

ECOSYSTEM PROCESSES AND LOWER TROPHIC LEVELS

Glen Canyon Environmental Studies
Interim Monitoring Progress Report

September 30, 1996

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GLEN CANYON ENVIRONMENTAL
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Submitted by

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FINAL

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Submitted to

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Cooperative Agreement 9-FC-40-07940

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GAME & FISH DEPARTMENT

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October 22, 1996

Dave Wegner
GCES Program Manager
Glen Canyon Environmental Studies
PO Box 22459
Flagstaff, AZ 86002-2459

Dear Dave:

Enclosed is an Arizona Game and Fish Department Glen Canyon Environmental Studies Interim Monitoring **Final Report** ready for outside review. Please send review comments directly to Andrew Ayers and Ted McKinney.

Ayers, A.D. and T. McKinney. 1996. Ecosystem processes and lower trophic levels. Glen Canyon Environmental Studies Interim Monitoring Progress Report.

Sincerely,

A handwritten signature in cursive script that reads "Bill Persons".

William R. Persons
GCES Coordinator

BP:bp

cc: Jim deVos, Chief of Research ✓
Andrew Ayers ✓
Ted McKinney ✓

Enclosure

GLEN CANYON ENVIRONMENTAL
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Richard



United States Department of the Interior

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Glen Canyon Environmental Studies
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IN REPLY REFER TO:

October 29, 1996

GLEN CANYON ENVIRONMENTAL
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FLAGSTAFF, AZ

MEMORANDUM

To: Mr. Michael Yard, Glen Canyon Environmental Studies
Mr. Larry Crist, Reclamation, Salt Lake City
Dr. Owen Gorman, Fish & Wildlife Service, Flagstaff

From: Dave Wegner

Subject: Review of Technical Report from Arizona Game & Fish Entitled "Ecosystem Processes and Lower Trophic Levels"

Enclosed for your information and review is a document prepared by Arizona Game & Fish Department entitled *Ecosystem Processes and Lower Trophic Levels*. This report was prepared by Andy Ayers and Ted McKinney in partial fulfillment of the Glen Canyon Environmental Studies interim flow monitoring program.

I would appreciate your review of this document by November 15, 1996. Please provide your comments in either written or electronic format. Thank you for your assistance. Regards.

enclosure

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INTRODUCTION

The purpose of this chapter is to summarize results from studies of ecosystem processes and lower trophic levels in the Glen Canyon Dam tailwater to Lee's Ferry during 1995. Investigations focused primarily on algal and macroinvertebrate standing stocks and lotic transport of fine particulate organic matter (FPOM) and zooplankton. Results represent continuation of the monitoring of periphytic algae and benthic macroinvertebrate standing stocks and of POM transport which were begun in August 1991, December 1992 and April 1993, respectively (Ayers and McKinney 1996a, 1996c, 1996d).

Previous investigations indicated that algal and macroinvertebrate standing stocks in the dewatered zone (zone of fluctuating flow elevations) were lower than those in the submerged (permanently-inundated) zone (Angradi and Kubly 1993, Ayers and McKinney 1996a, 1996c, Blinn et al. 1994, 1995). However, differences between the zones diminished during the interim flow regime (Ayers and McKinney 1996a, 1996c). POM transport studies indicated that lotic processing and autochthonous production of FPOM also occurred in the dam tailwater during the interim flows and increased in comparison with earlier discharge regimes (Angradi and Kubly 1994, Angradi et al. 1992a, Ayers and McKinney 1996b, 1996c).

METHODS

Macroinvertebrates

Transects (50 m) parallel to river flow were established on cobble bars at -14 mi and -4.1 mi and on a depositional site at -3.5 mi and reflect a downstream trend toward slower current velocity (Ayers and McKinney 1996b). Descriptions of transect locations are presented below.

The benthos was sampled at a depth of <1 m during the ascending limb of the daily hydrograph (Hess sampler; 0.087 m²) from the submerged (142 m³s⁻¹ flow elevation) and dewatered (227 m³s⁻¹ flow elevation) zones. Eight samples were collected haphazardly along transects. Samples were preserved in a 10% formaldehyde solution in the field. Samples were rinsed in the laboratory through a 250 µm sieve, and macroinvertebrates were sorted into nine groups: *Gammarus lacustris*;

oligochaetes; chironomid larvae and pupae; ostracods; nematodes; gastropods; turbellarians; bivalves and preserved in 95% ethanol.

Macroinvertebrate data were transformed using a $\log(x+1)$ (oligochaetes, chironomid larvae, ostracods and turbellarians) or a $\sqrt{x+1}+\sqrt{x}$ (*Gammarus* and gastropods) transformation (Sokal and Rohlf, 1981) and were analyzed using a 3 x 3 x 2 ANOVA with repeated measures. Means were discriminated using Duncan's Multiple Range Test. Chironomid pupae, nematode and bivalve data could not be normalized and were analyzed using Kruskal - Wallis ANOVA by Ranks Test. Means were discriminated using nonparametric Multiple Comparisons Tests (Zar 1984). Data from June 1995 were omitted from analyses due to missing data from -4.1 mi and -14 mi.

