Drifting Fine Particulate Organic Matter below Glen Canyon Dam in the Colorado River, Arizona

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ABSTRACT

The concentration and composition of drifting fine particulate organic matter (FPOM) in regulated rivers may be influenced by dam operations and site of collection within the river channel. We examined FPOM composition and biomass in the Colorado River, Arizona below Glen Canyon Dam along a 350 km reach during 15 collection trips over four years. Lotic zooplankton and detritus components were positively correlated with distance downriver from the dam, increased discharge, and near-shore habitats versus mid-channel locations. Lentic zooplankton also increased at higher discharges and in near-shore habitats but was negatively correlated with distance downriver. There is evidence the near-shore habitat provides a more stable environment than the mainstem for invertebrates which may enhance rearing and development of lentic zooplankton.

INTRODUCTION

Studies of drift in river and stream ecosystems indicate that coarse particulate organic matter (CPOM; >1mm) becomes fine particulate organic matter (FPOM; <1mm) as it travels downriver and is subject to biological, physical, and chemical processing (Vannote et al. 1980, Cushing et al. 1993, Shannon et al. 1996). The FPOM consists of living and dead animals, plants, and microorganisms, which provide an important food source in lotic ecosystems (Lieberman and Burke 1993, Wotton 1994). The concentration and composition of FPOM in regulated rivers are influenced by impoundment and dam operations, resulting in variable food availability for invertebrate and vertebrate fauna in these systems (Petts 1984, Angradi 1994).

The importance of zooplankton in FPOM is often overlooked as investigators examine total FPOM patterns in river systems (Lieberman and Burke 1993, Angradi and Kubly 1994), perhaps under the assumption that these organisms are absent in headwaters and mid-reaches of streams and rivers (Vannote et al. 1980, Ward and Stanford 1982). However, zooplankton has been found to contribute to the food supply in streams and rivers, especially below reservoirs (Chandler 1937, Ward 1975, Brown et al. 1989, Sabri et al. 1993). These organisms provide a valuable food source for invertebrates and fishes in lotic ecosystems (Lundberg et al. 1987, Muth and Snyder 1995).

Few studies have examined the contribution of FPOM to river systems below hydroelectric dams in the southwestern U.S.A. (Lieberman and Burke 1993, Angradi 1994, Angradi and Kubly 1994), and none of these studies have reported the composition and biomass of FPOM in response to varying discharge, distance from the dam, or channel habitat. Omission of such information from river ecosystem studies will result in an underestimate of available food and nutrients in these systems. Furthermore, this information is of interest in regard to dam management for endangered native and alien sport fish populations.

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We examined several aspects of FPOM drift in the Colorado River. Our objectives were: 1) to determine the composition and biomass of FPOM drift in the regulated Colorado River along a 350 km corridor below Glen Canyon Dam (GCD), 2) to examine the effect of discharge patterns on FPOM, 3) to examine the relationship between FPOM biomass estimates and distance from GCD, and 4) to compare FPOM between open river channel and vegetated near-shore habitats.

METHODS AND MATERIALS

Study Area

Our study included seven sites along the Colorado River beginning just below GCD, Arizona, which is 23.2 river kilometers (RKM) upstream from Lees Ferry (designated 0.0 RKM; 36°52'03''N, 111°35'40''W), and ending at Spring Canyon (327 RKM; Fig. 1). Glen Canyon Dam is a hypolimnial release hydroelectric structure with a maximum production discharge of 937 $m^3 \cdot s^{-1}$ (Stanford and Ward 1991).

The Colorado River flows from GCD through Glen Canyon for approximately 23 RKM to Lees Ferry, Arizona. This reach of the Colorado River is cool (7-12°C), clear, and nutrient-rich (Blinn et al. 1989, Angradi 1994). These conditions allow for prolific growth of the green alga Cladophora glomerata in the tailwaters (Czarnecki et al. 1976, Blinn and Cole 1991). In contrast, the river downstream from Lees Ferry is often turbid just below the confluence of the first tributary below GCD, the Paria River (0.1 RKM), where approximately three million tons of suspended sediments enter the Colorado River annually (Andrews 1991). The Secchi depth at Lees Ferry was >7 m during our study but decreased to <3.9 m below the Paria River confluence.

