and reported that stable habitat conditions are vital to the reproduction and young of the year survival of native fish.

Milner et al. (2000) examined newly formed streams resulting from glacial recession in Glacier Bay National Park, 36 - 1377 years in existence. This study is pertinent to the Colorado River below GCD because it is a “new” (< 40 y old) river since GCD was built, both have similar thermal regimes, and they share many of the same invertebrate taxa as the streams in Milner et al. (2000). Habitat stability and gradient were two significant variables in predicting invertebrate and fish density. Macroinvertebrate diversity was also positively linked with habitat stability in the Glacier Bay study, so the lack of taxa richness (Shannon et al. 2001) in Grand Canyon could also be related to GCD operations and habitat instability.

In conclusion, state and federal agencies responsible for the operation of GCD need to re-evaluate the current mandates and criteria for GCD discharges so that native fish can persist in a healthy river. Ricciardi and Rasmussen (1999) reported extinction rates for native fish in North America were 1000 times greater this century (40 out of 1061 fishes) than the historical background rate. River modification is the leading cause.

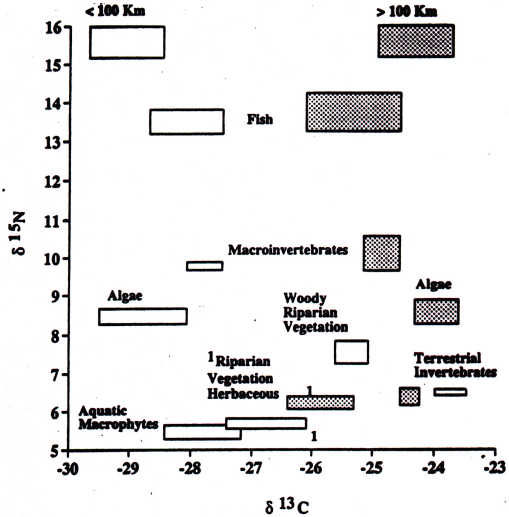
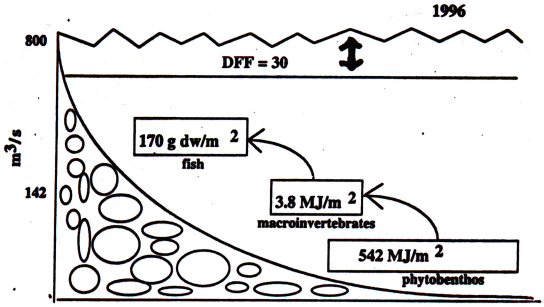


Figure 1. Dual isotope plot ($\delta^{13}C$ and $\delta^{15}N$) for the sectioned food web of the Colorado River through Grand Canyon National Park. The center of each box is the average $\delta^{13}C$ and $\delta^{15}N$ value and box size represents the standard error. Clear boxes indicate data collected in the upper 100 km and grey boxes indicate data collected from sites in the lower 100 km. 1 indicates riparian vegetation herbaceous.



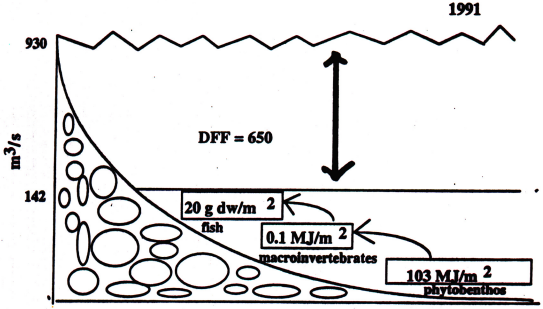


Figure 2. Benthic energy (MJ/m2) to potential fish biomass (g dw/m2) estimated at the Little Colorado River cobble bar (rkm 98.6) in the Colorado River, Grand Canyon for June 1991 and 1996. DFF is the discharge fluctuation factor.

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APPENDICES

These data are available in tabular in META-DATA/ASCII and SYSTAT format in ASCII through the Information Technology Department at the Grand Canyon Monitoring and Research Center, Flagstaff, Arizona.