Periphyton

Sampling transects parallel to river flow were established on cobble bars (-14 mi river right, -4.1 mi river right) and at a depositional site (-3.5 mi river right) (Figure 2.2.1) and reflected the downstream trend toward smaller, or finer substrate particles (Angradi and Kubly 1994). The following brief descriptions outline salient features at each site:

- 14 mi: Large cobbles abundant, forming a major portion of the substrate; little silt; comparatively high algal biomass (*Cladophora* dominates); river bed slopes gradually; comparatively high flow velocity.
- 4.1 mi: Similar to -14 mi, but cobbles tend to be smaller.
- 3.5 mi: Depositional zone with a few localized areas of small stone substrata; *Chara sp.* (probably *Chara contraria*) dominates, and, *Potamogeton sp.* (probably *Potamogeton pectinatus*; Blinn et al. 1994) is present to a lesser extent; low flow velocity; river bed slopes gradually.

Epilithon

Samples were collected quarterly at -14.0 mi and -4.1 mi (January, April, June and November 1995). Cobbles 10-20 cm diameter were collected haphazardly within fixed transects positioned parallel to river flow at levels corresponding to river flows of $142 \text{ m}^3\text{s}^{-1}$ (submerged zone) and $227 \text{ m}^3\text{s}^{-1}$ (dewatered zone). Cobbles were sampled ($n=15$ per flow level; 1-3 subsamples per cobble) by placing a 4.15 cm^2 cylinder haphazardly on the surface (Angradi and Kubly 1993, Angradi et al. 1992). Material within the cylinder was removed by cutting and scraping the rock surface and rinsing within

the cylinder with river water. Cylinder contents and rinse water were stored in plastic vials on ice until they were frozen in the laboratory pending analyses for chlorophyll *a*, pheophytin *a* and AFDW.

Samples were thawed immediately prior to analyses. Pheophytin-corrected chlorophyll *a* concentration of extracts was determined using a modification of Tett et al. (1975). Samples were placed directly on 47 mm glass microfiber (Whatman GF/F) filters, washed lightly with purified water and filtered (5 lb vacuum). The filter with sample was placed into a blender flask and blended for 1 min in 200 ml methanol. A 40 ml aliquot was boiled for 2 min in a water bath (80°C) and filtered (GF/F filter, 5 lb vacuum) into a 50 ml graduated cylinder. Methanol was added to the filtered extract to a final volume of 40 ml. Optical density of a 15 ml aliquot was determined using a Milton Roy Spectronic 21D. AFDW was determined by loss on ignition.

Epilithon biomass and chlorophyll *a* data were normalized using a $\log(x+1)$ transformation and analyzed using a 3 x 2 x 2 ANOVA with repeated measures and subsequent Duncan's Multiple Range Test. Data from June 1995 were omitted from analyses due to missing data from the 142 m³s⁻¹ flow elevation.

Epipelon

Chara/Potamogeton samples were collected quarterly at -3.5 mi from the 142 m³s⁻¹ and 227 m³s⁻¹ flow elevations January - November 1995. The macroalga *Chara* sp. and the angiosperm *Potamogeton* sp. were collected simultaneously in each sample due to their complex intergrowth in the beds. *Chara* sp. was consistently much more abundant than *Potamogeton* sp. in the transect (personal observation). Mile -3.5 was selected for sampling these benthic flora because they invaded the site during fall 1993 and became abundant and extensively distributed. The site appeared to be representative of areas in the river being colonized by these species. Samples were collected haphazardly along fixed 50 m transects parallel to river flow by securely placing a Hess sampler onto the substrate, removing all plant material within the sampler by hand and placing it into the collecting net. The net and material within it were rinsed briefly in the river to remove debris and sediment. Samples were removed from the collecting cylinder and stored in plastic ziplock bags on ice until they were frozen in the laboratory prior to analyses.

Following thawing, the total sample was drained and weighed. A 20 g subsample was homogenized in a blender for two minutes in 200 ml deionized water. A 10 ml aliquot of the homogenate was removed using a catheter syringe, transferred to a vacuum system and filtered (5 lb

vacuum; 4.7 cm glass fiber filter;). Syringe and plunger were rinsed lightly into the vacuum flask with deionized water. Filter and contents were analyzed for chlorophyll *a* and pheophytin *a* using methanol extraction (as described for epilithon analyses). AFDW of the unhomogenized portion of the sample was determined by loss on ignition.

Chara/Potamogeton biomass, chlorophyll *a* and pheophytin *a* data were normalized using a $\log(x+1)$ and analyzed using a 4 x 2 ANOVA with repeated measures and subsequent Duncan's Multiple Range Test.

FPOM

Sampling

Fine particulate organic mater (FPOM; 0.7 μm - 1,000 μm) was sampled quarterly from: Lake Powell (LP) forebay surface (1 m) and penstock depth (January - August 1995), from 75 m depth (January - April 1995), and from Glen Canyon Dam (GCD) draft tubes and the Colorado River at Lee's Ferry (January - December 1995). Water samples were collected in precleaned 5 gal polypropylene carboys. Lake Powell FPOM samples were collected with a diaphragm pump. Glen Canyon Dam FPOM samples were collected directly from central draft tube sampling ports. Lee's Ferry FPOM was sampled by pumping water from the river while traversing from one side of the river to the other along a transect perpendicular to the flow, raising and lowering the pump intake sinusoidally.