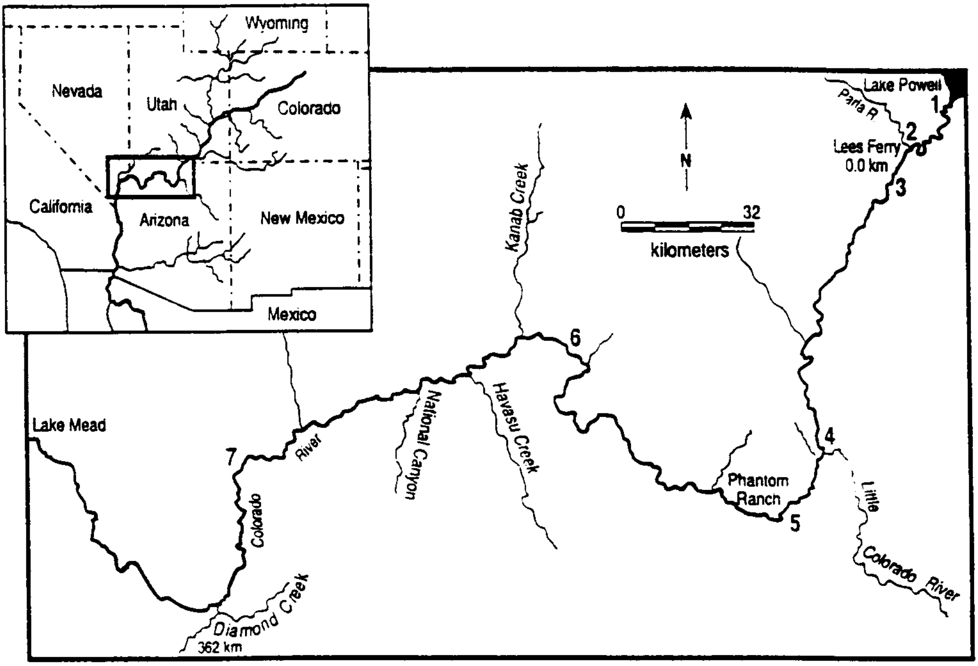

Figure 1. Map of drift collection sites (No. 1 - 7) in the Colorado River corridor through Grand Canyon National Park, Arizona.

Drift Collections

FPOM drift samples were collected during seasonal collection trips (spring, summer, and fall) over a four-year period which began in October 1995 and continued through June 1999 (n=325). Surface drift collections (0-0.5 m depth) were made in the river current with a circular tow net (30 cm diameter opening; 153 µm mesh) held in place behind a moored pontoon raft or secured to the river bank. Collections were taken in triplicate between approximately 900 h and 1700 h at each site.

Samples were preserved in 70% ETOH and sorted in the laboratory with a dissecting microscope into the following categories for biomass: 1) lentic zooplankton, including: Copepoda (Calanoida, Cyclopoida, Harpacticoida), Cladocera, Ostracoda, and 2) lotic zooplankton, which included: Gammarus lacustris, small Chironomidae, Oligochaeta, Tardigrada, etc. Samples were filtered through a 1 mm sieve to remove coarse particulate organic matter (CPOM). Depending on zooplankton density, samples were sorted in their entirety or were split with either 2 ml, 5 ml or 10 ml subsamples from a 100 ml dilution. Three subsamples were taken from samples which were split, and these values were averaged and extrapolated for the entire sample. Zooplankton was sorted for dry mass estimates and then converted to ash-free dry mass (AFDM) using a regression equation (AFDM = dry mass x 0.4932 + 0; $n = 20$; $r^2 = 0.84$; $F = 93.9$; $p < 0.001$). Densities for all zooplankton categories were also recorded. The remaining organic material was filtered onto glass microfiber filters (Whatman® GF/A) with a Millipore Swinex® system. These filters were then dried at 60°C and combusted for 1 h at 500°C to obtain an AFDM for all detritus. The condition, reproductive state, and presence of nauplii were documented.

We examined FPOM patterns in the vegetated near-shore habitat to compare with FPOM estimates in the open river channel. Near-shore habitat is defined as vegetated shoreline area (composed primarily of Equisetum spp.) with

