

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

Ted R. Angradi  
USDA Forest Service  
Timber and Watershed Laboratory  
Box 404,  
Parsons, West Virginia, 26287  
and

Dennis M. Kubly  
Arizona Game and Fish Department  
2222 West Greenway Road  
Phoenix, Arizona 85025

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## ABSTRACT

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

## INTRODUCTION

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

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

Glen Canyon Dam on the Colorado River regulates flows for 400 km between Lake Powell and Lake Mead. This reach includes Glen Canyon, which extends for 25 km below the dam, and Grand Canyon which extends thence to Lake Mead. The influence of the existence (since 1963) and operation of Glen Canyon Dam on downriver ecosystems in Glen and Grand Canyons has come under scrutiny in recent years (National Research Council [NRC] 1987, 1991; United States Department of the Interior 1987). Two potential effects of dam operations on downriver resources which involve POM dynamics have been identified: (1) the flow

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regime may affect the availability of suspended particles eaten by introduced trout and native fishes (NRC 1987, Minckley 1991); (2) water releases may influence the export of organic matter from the Glen Canyon reach to Grand Canyon where it may be processed and assimilated by primary and secondary producers (NRC 1987).

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

#### SITE DESCRIPTION AND METHODS

POM samples were collected from penstocks within Glen Canyon Dam on the Colorado River, and from the 25 km tailwater reach between the dam and Lee's Ferry, Arizona. Glen Canyon Dam forms Lake Powell, a long (300 km), deep (average depth = 51 m), warm monomictic reservoir that retains virtually all of the 44-154 million Mg annual suspended sediment input (Evans and Paulson 1983). Water releases from the reservoir are hypolimnial (from a depth of ca. 48-52 m during this study). As a result, released water is perennially cold (7-11 C), chemically stable, and transparent (Stanford and Ward 1991).

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

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

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

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

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

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

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

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

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

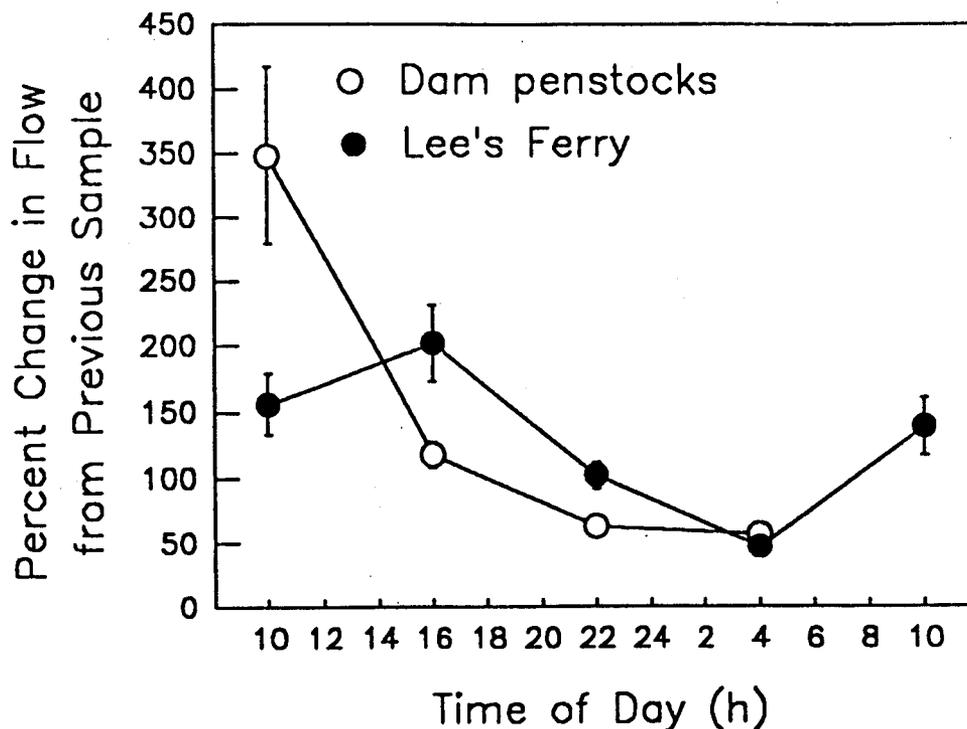


Figure 1. Mean ( $\pm$ SE) percent change in flow between diel POM samples at Lee's Ferry and Glen Canyon Dam (GCD) for September 1990 - December 1991 excluding dates on which flow did not vary. At Lee's Ferry, 1000 h and 1600 h samples were during ascending flow; flows during the 2200 h sample were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