Analyses

FPOM chlorophyll *a* (pheophytin-corrected) content was determined by filtering three 3 L subsamples onto preweighed, glass fiber filter paper (0.7 μm pore size). A saturated solution of MgCO_3 (100 μl) was added to the final 200 ml being filtered. Filters were placed into petri dishes, wrapped in foil and frozen until analyzed. Samples were analyzed within one week of collection. Thawed samples (previously filtered) were homogenized in a hand-held glass homogenizer (20 ml) in 20 ml methanol. Contents were transferred to a 250 ml beaker and the homogenizer rinsed with an additional 20 ml methanol. The homogenate was boiled in a water bath (80°C) for 2 min. A 40 ml aliquot was filtered (10-12 lb vacuum) into a 50 ml graduated cylinder. Optical density of a 15 ml aliquot was read at 480 nm, 750 nm, 666 nm and again at 750 nm against a methanol blank. The

aliquot then was acidified with 122 μ l of 1N HCl, vortexed and optical density read at the above wavelengths after 90 sec (Tett et al. 1975).

FPOM biomass was determined by filtering three 3 L sub-samples onto preweighed, preburned glass fiber filter paper (0.7 μ m pore size). Ash free dry weight (AFDW) then was determined by loss on ignition. Samples were dried at approximately 100°C for 24 hr then desiccated to a constant weight. Samples were ashed for 2 hr (500°-525°C) cooled, then desiccated to a constant weight.

FPOM biomass data were analyzed by location and month with Kruskal-Wallis ANOVA. Data were further analyzed by location and month using nonparametric Multiple Comparisons Tests (Zar 1984).

FPOM chlorophyll *a* data were normalized using a $\log(x+1)$ transformation and compared using a 2 x 5 (January vs April, all locations), 3 x 4 (January - August, Lake Powell surface and penstock depths, GCD draft tubes and Lee's Ferry) and 4 x 2 (January - December, GCD draft tubes and Lee's Ferry) analysis of variance with repeated measures. Data were further analyzed using Duncan's Multiple Range Test.

Zooplankton

Single zooplankton samples were collected in the forebay of LP 200 m in front of the dam from the surface and penstock depth, from #6 draft tube in GCD, and from Lee's Ferry on the Colorado River (January 1995). Beginning April 1995 a 0-60m vertical tow replaced the surface collection. Duplicate samples were taken at all locations in August 1995, and triplicate collections were taken from GCD draft tubes and Lee's Ferry in December. Collections from the forebay of Lake Powell were discontinued due to insufficient funding. Zooplankton were collected between 09:00 and 17:00 hrs by pumping (or drawing from draft tubes) 100 L of water through an 80 μ m plankton net and preserving in 70% ethanol. We conducted vertical zooplankton tows by lowering a 11.5 cm diameter 80 μ m plankton net with a 450 g weight suspended from the bottom of the collection cup to a depth of 60 m and retrieved at 10 cm/sec. Samples were preserved in 70% ethanol. In the laboratory, samples were poured into a 53 micron sieve, rinsed, transferred into a 50 ml graduated cylinder and the volume brought to 50 ml with water. Five 1 ml subsamples were

counted from each sample, and a mean density was calculated and used as the density value for each sample. Zooplankton other than nauplii were keyed to genus; nauplii were grouped together.

Zooplankton data from August were analyzed by a 4 x 5 (location x taxa) ANOVA. Data from the GCD draft tube and Lee's Ferry for August and December were analyzed by a 2 x 2 x 5 (month x location x taxa) ANOVA. Data were further analyzed using Duncan's Multiple Range Test.

RESULTS

Glen Canyon Dam Releases

Minimum and maximum daily releases from Glen Canyon Dam (GCD) in 1995 are shown in figure 1. Minimum releases averaged 271 m^3s^{-1} January 1 through February 28, 211 m^3s^{-1} March 1 through May 31, 448 m^3s^{-1} June 1 through September 30 and 326 m^3s^{-1} October 1 through December 31. Maximum releases averaged 443 m^3s^{-1} , 359 m^3s^{-1} , 548 m^3s^{-1} and 515 m^3s^{-1} during the same time periods.

