EFFECTS OF GLEN CANYON DAM OPERATIONS ON *Gammarus lacustris* IN THE GLEN CANYON DAM TAILWATER

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Andrew D. Ayers and Ted McKinney

Arizona Game and Fish Department
2221 West Greenway Road
Phoenix, Arizona 85023

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INTRODUCTION

The Glen Canyon Environmental Studies (GCES) were initiated in 1982 in response to potential changes in the Bureau of Reclamation management of water flowing in the Colorado River through Glen Canyon Dam and environmental concerns relating in part to dam operations. Research under Phase I (GCES I) extended from 1982-1988 and provided the basis for implementation in 1988 of further investigations under Phase II (GCES II). Phase II studies were designed to incorporate testable hypotheses and develop an information base necessary to evaluate operations of Glen Canyon Dam. Patten (1991) provided a broad perspective of the history of GCES I and of GCES II projected studies and objectives.

On January 4, 1994, a draft Environmental Impact Statement concerning operations of Glen Canyon Dam was filed with the Environmental Protection Agency, based upon information and data gathered during GCES I and GCES II studies. Angradi et al. (1992) addressed the scope and background of GCES I investigations, emphasizing research conducted during controlled flows from June 1990 through July 1991. Since August 1991, releases from Glen Canyon Dam have followed interim flow criteria mandated by the Secretary of the Interior. The interim flow regime has restricted minimum and maximum releases from the dam to $142m^3s^{-1}$ (5,000 cfs) and $568m^3s^{-1}$ (20,000) cfs, respectively (Angradi et al. 1992). Daily ranges vary dependent upon total monthly flows but may not exceed $227m^3s^{-1}$ (8,000 cfs), while hourly increases and decreases are limited to $71m^3s^{-1}$ (2,500 cfs) and $43m^3s^{-1}$ (1,500 cfs), respectively. Errors not to exceed 10% are permitted, recognizing difficulty in controlling releases.

Purpose of the present report is to provide information concerning investigations carried out during the interim flow regime within the tailwaters of Glen Canyon Dam to Lee's Ferry (25 km downstream). Particularly, these studies have emphasized driving variables (flow components as related to dam discharge) in relation to response variables (ecosystem processes and lower trophic levels). Our use of the terms ecosystem and trophic level incorporate descriptions provided by Poole (1974). Ecosystem processes and trophic levels addressed are those which affect and/or represent directly the provisioning of food resources to the fishes for which the Arizona Game and Fish Department and other resource management agencies have legislatively mandated responsibilites.

Numerous reports have addressed effects of fluctuating flows and water levels on benthic organisms in tailwaters of hydroelectric facilities (Cushman 1985, Fisher and LaVoy 1972, Garcia de Jalon et al. 1988, Trotzky and Gregory 1974), but fewer have provided information regarding *G. lacustris* (Ayers and McKinney 1996a, Angradi and Kubly 1993, Blinn et al. 1992,1994, 1995, Leibfried and Blinn 1987). Glen Canyon Dam operations have major influence on the phytobenthos, epiphyton and macroinvertebrates in the tailwaters (Angradi et al. 1992, Ayers and McKinney 1996a, 1996b, Blinn et al. 1992, 1994, 1995). Standing crops and production of the amphipod and other macroinvertebrates are lower in the zone of fluctuating flows in Glen Canyon (Angradi and Kubly 1993, Ayers and McKinney 1996a, 1996b, Blinn et al. 1994, Leibfried and

Blinn 1987). *G. lacustris* might be expected to recolonize denuded/depauperate areas through drift or movement up/across current (Hultin 1971, Mackay 1992, Minckley 1964, Waters 1964) during periods of inundation, but relative paucity of *C. glomerata* and its epiphytic diatoms may influence recolonization (Ayers and McKinney 1996a, 1996b, Blinn et al. 1994, 1995, Shannon et al. 1994). Stranding of *G. lacustris* is a possible source of loss (mortality, emigration) to populations and may occur as flow levels decline in Glen Canyon on sites with cobble and smaller stone substrates (Blinn and Cole 1991, Ayers and McKinney unpublished data). However, no stranding has been observed at depositional sites with sandy/silt substrate supporting *Chara* spp/ *Potamogeton* spp. and high amphipod densities (McKinney and S. Rogers, personal observation).