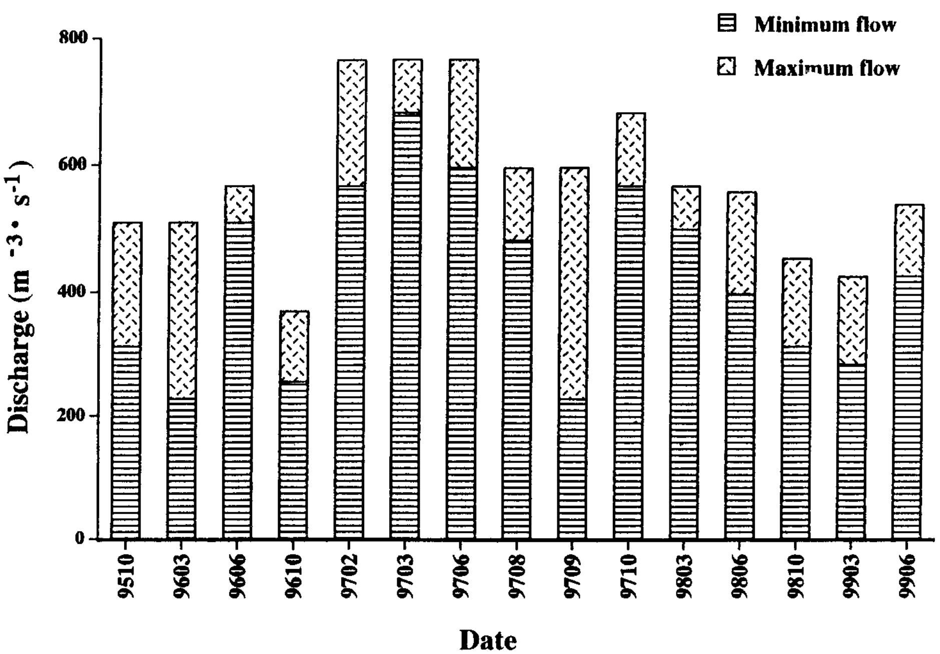

Figure 2. Minimum and maximum discharge ($m^{-3} \cdot s^{-1}$) in the Colorado River during the study collections October 1995 - June 1999.

lowered current velocities (< 0.05 $m^3 \cdot s^{-1}$). In recent years, near-shore habitats became extensive below GCD due to a rare period of flow regimes with reduced daily fluctuations. One such period occurred from April 1995 to September 1997. Additional drift samples ($\underline{n}$ = 66) were collected from October 1997 to November 1998 for the purpose of comparing FPOM components between the two habitats of vegetated near-shore versus open river channel. A hand bilge pump was used to draw 45 L of river water from the vegetated shoreline into a bucket that was then poured through the 153 μm mesh drift net. Collections were made from a raft to minimize disturbance to this low velocity habitat. These samples were processed in the same manner as described above for FPOM collections.

We investigated whether any diurnal change in zooplankton mass occurred at Lees Ferry by collecting at six-hour intervals (0600, 1200, 1800, and 2400 $\underline{n}$ = 27) for three days (25 April - 27 April 1997). The purpose of these interval collections was to determine if migration patterns could be detected downstream. The same protocol for FPOM collections was followed.

Current velocity was measured for volumetric calculations (mass $\cdot m^{-3} \cdot s^{-1}$) using a Marsh-McBirney electronic flow meter. River discharge was determined from United States Geological Survey gauge data (USGS Web site; Fig. 2). The duration of all drift collections averaged 43.6 sec (+ 1.8 SE) with an average of 1.8 $m^3 \cdot s^{-1}$ (± 0.1 SE) of water sampled through nets. The standard sampling error was within ± 10% of the mean total drifting mass (51.0 ± 4.0 mg $\cdot m^{-3} \cdot s^{-1}$; Culp et al. 1994).

Statistical Analyses

Multivariate analyses of variance (MANOVA) were used to analyze multiple response variables (biomass and density estimates) against predictor variables (abiotic parameters) for significant discharge and spatial trends in FPOM drift patterns. Regression analysis was used to determine linear relationships of FPOM estimates with increased discharge and distance downstream. All calculations were performed with SYSTAT® computer software on $\log_{10+1}$ transformed data (Statistics, version 5.2, SYSTAT, Inc. 1992, Evanston, Illinois).

RESULTS

Channel FPOM Patterns

Fine particulate organic matter (FPOM) changed significantly over discharge, distance, and time ($\underline{p} < 0.001$; Table 1). Multiple regression of FPOM ash-free dry mass (AFDM) showed significant association ($\underline{p} < 0.01$) of FPOM components (lentic zooplankton, lotic zooplankton, and detritus) with both discharge and distance downstream from GCD (Table 2). Lotic zooplankton and detritus drift increased in biomass both with distance from the dam and higher discharge. While lentic zooplankton also increased with discharge, it decreased in biomass at downstream sites (Figs. 3 and 4). A positive correlation ($\underline{p} < 0.001$) occurred between lotic zooplankton and detritus. Lentic zooplankton showed a weak negative correlation with detritus (Table 2).

Discharge changed significantly ($\underline{p} < 0.001$) between and within seasonal collection trips. Flows ranged from 226 - 765 $m^{-3} \cdot s^{-1}$ during the 1995 - 1999 sampling period with large discharge fluctuations of 65 - 377 $m^{-3} \cdot s^{-1}$ within single collection trips (Fig. 2). Multivariate analysis showed significant ($\underline{p} < 0.001$) differences in FPOM biomass both between and within collection trips 1995 - 1999 (Fig. 5).

Detritus contributed over two orders of magnitude greater FPOM biomass (74.0 mg $\cdot m^{-3} \cdot s^{-1}$; SE ± 5.9) than lentic or lotic zooplankton (0.53 mg $\cdot m^{-3} \cdot s^{-1}$; ± 0.04 and 0.32; ± 0.02, respectively). Detritus increased with distance from GCD,

Table 1. Results of MANCOVA analysis of fine particulate organic matter (FPOM) ash-free dry mass from collection trips by discharge and distance downstream. Composition of FPOM analyzed included lentic zooplankton (Z), lotic zooplankton (R), and detritus (D).