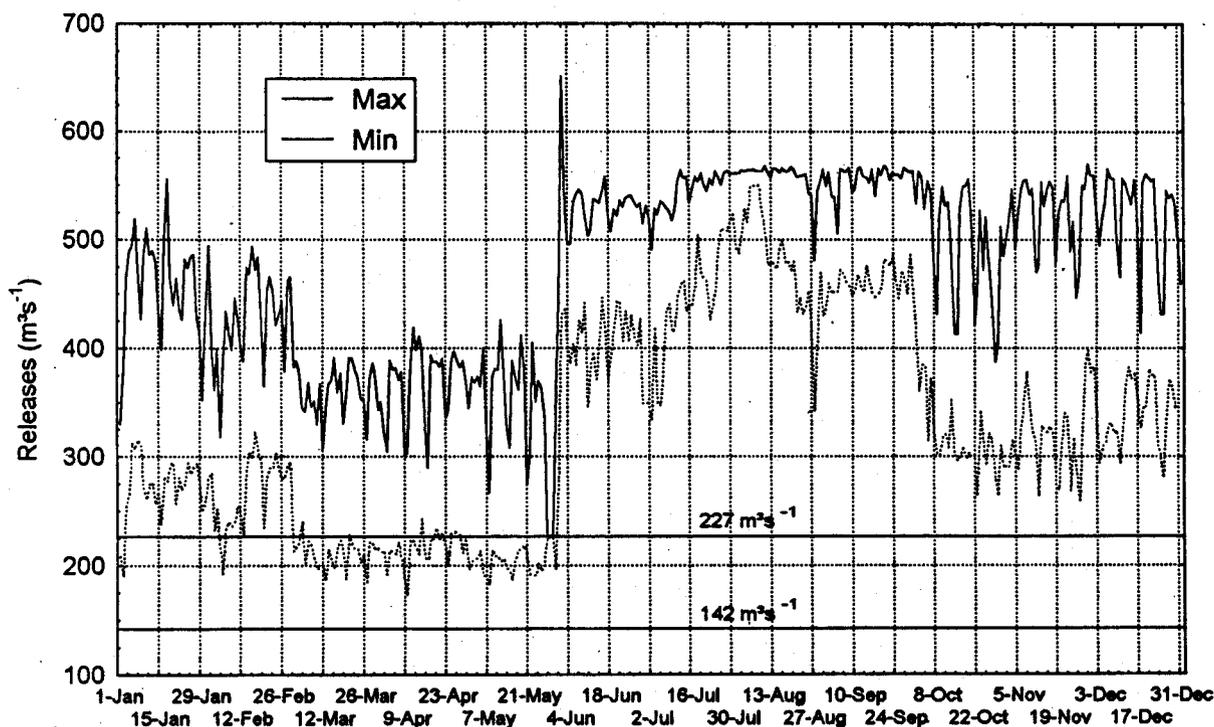


Figure 1. Glen Canyon Dam daily minimum and maximum releases (m^3s^{-1}) during 1995. Horizontal lines indicate the fluctuating ($227 \text{ m}^3\text{s}^{-1}$) and permanently inundated ($142 \text{ m}^3\text{s}^{-1}$) flow zones.

Benthic Invertebrates

No significant differences in invertebrate densities were found between flow elevations (Table 1). Densities of *Gammarus lacustris*, chironomid larvae and pupae, were greatest at -14 mile ($p < 0.05$) while densities of oligochaetes, ostracods and turbellarians were lowest at -14 mile ($p < 0.05$) (Table 1). Densities of nematodes were greatest at -3.5 mile while gastropod densities were greatest at -4.1 mile ($p < 0.05$). November found the greatest densities of *Gammarus lacustris* and turbellarians ($p < 0.05$) while gastropod densities peaked in January ($p < 0.05$). Densities of chironomid larvae and pupae were lowest in January ($p < 0.05$). Gastropod densities were lowest in April ($p < 0.05$) with the lowest densities at -3.5 mile ($p < 0.05$). We found bivalve density low (generally less than $11/m^2$) with no differences by mile or month.

Periphyton

Epilithon

No differences in periphyton biomass were found between river miles or flow elevations (Table 2). Periphyton biomass was higher in April than in January or November ($p < 0.05$). Periphyton chlorophyll *a* was higher at -14 mile than at -4.1 mile ($p < 0.05$) and was higher at the $142 \text{ m}^3\text{s}^{-1}$ flow elevation ($p < 0.05$) (Table 2). Chlorophyll *a* was highest in April and lowest in January ($p < 0.05$).

Epipelon

Chara/Potamogeton biomass and chlorophyll *a* were higher and pheophytin *a* lower at the $142 \text{ m}^3\text{s}^{-1}$ flow elevation ($p < 0.05$) (Table 3). Biomass and chlorophyll *a* were highest and pheophytin *a* was lower in November ($p < 0.05$).

FPOM

FPOM biomass was higher at the surface of Lake Powell than at penstock and 75 m depths ($p < 0.05$) (Table 4). At the surface of Lake Powell and at Lee's Ferry, biomass was higher in August than in January ($p < 0.05$) and biomass in the GCD draft tubes was higher in December than in January

($p < 0.05$). FPOM chlorophyll a was higher at the surface of Lake Powell than at penstock and 75m depths ($p < 0.05$). FPOM chlorophyll a was higher at Lee's Ferry than that at GCD draft tubes ($p < 0.05$). No significant differences were found between the penstock depth in the forebay of Lake Powell and the GCD draft tube ports (Table 4). FPOM chlorophyll a at surface and penstock depths in the forebay of Lake Powell peaked in April ($p < 0.05$). FPOM chlorophyll a from the GCD draft tubes was highest in December and lowest in August ($p < 0.05$), while at Lee's Ferry highest values were found in April and the lowest in January and August ($p < 0.05$).