## RESULTS

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

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

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

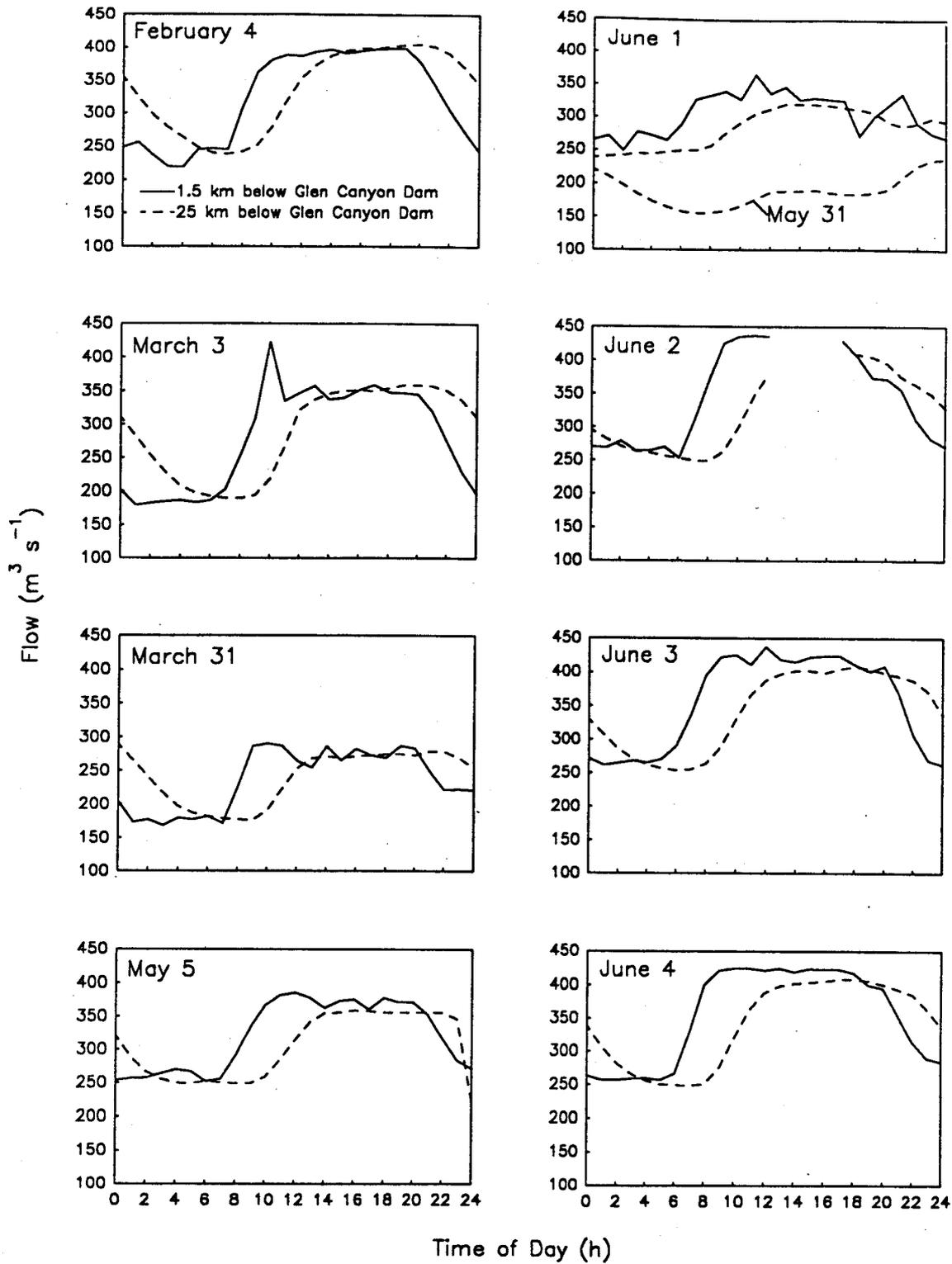


Figure 2. Daily hydrographs at Lee's Ferry and 1.5 km below Glen Canyon Dam (GCD) for 1992 dates when longitudinal FPOM samples were collected (for February - May, the hydrographs for the first sample day are shown). Missing are data from the upper gauge on May 31, and data from both gauges for several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