Source	Wilks' Lambda	F-statistic	df	p	Response Variables
Trip	0.29	11.10	42, 908	<0.0001	Z, R, D
Discharge	0.91	10.46	3, 306	<0.0001	Z, R, D
Kilometer	0.61	65.49	3, 306	<0.0001	Z, R, D

averaging 29.5 mg $\cdot$ m^{-3} $\cdot$ s^{-1} (± 6.3) in the first three collection sites below the dam and up to 137.4 mg $\cdot$ m^{-3} $\cdot$ s^{-1} (±14.1) at the last sites ~300 km downstream (Fig. 4). Lotic zooplankton followed similarly with 0.26 mg $\cdot$ m^{-3} $\cdot$ s^{-1} (± 0.03) in the first sites increasing to 0.41 (± 0.06) mg $\cdot$ m^{-3} $\cdot$ s^{-1} at the last sites. In contrast, lentic zooplankton from Lake Powell showed a pattern of decline with distance downstream (0.65 to 0.39 mg $\cdot$ m^{-3} $\cdot$ s^{-1}; ± 0.06). Most of the decrease in lentic zooplankton occurred between the first two sites below GCD, the same river stretch with a large increase in lotic zooplankton. In fact, both lentic and lotic zooplankton significantly changed ($p < 0.001$) in biomass and abundance between the first two collection sites. Lentic zooplankton dropped by 55%; lotic zooplankton increased by >100%.

Zooplankton densities were positively associated with biomass ($p < 0.001$) and followed the same trends as biomass along the distance, discharge, and time gradients throughout the study. Lentic zooplankton densities significantly decreased with distance from GCD, while lotic zooplankton densities increased with distance ($p < 0.001$). All zooplankton densities increased with discharge. Zooplankton densities were significantly ($p < 0.001$) different both between season and within season as with biomass estimates. Overall, zooplankton was dominated by Cyclopoida, Calanoida, and Cladocera which contributed 91.6% of the overall density and exhibited the strongest patterns against the predictor variables (Table 3; Fig. 6). Harpacticoida and Ostracoda were represented in low numbers (<10 $\cdot$ m^{-3} $\cdot$ s^{-1}). Condition of zooplankton was consistently good with little or no degradation noted in any collections. Reproductive structures were rarely noted (<1%); however, when present they consisted of egg sacs on female copepods. Copepod nauplii were rarely encountered.

Interval collections showed no diurnal difference in biomass for the FPOM components of lotic or lentic zooplankton and detritus. Discharge was steady during the three days of collection averaging 610 m^3 $\cdot$ s^{-1} (± 2.7), removing it as a possible variable affecting FPOM patterns. Although biomass differences between intervals were non-significant ($p = 0.265$), the midnight (2400) collections did show a pattern of reduced biomass (0.0083 mg; ± 0.0012) compared to all other sampling times (0.0123 mg; ± 0.0010).

Near-shore FPOM Patterns

Lentic zooplankton, lotic zooplankton, and detritus had significantly ($p < 0.001$) greater biomass in the near-shore habitat versus the river channel. Near-shore samples averaged 11-fold greater biomass for each of the three components (Fig. 7). Zooplankton densities were also significantly ($p < 0.001$) greater in the near-shore habitat, with eight-fold the number of individuals than in the channel.

Table 2. Multiple regression analysis of the relationship of fine particulate organic matter (FPOM) components (AFDM) with each other, discharge, and distance downriver. Components of FPOM analyzed included lentic zooplankton (Z), lotic zooplankton (R), and detritus (D).

Response Variables	Association	Predictor Variables	Probability
Lentic Zooplankton	+	R	< 0.001
	+	Discharge	< 0.001
	-	Distance	< 0.001
	-	D	NS
Lotic Zooplankton	+	Z	< 0.001
	+	D	< 0.001
	+	Discharge	< 0.01
	+	Distance	< 0.01
Detritus	+	R	< 0.001
	+	Discharge	< 0.01
	+	Distance	< 0.001
	-	Z	NS