Zooplankton

Highest densities of adult copepods, nauplii, rotifers and cladocerans were found in the epilimnion within Lake Powell (Table 5). Densities of copepod adults were highest during December, but densities of copepod nauplii were highest during summer. At GCD draft tubes and Lee's Ferry, adult copepod densities were higher in December than in August, while copepod nauplii and rotifers densities were higher in August than in December ($p < 0.05$) (Table 5). Densities of adult copepods were greater in December than August, and densities of copepod nauplii were greater in August than December, at GCD draft tubes than at Lees ferry ($p < 0.05$). Cladoceran densities at Lee's Ferry exceeded those from dam draft tubes during winter and spring.

Table 1. Mean (SD) benthic invertebrate densities (#/m²) at -3.5 mi, -4.1 mi and -14.0 mi, 142 m³s⁻¹ and 227 m³s⁻¹ flow elevations. January - November 1995.

River mile	Flow Elevation	1/29/95	4/30/95	6/26/95	11/19/95
<i>Gammarus lacustris</i>					
-3.5 mi	142 m ³ s ⁻¹	2126 (726)	330 (224)	1502 (1236)	3268 (1184)
	227 m ³ s ⁻¹	716 (74)	540 (178)	448 (422)	1751 (1208)
-4.1 mi	142 m ³ s ⁻¹	1149 (354)	651 (173)		1900 (190)
	227 m ³ s ⁻¹	674 (222)	441 (48)		3736 (2202)
-14.0 mi	142 m ³ s ⁻¹	2966 (139)	1946 (735)		6057 (5605)
	227 m ³ s ⁻¹	697 (53)	1195 (1287)		8498 (5554)
<i>Oligochaetes</i>					
-3.5 mi	142 m ³ s ⁻¹	1548 (1958)	471 (279)	12644 (17134)	1448 (1019)
	227 m ³ s ⁻¹	3510 (5860)	820 (1204)	1490 (966)	153 (186)
-4.1 mi	142 m ³ s ⁻¹	1847 (362)	946 (471)		1808 (314)
	227 m ³ s ⁻¹	391 (181)	272 (232)		1713 (467)
-14.0 mi	142 m ³ s ⁻¹	103 (61)	123 (89)		287 (263)
	227 m ³ s ⁻¹	187 (146)	356 (304)		682 (256)
<i>Chironomid Larvae</i>					
-3.5 mi	142 m ³ s ⁻¹	19 (18)	406 (241)	4100 (3000)	824 (139)
	227 m ³ s ⁻¹	287 (150)	2575 (1356)	4989 (2765)	157 (104)
-4.1 mi	142 m ³ s ⁻¹	61 (27)	241 (41)		437 (260)
	227 m ³ s ⁻¹	38 (35)	226 (137)		969 (374)
-14.0 mi	142 m ³ s ⁻¹	149 (30)	1261 (466)		713 (704)
	227 m ³ s ⁻¹	57 (41)	5816 (4489)		877 (336)
<i>Chironomid Pupae</i>					
-3.5 mi	142 m ³ s ⁻¹	0	19 (13)	433 (471)	8 (7)
	227 m ³ s ⁻¹	0	103 (94)	230 (100)	4 (7)
-4.1 mi	142 m ³ s ⁻¹	4 (7)	11 (0)		38 (7)
	227 m ³ s ⁻¹	8 (13)	8 (7)		57 (20)
-14.0 mi	142 m ³ s ⁻¹	34 (11)	207 (161)		34 (20)
	227 m ³ s ⁻¹	11 (11)	119 (77)		61 (27)

Table 1 Continued. Mean (SD) benthic invertebrate densities (#/m²) at -3.5 mi, -4.1 mi and -14.0 mi, 142 m³s⁻¹ and 227 m³s⁻¹ flow elevations. January - November 1995.