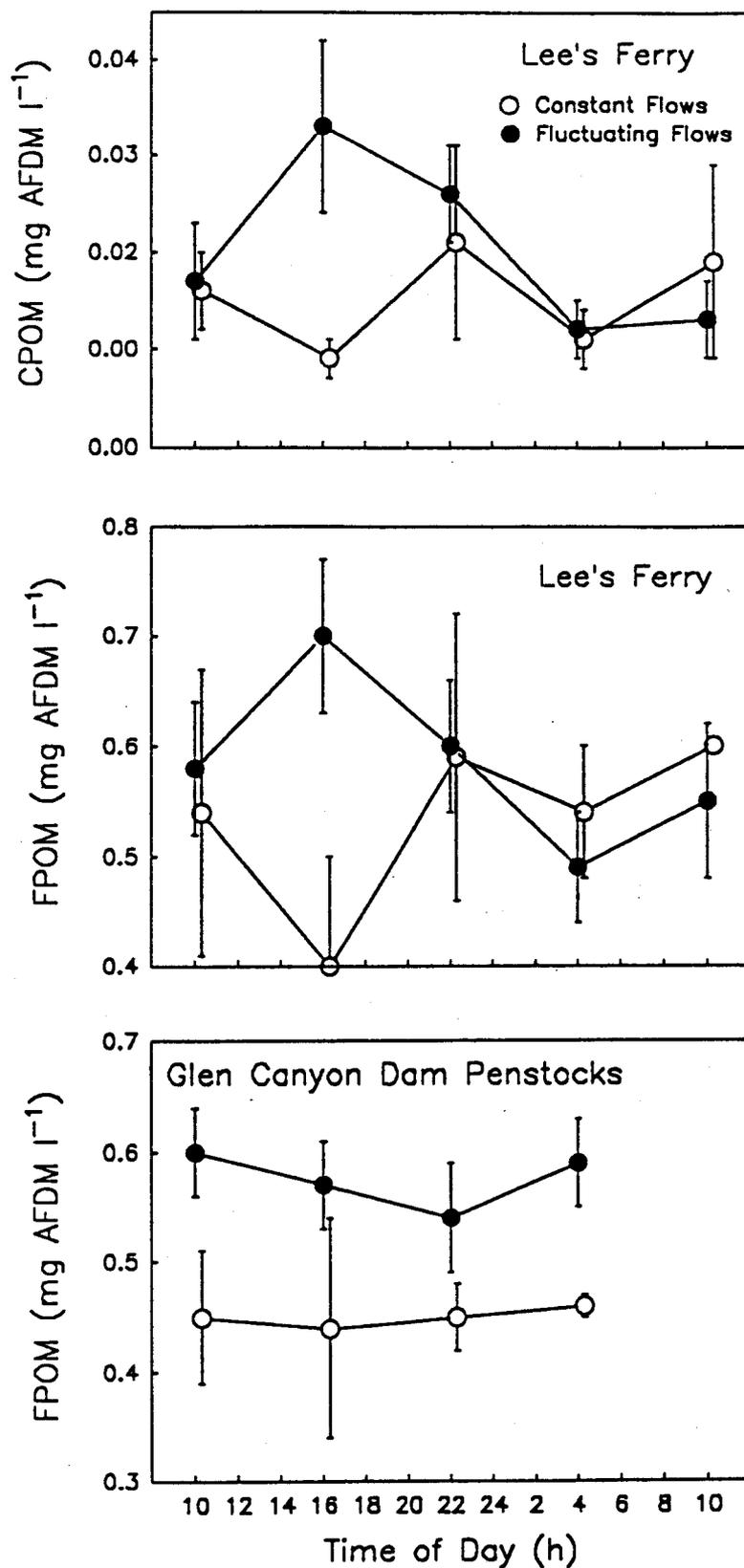


Figure 3. Diel variation in POM concentration in Glen Canyon. Values are means ( $\pm$ SE) pooled across sample dates (September 1990 - December 1991). Dates of constant flows are given in Table 1. CPOM was not collected from penstocks.