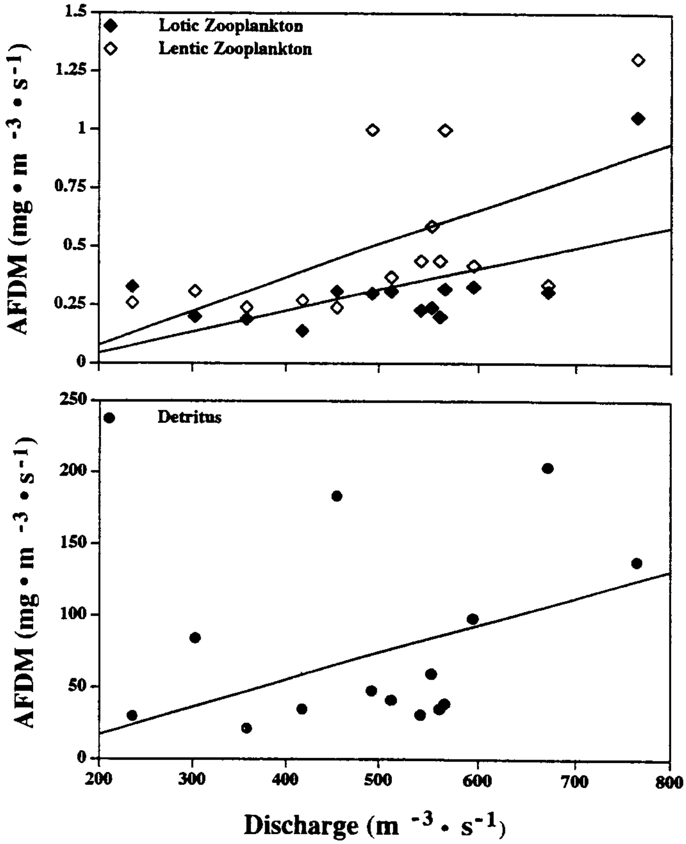

Figure 3. The positive relationship of FPOM components (lentic and lotic zooplankton, detritus: AFDM mg · m^{-3} · s^{-1}) with discharges of 200 - 800 m^{-3}· s^{-1} during 15 collection trips along the mainstem Colorado River.

Table 3. Densities of lentic zooplankton taxa in the Colorado River at seven sites along a transect of 352 kilometers below Glen Canyon Dam. Lotic zooplankton taxa included Chironomidae, Oligochaeta, Gammarus lacustris, and Tardigrada.

Taxa	Mean Density	± SE	Relative %
Calanoida	76	7	11.3
Cyclopoida	456	27	68.4
Harpacticoida	8	1	1.2
Cladocera	72	10	10.8
Ostracoda	2	0.3	0.3
Miscellaneous lotic zooplankton	53	4	8

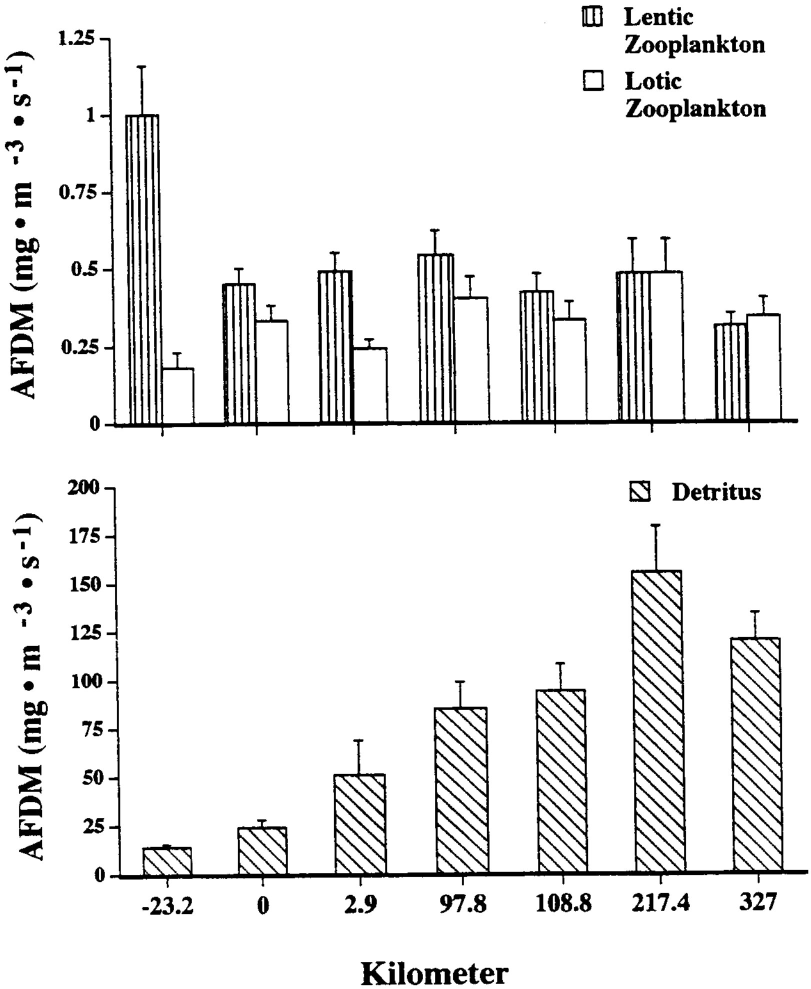

Figure 4. Mean drift of FPOM components (lentic and lotic zooplankton, detritus: AFDM mg · m^{-3} · s^{-1}, ±SE) at seven collection sites in the mainstem Colorado River during October 1995 - June 1999.