River mile	Flow Elevation	1/29/95	4/30/95	6/26/95	11/19/95
Ostracods					
-3.5 mi	142 m ³ s ⁻¹	169 (192)	38 (29)	1165 (1759)	92 (11)
	227 m ³ s ⁻¹	126 (181)	211 (178)	556 (688)	253 (70)
-4.1 mi	142 m ³ s ⁻¹	326 (77)	720 (244)		27 (29)
	227 m ³ s ⁻¹	184 (70)	1065 (819)		8 (13)
-14.0 mi	142 m ³ s ⁻¹	61 (24)	15 (18)		8 (13)
	227 m ³ s ⁻¹	103 (53)	203 (123)		27 (29)
Nematodes					
-3.5 mi	142 m ³ s ⁻¹	322 (178)	1349 (522)	1180 (774)	498 (389)
	227 m ³ s ⁻¹	1176 (551)	471 (150)	1701 (1730)	529 (737)
-4.1 mi	142 m ³ s ⁻¹	57 (12)	23 (40)		54 (65)
	227 m ³ s ⁻¹	4 (7)	4 (7)		96 (35)
-14.0 mi	142 m ³ s ⁻¹	8 (13)	0		8 (13)
	227 m ³ s ⁻¹	0	4 (7)		0
Gastropods					
-3.5 mi	142 m ³ s ⁻¹	65 (59)	4 (7)	57 (30)	123 (44)
	227 m ³ s ⁻¹	84 (57)	23 (11)	46 (30)	57 (30)
-4.1 mi	142 m ³ s ⁻¹	835 (115)	249 (58)		96 (13)
	227 m ³ s ⁻¹	280 (48)	130 (37)		333 (257)
-14.0 mi	142 m ³ s ⁻¹	134 (57)	103 (30)		57 (30)
	227 m ³ s ⁻¹	65 (27)	57 (23)		172 (155)
Turbellarians					
-3.5 mi	142 m ³ s ⁻¹	510 (206)	69 (90)	107 (146)	874 (202)
	227 m ³ s ⁻¹	444 (103)	161 (87)	27 (24)	1502 (932)
-4.1 mi	142 m ³ s ⁻¹	1153 (54)	433 (210)		1188 (427)
	227 m ³ s ⁻¹	536 (157)	203 (139)		1123 (344)
-14.0 mi	142 m ³ s ⁻¹	4 (7)	4 (7)		8 (7)
	227 m ³ s ⁻¹	4 (7)	27 (7)		54 (65)

Table 1 Continued. Mean (SD) benthic invertebrate densities (#/m²) at -3.5 mi, -4.1 mi and -14.0 mi, 142 m³s⁻¹ and 227 m³s⁻¹ flow elevations. January - November 1995.

River mile	Flow Elevation	1/29/95	4/30/95	6/26/95	11/19/95
Bivalves					
-3.5 mi	142 m ³ s ⁻¹	8 (7)	4 (7)	61 (59)	0
	227 m ³ s ⁻¹	4 (7)	4 (7)	0	0
-4.1 mi	142 m ³ s ⁻¹	0	4 (7)		8 (13)
	227 m ³ s ⁻¹	11 (11)	0		4 (7)
-14.0 mi	142 m ³ s ⁻¹	0	0		0
	227 m ³ s ⁻¹	0	0		0

Table 2. Mean (SD) epilithon biomass (g/m²) and chlorophyll *a* (mg/m²) at -4.1 mi and -14.0 mi, 142 m³s⁻¹ and 227 m³s⁻¹ flow elevations. January - November 1995.

River mile	Flow Elevation	1/29/95	4/30/95	6/26/95	11/19/95
Biomass					
-4.1 mi	142 m ³ s ⁻¹	76.0 (33.3)	145.6 (59.9)		115.7 (47.5)
	227 m ³ s ⁻¹	108.6 (40.3)	200.2 (69.5)	113.1 (55.1)	128.3 (75.9)
-14.0 mi	142 m ³ s ⁻¹	117.8 (21.7)	147.7 (49.8)		127.9 (33.4)
	227 m ³ s ⁻¹	84.7 (42.8)	102.8 (45.1)	113.4 (60.3)	97.59 (24.3)
Chlorophyll <i>a</i>					
-4.1 mi	142 m ³ s ⁻¹	503.9 (236.6)	2462.5 (840.8)		903.2 (348.4)
	227 m ³ s ⁻¹	275.7 (102.5)	1124.6 (400.4)	229.8 (99.5)	924.4 (495.8)
-14.0 mi	142 m ³ s ⁻¹	1317.9 (326.9)	2237.0 (797.0)		768.5 (227.2)
	227 m ³ s ⁻¹	765.9 (255.6)	2377.5 (990.9)	953.4 (365.6)	786.5 (274.5)

Table 3. Mean (SD) epipelton biomass (g/m^2), chlorophyll α and pheophytin α (mg/m^2) at -3.5 mile, $142 \text{ m}^3\text{s}^{-1}$ and $227 \text{ m}^3\text{s}^{-1}$ flow elevations. January - November 1995.

	Flow				
	Elevation	1/29/95	4/30/95	6/26/95	11/19/95
Biomass	$142 \text{ m}^3\text{s}^{-1}$	191.4 (133.7)	69.9 (27.0)	81.0 (25.2)	217.5 (40.2)
	$227 \text{ m}^3\text{s}^{-1}$	52.5 (14.3)	26.6 (9.5)	52.1 (9.1)	113.0 (38.6)
Chlorophyll α	$142 \text{ m}^3\text{s}^{-1}$	585.4 (146.3)	455.0 (501.1)	380.2 (198.5)	1232.2 (356.2)
	$227 \text{ m}^3\text{s}^{-1}$	95.5 (54.8)	83.7 (61.3)	240.5 (77.3)	784.7 (338.5)
Pheophytin α	$142 \text{ m}^3\text{s}^{-1}$	4.3 (1.6)	3.4 (1.8)	8.7 (5.3)	2.5 (1.6)
	$227 \text{ m}^3\text{s}^{-1}$	11.8 (9.2)	10.0 (3.5)	13.8 (3.4)	7.1 (2.5)

Table 4. Mean (SD) FPOM biomass and chlorophyll α (mg/m^3), at the Lake Powell forebay surface (LPS), penstock (LPP) and 75 m (LP75) depths, Glen Canyon Dam draft tubes (GCDdt) and Lee's Ferry (LF). January - December 1995.