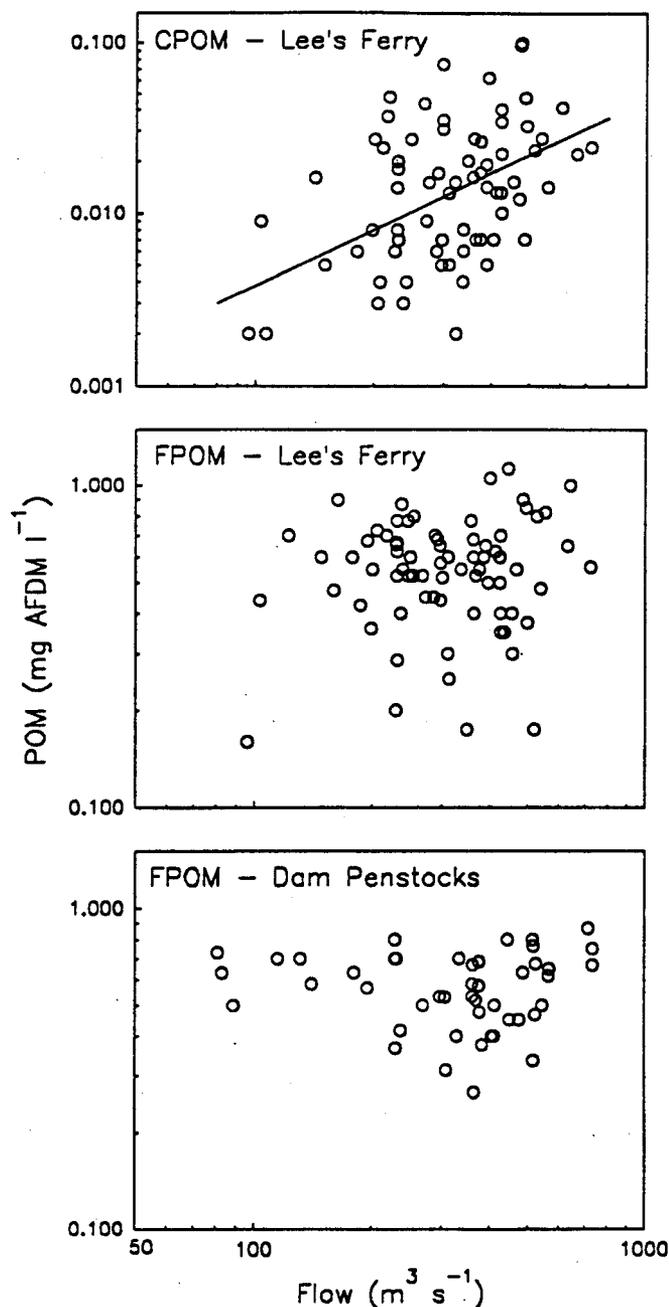


Figure 4. Plots of POM concentration versus flow for all dates combined (September 1990 - December 1991). Regression was significant for CPOM only;  $\text{Log}_{10} \text{CPOM} = -4.33 + 0.98 \text{Log}_{10} \text{Flow}$ ,  $r^2 = 0.21$ .