Both zooplankton categories in the near-shore habitat showed little change in biomass as related to discharge, distance, or time. Detritus showed no change in biomass over distance; however, it significantly increased with discharge and varied between collection trips ($p < 0.001$).

DISCUSSION

The composition of FPOM drift in the Colorado River below GCD is dominated by detrital material, as has also been found in the lower Colorado River below Laughlin, Nevada (Lieberman and Burke 1993). Consequently, patterns of total FPOM followed those established by the detrital material. However, when components of FPOM were examined individually, lentic and lotic zooplankton showed differences in patterns compared to each other and to detritus in the mainstem and near-shore habitats.

In contrast to the findings of Haury (1988), both the detrital and zooplankton components of FPOM drift in our study were related to distance from the dam. Detrital biomass increased with distance from the dam, as was found by Angradi and Kubly (1994) in the Glen Canyon reach of the Colorado River. This is likely due to further degradation of coarse particulate organic matter into FPOM as it travels downstream (Ward et al. 1994). The increases in detrital material and lotic zooplankton are likely connected as successive rapids churn up benthic material, which is then continually added to river drift (Shannon et al. 1996).

A decrease in the limnetic zooplankton FPOM biomass downriver from dams and reservoirs is commonly observed (Ward 1975, Keefer and Maughan 1985). Often this decrease in zooplankton is dramatic with a 25-98% decrease within the first 8 km downriver of the reservoir (Chandler 1937, Armitage and

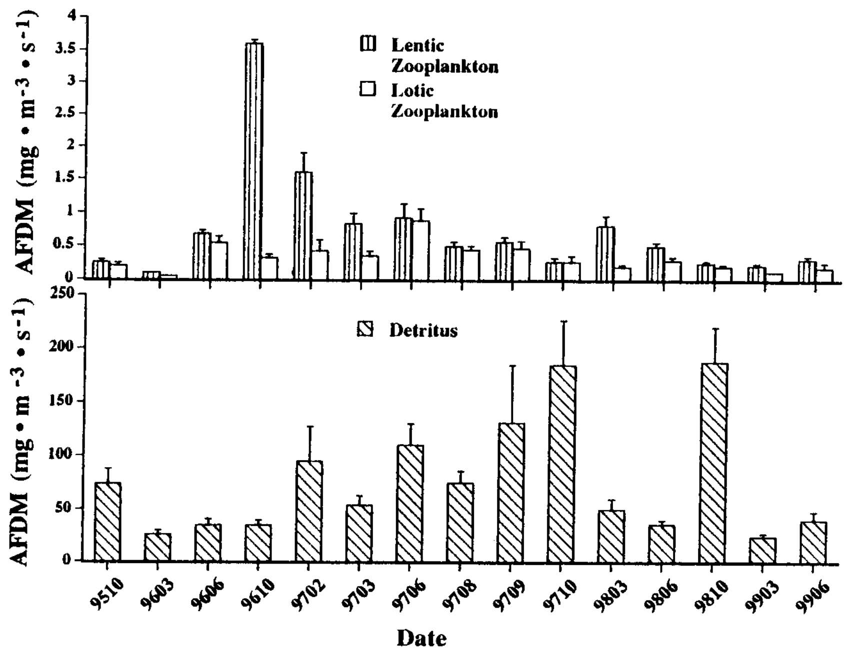

Figure 5. Mean drift of FPOM components (lentic and lotic zooplankton, detritus: AFDM mg · m^{-3} · s^{-1}, ±SE) during 15 collection trips at seven collection sites in the mainstem Colorado River during October 1995 - June 1999.

Capper 1976). This was supported by our study which revealed a major decrease of Cyclopoid and Calanoid copepods and cladocerans in the first 24 km below GCD and then a gradual decline for the remaining 325 km downriver to the last site. This large decrease in the zooplankton biomass may be attributed to a variety of factors. One possibility is that many of the zooplankters being released by the dam are destroyed by several riffles present in the Glen Canyon reach, as has been noted by other investigators in response to rapids (Armitage and Capper 1976). It is also possible that the zooplankton released by the dam is being consumed by invertebrates and fishes inhabiting the Glen Canyon reach. The GCD tailwaters support an alien trout fishery dominated by rainbow trout (Minckley 1991). Minckley (1973) indicated that larvae of rainbow trout, as well as native bluehead and flannelmouth suckers, consume zooplankton in the Colorado River, and