Location		1/20/95	4/15/95	8/23/95	12/18/95
LPS	Biomass	255.6 (50.9)	633.3 (176.4)	855.6 (83.9)	
	Chlorophyll α	0.460 (0.237)	1.420 (0.158)	0.988 (0.068)	
LPP	Biomass	166.7 (152.8)	177.8 (157.5)	255.6 (221.9)	
	Chlorophyll α	0.125 (0.125)	0.230 (0.158)	0.146 (0.130)	
LP75	Biomass	200.0 (33.3)	288.9 (19.2)		
	Chlorophyll α	0.021 (0.036)	0.0 (0.0)		
GCDdt	Biomass	244.4 (38.5)	322.2 (19.2)	388.9 (19.2)	444.4 (69.4)
	Chlorophyll α	0.292 (0.036)	0.209 (0.181)	0.063 (0.109)	0.668 (0.036)
LF	Biomass	300.0 (0.0)	622.2 (101.8)	811.1 (283.5)	500.0 (33.3)
	Chlorophyll α	0.627 (0.109)	2.716 (0.096)	0.648 (0.096)	1.128 (0.063)

Table 5. Mean (SD) zooplankton densities (#/m³) at Lake Powell (LP) 0-60m and penstock depths, Glen Canyon Dam (GCD) draft tubes and Lees Ferry. January - November 1995. * Surface collection only.

Location	1/19/95	4/14/95	8/22/95	12/18/95
Copepod Adults				
LP 0-60m	8600*	2808	2688 (806)	
LP penstock	700		1100 (283)	
GCD draft tubes	900	900	1250 (354)	3367 (814)
Lee's Ferry	100	500	1400 (566)	1333 (208)
Copepod Nauplii				
LP 0-60m	3400*	3033	15420 (3245)	
LP penstock	900		12600 (5940)	
GCD draft tubes	4000	4000	11200 (1131)	3433 (929)
Lee's Ferry	1200	3400	7350 (495)	2567 (208)
Rotifers				
LP 0-60m	100*	1155	1966 (1169)	
LP penstock	0		450 (212)	
GCD draft tubes	0	400	1100 (141)	133 (58)
Lee's Ferry	0	600	1200 (566)	100 (0)
Cladocerans				
LP 0-60m	100*	48	144 (91)	
LP penstock	0		0	
GCD draft tubes	0	0	200 (141)	67 (115)
Lee's Ferry	1200	100	200 (283)	67 (115)

DISCUSSION

Densities of benthic macroinvertebrates were similar in the dewatered (fluctuating flow elevation) and submerged (permanently-inundated) zones. However, earlier investigations showed that benthic macroinvertebrate concentrations were lower in the dewatered zone downstream from Glen Canyon Dam (Angradi and Kubly 1993, Angradi et al. 1992b, Ayers and McKinney 1996a, 1996b, Blinn et al. 1992, 1994, 1995). Similarity in zoobenthic densities between the dewatered and submerged zones during 1995 may reflect the influence of higher minimum flows and increased food and habitat for the invertebrates (Ayers and McKinney 1996a, 1996c, Blinn et al. 1992, 1994).

Consistent with previous results (Ayers and McKinney 1996a, 1996b), densities of benthic macroinvertebrates exhibited spatial and temporal variability. Densities of *Gammarus* and chironomids were greatest at -14 mi, while those of oligochaetes, ostracods, snails and flatworms tended to be lower at this site than elsewhere. During 1992 to about mid-1994, amphipod densities at -3.5 mi exceeded those at -14 mi (Angradi et al. 1992b, Ayers and McKinney 1996a, 1996b). Standing stock of *Gammarus* tended to decline and remain low after late 1993 at -3.5 mi, while densities at -14 mi remained comparatively stable (Ayers and McKinney 1996a, 1996b). Standing stocks of benthic macroinvertebrates other than *Gammarus* showed no consistent trends in present or earlier studies (Ayers and McKinney 1996a, 1996b).

Angradi et al. (1992b) reported that densities of the amphipod at -3.5 mi were high in 1992, although periphyton biomass at the site was low. Submerged macrophytes did not colonize extensively at -3.5 mi until late 1993 (Ayers and McKinney 1996c), and Angradi et al. (1992b) suggested that periphyton biomass is not the only determinant of *Gammarus* densities. Abiotic variables apparently do not primarily regulate stream biota, but periphyton is strongly regulated by herbivores in lotic systems (Feminella and Hawkins 1995). However, interactions between benthic algae and herbivory are complex and influenced by numerous factors (Biggs 1996, Lamberti 1996). Algal biomass provides an index of how much food is potentially available to herbivores in a system at a point in time but provides no information on how large a herbivore population can be supported by that biomass (Steinman and Lamberti 1996).