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

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

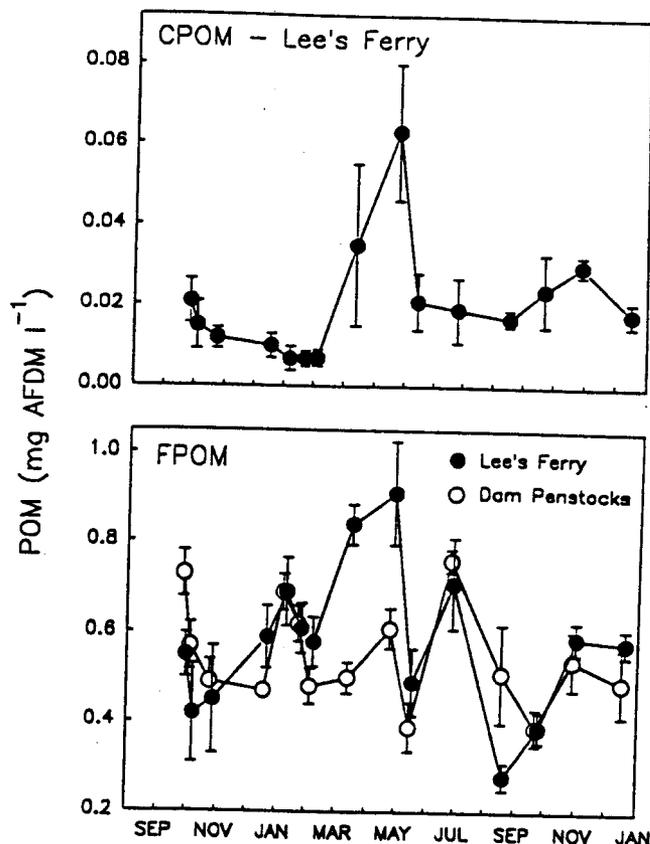


Figure 5. Among-sample date variation in CPOM and FPOM concentration in Glen Canyon (September 1990 - December 1991). Values are means ( $\pm$ SE) pooled across time of day, excluding the second 1000 h sample at Lee's Ferry.

As for concentration, total export of POM ( $\text{g AFDM s}^{-1}$ ) from the tailwater reach was highest in spring (Table 1). For several samples, inputs to the reach substantially ( $> 50\%$ ) exceeded outputs. When the effects of the spring 1991 data are excluded, there is little net export from the reach (Table 1). Of the three sample dates in which flow did not vary much (October 23-24, 1990; December 17-18, 1990; May 28, 1991), there was net export from the reach only in the May sample. There is little evidence that during fluctuating flows, flow regime influenced POM concentration. For example, total POM concentration at Lee's Ferry was not correlated with discharge range ( $r^2 = 0.11$ ,  $n = 15$ ).

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

On June 2, a large increase (ca. twice ambient) in FPOM concentration was measured at the site 6 km downriver from the dam. On the next two days an elevated FPOM concentration (ca. three-four times ambient) was measured at sites 15-18 km below the dam (Figure 6). In each case the increase diminished downriver. As a result of a shift to a new release schedule at the dam, peak discharge on June 2, the first day of elevated FPOM concentration, was higher ( $> 400 \text{ m}^3 \text{ s}^{-1}$ ) than on any previous day since early March 1992 (Figure 2). Our observations indicate that these elevated peak flows partially flushed a large (ca. 1.5 ha) backwater located just upriver of the sample station. Flushed material was concentrated in large main-channel eddies further downriver (15-18 km below the dam). The effects

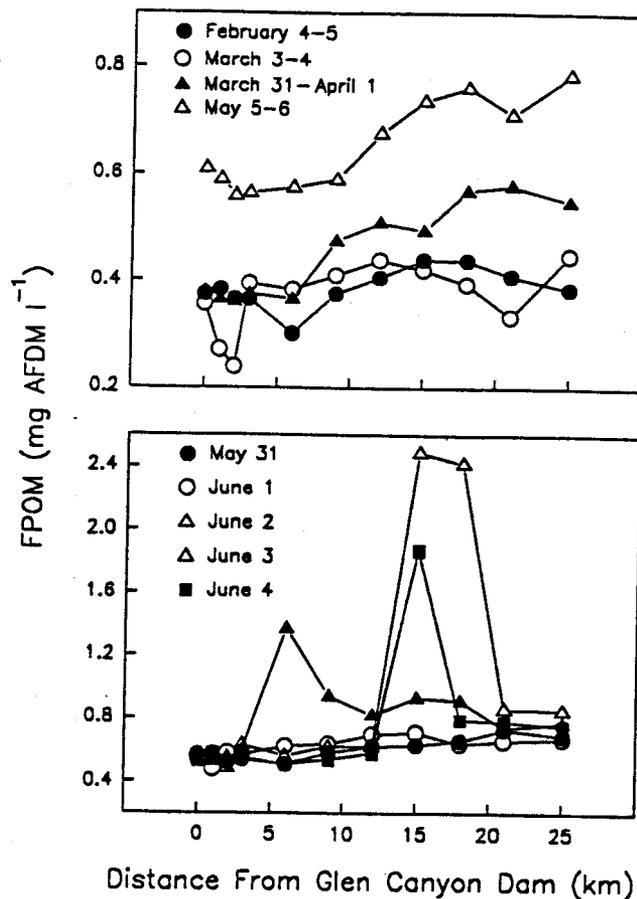


Figure 6. Longitudinal variation in mean FPOM concentration ( $n = 10$  except in June,  $n = 5$ ) in Glen Canyon, February - June 1992. Error bars were omitted for clarity. Samples for 0 km were collected from Glen Canyon Dam penstocks.