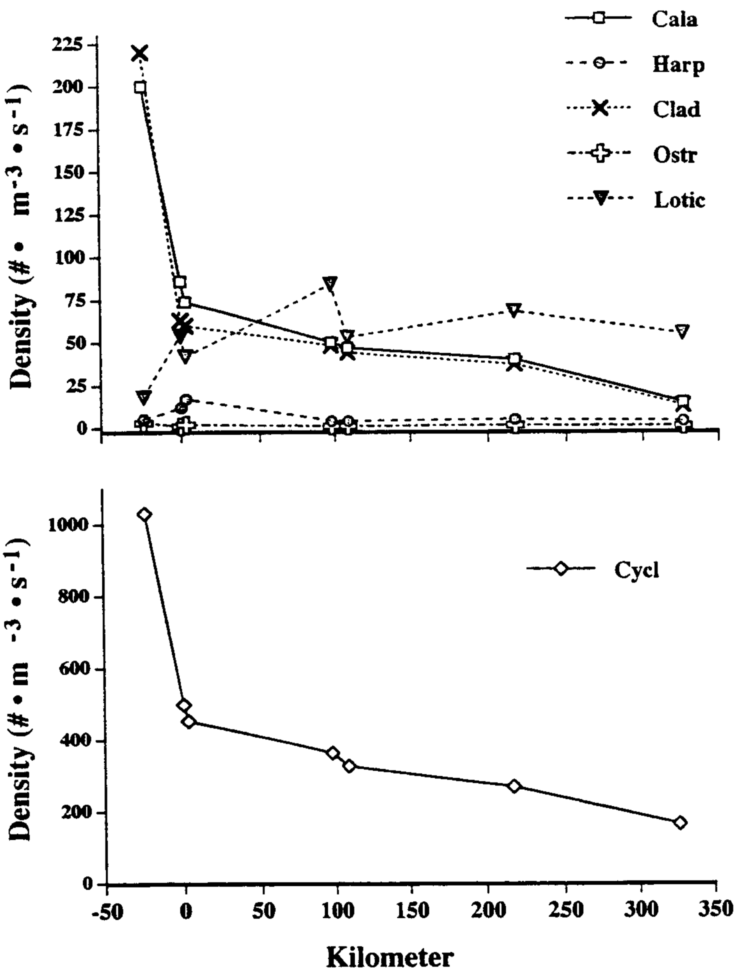

Figure 6. Average FPOM density distribution from Glen Canyon Dam (-23.2 Rkm) to Spring Canyon (Rkm 327) during 15 collection trips at seven collection sites in the mainstem Colorado River during October 1995 - June 1999. Abbreviations are defined as Cala = Calanoida, Harp = Harpacticoida, Clad = Cladocera, Ostr = Ostracoda, Lotic = lotic zooplankton, and Cycl = Cyclopoida.

Angradi (1994) confirmed that trout in the Colorado River consume zooplankton from Lake Powell. Other studies have indicated zooplankton as a food source for invertebrates and fishes in flowing waters (Ward 1975, Armitage 1976, Lundberg et al. 1987, Muth and Snyder 1995). Chandler (1937) demonstrated that vegetation may act as a strainer to remove zooplankton from running water, a possibility in the Glen Canyon reach due to prolific growth of algae and aquatic macrophytes (Shannon et al. 2000). The aquatic vegetation may also be linked to the substantial increase in lotic zooplankton by providing habitat for rearing and nutrition from algae and associated epiphytes. Thus, it is probable that some combination of these factors is working to both decrease lentic and increase lotic zooplankton abundances and biomasses in the Glen Canyon reach.

The removal of zooplankton from the river in the Glen Canyon reach was especially pronounced in regard to the densities of cyclopoid copepods and cladocerans. This may be due to the life history traits of these organisms. Cladocerans are very susceptible to vertebrate predators, and both cladocerans and copepods are moderately susceptible to invertebrate predators (Allan 1976). Alternatively, these taxa may have an affinity for vegetation, as they are commonly found in lentic habitats (Pennak 1953), and may become entangled in the masses of Cladophora glomerata and other algae in the Glen Canyon reach.

The densities of the zooplankton component of FPOM showed that cyclopoid copepods dominated zooplankton densities. Calanoid copepods and cladocerans were well represented but did not dominate the zooplankton densities at any site. This is in contrast to the findings of Haury (1988) that calanoid copepods were the dominant zooplankters in the Colorado river below GCD and cladocerans were the least abundant. Since no collections of zooplankton were taken from Lake Powell during our study, it is not possible to determine whether or not our compositional patterns were a reflection of lake populations or a reflection of their ability to survive in the river. However, Shiel and Walker (1982) found that plankton from reservoirs of regulated rivers pass downriver with little change in zooplankton composition.

Condition of zooplankton was consistently good at all sites and during all collection periods, in contrast to Haury (1988) who found a significant decrease in plankton condition at downriver sites. Although a decrease in the number of zooplankters was detected at downriver sites in our study, no intermediate stages were seen where condition of zooplankton deteriorated. It is possible that these two studies used different criteria to determine condition. In our study, most zooplankters were whole or consisted of unidentifiable parts, which were then considered part of detrital material.