Biomass of epilithon also was comparable in the dewatered and submerged zones, but chlorophyll *a* densities were lower in the dewatered zone. Angradi and Kubly (1993) also reported that chlorophyll *a* was more sensitive to exposure than was biomass, but the mechanisms of

phytopigment destruction are uncertain. The lower chlorophyll *a* values in January and April coincide with lower minimum flows and greater exposure. Determination of biomass precludes distinction of algal material from other organic material in the sample. Chlorophyll *a* densities, however, are related to algal matter, and lower chlorophyll *a* levels indicate a negative impact on the algal assemblage (Angradi and Kubly 1993, Blinn et al. 1994, 1995). In contrast to present results, both indices of standing stock were lower in the dewatered zone in earlier studies during the interim flow regime (Angradi et al. 1992a, Angradi and Kubly 1993, Ayers and McKinney 1996c, Blinn et al. 1994), but differences between the flow zones diminished after mid- 1993 (Ayers and McKinney 1996c). Also, standing stock at -14 mi was greater than at -4.1 mi prior to (Ayers and McKinney 1996c) but not during 1995. Comparative results for these sites possibly reflect fewer sampling periods during 1995 but are consistent with progressive changes in epilithon standing stock during interim flows (Ayers and McKinney 1996c, Blinn et al. 1994).

Submerged macrophytes colonized extensively in the dam tailwater during interim flows (Ayers and McKinney 1996c) and appear to be more adversely impacted than epilithon by fluctuating flow levels, possibly due in part to relative instability of the depositional substrate (Peterson 1996). Consistent with previous results (Ayers and McKinney 1996c), biomass and chlorophyll *a* densities of *Chara/Potamogeton* were lower in the dewatered zone. This difference between flow zones continued throughout 1995 despite the higher minimum flows from June 1 through December 31.

Concentrations, vertical distribution and seasonal changes of FPOM biomass and chlorophyll *a* in the Lake Powell forebay and concentrations and seasonal changes in the dam discharge and at Lee's Ferry during 1995 were similar to those during 1993-1994 (Ayers and McKinney 1996c). Autochthonous processing and production of FPOM in the dam tailwater increased during interim the interim flow regime (Angradi and Kubly 1994, Ayers and McKinney 1996c) and continued to occur during 1995. The increased autochthonous production and processing is consistent with greater primary production below Glen Canyon Dam during interim flows (Ayers and McKinney 1996c, Blinn et al. 1994) and does not appear to reflect changes among months or years in primary production in the reservoir forebay.

Comparing results from 1995 with those during 1993-1994 for the same months (Ayers and McKinney 1996d), assemblages and densities and seasonal patterns of change of zooplankton were generally similar at the various sampling locations. Downstream reductions in densities of copepod adults and nauplii between dam draft tubes and Lee's Ferry during winter or summer also were

apparent in 1995 and 1993-1994 (Ayers and McKinney 1996d), likely reflecting filtration of the zooplankton by benthic flora. Densities of cladocerans at Lee's Ferry increased above those in the dam discharge during winter and spring 1995. Similar results were obtained during 1993-1994 (Ayers and McKinney 1996d), indicating that autochthonous production by the taxa occurs in the tailwater.

Blinn et al. (1994) concluded that reduced daily discharge fluctuations and ramping rates during interim flows generally increased standing stocks of algae and macroinvertebrates below Glen Canyon Dam. Our findings are consistent with this conclusion and further indicate that differences decreased between standing stocks of epilithon and macroinvertebrates in the dewatered and submerged zones during interim flows. However, we collected samples in lower areas of the dewatered zone which experience comparatively little atmospheric exposure due to fluctuating flow elevations. Our results do not represent reduced influence of exposure, per se, on the lotic biota. Numerous investigations (e.g. Angradi and Kubly 1993, Blinn et al. 1994, 1995) have shown negative impacts of atmospheric exposure on benthic algae and macroinvertebrates. Peterson (1996), however, observed that *Cladophora* (dominant epilithic alga in the tailwater) is tolerant of periodic emersion, and Angradi and Kubly (1993) suggested that epilithon from the dewatered zone was more tolerant of exposure than epilithon from the submerged zone.

CONCLUSIONS

Our results are in agreement with those of Blinn et al. (1994) that the interim flow regime generally has increased standing stocks of benthic algae and macroinvertebrates in the Glen Canyon Dam tailwater. However, in depositional habitat, *Gammarus* standing stock trended downward during interim flows while periphyton biomass increased and changed compositionally. Also, submerged macrophytes appear to be less resistant to dewatering than is epilithon. Concurrent spatial and temporal variability of benthic algae and macroinvertebrates in lotic systems is an important consideration in assessing the biotic community and designing monitoring programs (Biggs 1996, McElravy et al. 1989, Resh and Rosenberg 1989).

Less energetic flows during the interim flow regime also have promoted lotic detrital processes and autochthonous production of FPOM in the dam tailwater. Increased FPOM

processes, production and transport in the tailwater potentially influence and are influenced by the lotic biotic community (Angradi 1993, Ayers and McKinney 1996c, Cushing et al. 1993, Steinman 1996, Thorp and DeLong 1994).

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