were short-lived and local; the FPOM concentration at Lee's Ferry on these dates was similar to dates when no backwater flushing occurred.

## DISCUSSION

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

The effects of diel flow variation on FPOM concentration were less than for CPOM. FPOM concentration in penstocks at the dam did not vary with flow, and was largely independent of the volume of water withdrawn from Lake Powell. FPOM concentration at Lee's Ferry was only weakly related to flow, suggesting that FPOM exported from Lake Powell dampens diel (i.e., flow-related) variation in FPOM concentration. Seasonal variation in the POM concentration in the dam forebay at penstock intake depth is probably low (Angradi et al. 1992) suggesting that limnologic processes in Lake Powell, which is intensely stratified most of the year (Stanford and Ward 1991), may dampen seasonal variation in

downriver POM concentration.

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

FPOM sampling at intermediate sites between the dam and Lee's Ferry indicated a moderate (ca. 25 %) downriver increase in FPOM concentration within the reach in spring. An initial decline in FPOM concentration in the first few km below the dam on some dates suggests that a part of the FPOM from the reservoir was deposited in the relatively slack water in the large (0.25 km<sup>2</sup>) pool just below the dam. Net export of POM in late winter and spring resulted from processes in the tailwater rather than from depressed FPOM concentration in water releases (Figure 5).

In Glen Canyon, where epilithon biomass on cobble substrates is high, a positive relationship between cumulative upriver area of cobble substrate and epilithon-derived POM would be predicted (Swanson and Bachmann 1976). However, cobble substrates in Glen Canyon are largely restricted to the upstream half of the tailwater (about 85% are in the first 12 km), and the bottom area colonized by algae decreases substantially between the dam and Lee's Ferry (T. R. Angradi, personal observation). Whereas cumulative upstream algal production increases in the downriver direction, it is at a decreasing rate, and high concentrations—compared to dam penstocks—of river-derived POM do not develop.

The strong temporal concordance between Lee's Ferry and dam penstock FPOM concentrations, and lack of concordance with CPOM concentration (Figure 5) indicate that the measured FPOM concentration at Lee's Ferry resulted from lotic organic matter inputs in excess of the lentic inputs which remain entrained through the reach.

The effects of benthic POM storage on POM dynamics in the reach are poorly understood. Longitudinal sampling (Figure 6) revealed no consistent interruption—POM source or sink—in the progressive, albeit slight, downriver increase in FPOM concentration except in June when side channels were flushed by elevated peak flows. Our observation that the importance of backwaters as contributors of POM to the river is contingent on antecedent flow conditions agrees with the findings of Lieberman and Burke (1991). They reported that the abundant backwaters of the lower Colorado River appeared to have little effect on thalweg POM concentration except during storm events. The effects of backwater flushing appear to be short-lived; sustained high flows flush out stored POM in a day or two.