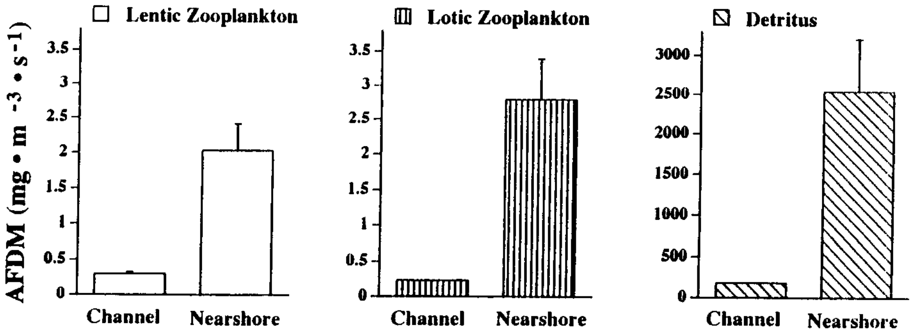

Figure 7. Comparison of mean drift of FPOM components (lentic and lotic zooplankton, detritus: AFDM mg $\cdot$ m^{-3} $\cdot$ s^{-1}, ±SE) in the nearshore versus open river channel habitats collected October 1997 - November 1998 (n = 66).

Reproductive structures were rarely seen (<1%) on zooplankters during this study in both the channel and near-shore habitats. When present they consisted of egg sacs on female copepods and tardigrada. Copepod nauplii were rarely encountered and did not make up a notable proportion of the total copepod abundance. Lack of literature on these aspects of zooplankton in rivers below hydroelectric dams makes it difficult to determine if these are normal patterns of reproductive structures and nauplii. While no conclusions can be made about the importance of these findings, it is possible that this is an indication that lentic zooplankton cannot survive and reproduce under the cold temperature conditions of this regulated river.

The positive association of FPOM biomass and abundance with discharge throughout the study corroborate with other workers (Ward 1975, Sabri et al. 1993) but is in contrast with Haury (1988). The peak in total FPOM biomass in October 1996 is not easily explained based on our data, and studies are lacking on seasonal variation of FPOM biomass in rivers below dams. However, this may be a reflection of the late fall degradation of benthic plants and animals in the river and their release into the river FPOM drift (Ward et al. 1994). Seasonal changes in FPOM are dampened due to the overriding effects of dam operations; therefore variation may be more a function of increased discharge or possibly a combination of discharge with seasonal changes in abundance in lentic zooplankton and tributary contributions to detrital material.

The increase of FPOM biomass by an order of magnitude in the near-shore collections suggests that this is a more stable habitat than the river channel. In addition, the lack of zooplankton response to discharge, distance, or time indicates this habitat, if allowed to develop, could become an important habitat for both invertebrate and fish colonization. Because the criteria for near-shore development are steady discharge regimes or reduced fluctuations in flow, modifications in dam operations would be necessary. Management accommodations that would allow further study of this important habitat are recommended. We were only able to sample this habitat for one year prior to its deterioration due to resumption of fluctuating flow regimes.

Vegetated near-shore habitats have attributes similar to backwaters for young fish (Minckley 1991). Backwater habitats have slow water velocity, high food base, adequate cover from predators, and warmer water than the channel which are conducive to rearing young fish. Near-shore emergent vegetation provides slow water velocity and cover for young fish, with the shoreline topography also providing more exit and entry points for fish than a backwater. The near-shore food base is abundant with a substantially greater zooplankton population than the channel. Several data-logging thermisters testing for near-shore warming were damaged so our data is inconclusive. However, hand held thermometers indicated a 2 - 3°C increase in the vegetated areas compared to the channel.

Isotopic analysis of particulate organic matter in the Colorado River below GCD indicates ultra fine particulate organic matter and a large portion of the zooplankton components of FPOM are derived from Lake Powell (Angradi 1994, Blinn et al. 1999, Shannon et al. 2000). Other studies of rivers below impoundments have also found large numbers of lentic zooplankton being exported from reservoirs (Novotny and Faler 1982, Petts 1984, Herlong and Mallin 1985). These studies highlight the importance of examining limnetic zooplankton regarding its contributions and influence on the river biota.

Although FPOM drift contributes only a small amount of organic material to the Colorado River below GCD, it should be considered an important food source for invertebrates and fishes. While invertebrate and vertebrate fauna at upriver sites will benefit from the contribution of lentic zooplankton from Lake Powell, downriver fauna may utilize the fine detrital material abundant in these reaches. Degradation of all FPOM components may contribute more nutrients to the ecosystem, thus enhancing growth of primary producers which will benefit higher trophic level links in the Colorado River system.

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