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

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

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

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## LITERATURE CITED

- ANGRADI, T. R., R. W. CLARKSON, D. A. KINSOLVING, D. M. KUBLY, and S.A. MORGENSEN. 1992. Glen Canyon Dam operations and the Colorado River: responses of the aquatic biota to dam operations. Interim Report for the Bureau of Reclamation, Upper Colorado Region, Glen Canyon Environmental Studies, Flagstaff, Arizona. Cooperative Agreement 9-FC-40-07940, Arizona Game and Fish Department, 2222 West Greenway Road, Phoenix.
- BLINN, D. W., and G. A. COLE. 1991. Algal and invertebrate biota in the Colorado River: comparison of pre- and post-dam conditions, Pp. 102-123. In: Colorado River Ecology and Dam Management, Proceedings of a National Research Council Symposium, May 24-25, 1990, Santa Fe, New Mexico. National Academy Press, Washington, D.C.
- CUSHMAN, R. M. 1985. Review of ecological effects of rapidly varying flow downstream from hydroelectric facilities. North American Journal of Fisheries Management 5:330-339.
- EVANS, T. D., and L. J. PAULSON. 1983. The influence of Lake Powell on the suspended sediment-phosphorus dynamics of the Colorado River inflow to Lake Mead. In: V. D. Adams and V. A. Lamarra (eds.), Aquatic Resource Management of the Colorado River Ecosystem. Ann Arbor Scientific Publishers, Ann Arbor, Michigan.
- FERGUSON, R. I. 1987. Accuracy and precision of methods for estimating river loads. Earth Surfaces and Landforms 12:95-104.
- JOHNSON, R. R. 1991. Historic changes in vegetation along the Colorado River in the Grand Canyon. Pp. 178-206. In: Colorado River Ecology and Dam Management, Proceedings of a National Research Council Symposium, May 24-25, 1990, Santa Fe, New Mexico. National Academy Press, Washington, D.C.
- KONDRATIEFF, P. F., and G. M. SIMMONS, Jr. 1984. Nutritive quality and size fractions of natural seston in an impounded river, Archives für Hydrobiologia 101:401-412.
- LIEBERMAN, D. and T. BURKE. 1991. Limnology and drift of particulate organic matter through the lower Colorado River. REC-ERC-91-1, U.S. Bureau of Reclamation, Boulder City, Nevada.
- MINCKLEY, W. L. 1991. Native fishes of the Grand Canyon region: an obituary? Pp. 124-177. In: Colorado River Ecology and Dam Management, Proceedings of a National Research Council Symposium, May 24-25, 1990, Santa Fe, New Mexico. National Academy Press, Washington, D.C.
- NATIONAL RESEARCH COUNCIL. 1987. River and dam management: a review of the Bureau of Reclamation's Glen Canyon Environmental Studies. National Academy Press, Washington, D.C.
- NATIONAL RESEARCH COUNCIL. 1991. Colorado River Ecology and Dam Management. Proceedings of a Symposium, May 24-25, 1990, Santa Fe, New Mexico. National Academy Press, Washington, D.C.
- PAULSON, L., and J. BAKER. 1984. The limnology in reservoirs on the Colorado River. Technical Report No. 11, Lake Mead Limnological Center, University of Nevada, Las Vegas.
- PEMBERTON, E. L. 1976. Channel changes in the Colorado River below the Glen Canyon Dam. Proceedings of the 3rd Interagency Sedimentation Conference. Sedimentation Council of the Water Resource Council, Denver, Colorado.
- PETTS, G. E. 1984. Impounded rivers, perspectives for ecological management. John Wiley and Sons, Chichester, England.
- STANFORD, J. A. and J. V. WARD. 1991. Limnology of Lake Powell and the chemistry of the Colorado River. Pp 75-101. In: Colorado River Ecology and Dam Management, Proceedings of a National Research Council Symposium, May 24-25, 1990, Santa Fe, New Mexico. National Academy Press, Washington, D.C.
- SWANSON, C. D., and R. W. BACHMANN. 1976. A model of algal exports in some Iowa streams. Ecology 57:1076-1080.
- UNITED STATES DEPARTMENT OF THE INTERIOR. 1987. Glen Canyon Environmental Studies Final Report. U.S. Bureau of Reclamation, Flagstaff, Arizona.
- USHER, H. D. and D. W. BLINN. 1990. Influence of various exposure periods on the biomass and chlorophyll *a* of *Cladophora glomerata* (Chlorophyta). Journal of Phycology 26:244-249.
- VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, and C. E. CUSHING. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.
- WARD, J. V. 1976. Comparative limnology of differentially regulated sections of a Colorado Mountain River. Archives für Hydrobiologia 78:319-342.
- WEBSTER, J. R., E. F. BENFIELD, and J. CAIRNS, Jr. 1979. Model predictions of effects of impoundment on particulate organic matter in a river system. Pp. 339-364. In: J. V. Ward and J. A. Stanford (eds.). The Ecology of Regulated Streams. Plenum Press, New York.