Gammarus lacustris is a cold-stenothermous amphipod crustacean which is widespread in Asia, Europe and North America. The species was first introduced during 1968 into the tailwaters of Glen Canyon Dam and provides an important food source for Colorado River exotic and native fishes (Angradi 1994, Angradi et al. 1992, Blinn and Cole 1991, Leibfried 1988, Stone and Rathbun 1969). Life history of *G. lacustris* is poorly understood (de March 1982, Hynes 1955, Hynes and Harper 1972, Marchant 1981, Mathias et al. 1982), but breeding activity may generally be limited to winter-spring-summer, with young hatching during spring-summer. Under laboratory temperatures of 15°C - 27°C, *G. lacustris* matured sexually in about 3-5 months (Smith 1973). However, age at sexual maturity may approach 2 yr in lotic systems with seasonally varying water temperatures (Hynes and Harper 1972, Marchant 1981). Individuals become sexually mature during February-March, breed through and die during June-July, and females may produce several clutches annually. Short day length or reduced light and temperature may be factors influencing reproductive activity (de March 1982, Smith 1973).

Waters (1965) reported that *G. lacustris* densities were much lower in riffles than in sandy areas, and other work indicates that *Gammarus* spp. may select for finer-particle substrates (Waters 1984, Gee 1982). However, both organic and inorganic fractions of stream substratum may influence habitat selection by the species (Gee 1982, Marchant 1981, Rees 1972, Waters 1965). In the Colorado River below Glen Canyon, distributions of *Cladophora glomerata* and *G. lacustris* were positively correlated, and epiphytic diatoms were the determinant of substratum choice (Shannon et al. 1994). Epiphytic diatoms associated with *C. glomerata* comprise a major portion of the diet of *G. lacustris* (Blinn et al. 1992, Pinney 1991), and stable isotope analyses indicated that the amphipod represents an intermediate trophic level between algae and fish (Angradi 1994). Data concerning microfauna associated with *C. glomerata* remain limited (Dodds and Gudder 1992, Whitton 1970).

Present studies were designed to assess effects of dam operations during interim flows on *G. lacustris* in Glen Canyon Dam tailwaters and to provide a baseline of data for future monitoring. Specific objectives were to determine regarding the amphipod: 1) distribution, standing crops and life history and 2) whether a relationship exists between dam operations and distribution, standing crops and life history.

METHODS

Gammarus lacustris were sampled in the benthos monthly from May 1992-October 1993 and quarterly from January-July 1994 using a Hess sampler (0.087 m^2) at the 5,000 cubic feet per second (cfs) (permanently inundated) and 8,000 cfs (intermittently dewatered) flow elevations. Linear transects (50 m) were established parallel to river flow at each site (-14 mi, -9 mi bank side and river side, -4.1 mi and -3.5 mi) and river elevation. Eight samples were collected haphazardly along each transect (4 samples each from -9 mi bank side and river side) and preserved in a 10% formaldehyde solution. After sampling a site, five flow velocity measurements were taken (Swoffer Model 2100 current velocity meter) along each transect 10 cm above the substrate. In the laboratory, samples were rinsed (tap water) in a 250 *um* sieve, and contents were placed into a dissecting pan and amphipods picked, counted and preserved in 95% ethanol. Preserved amphipods (from May 1992-May 1993) were sent to a contract laboratory for length measurements (grouped into 1 mm size classes), sexing and egg enumeration. Biomass data were derived following procedures outlined in Waters and Hokenstrom (1980).

Sampling locations were selected to reflect different habitats found within the dam tailwater. The upriver (-14 mi) and downriver (-9 mi, -4.1 mi, -3.5 mi) sites exhibit differences in flow velocities (Table 2.4.4), algal biomass and composition and a general downstream trend toward smaller/finer substrate particles (Angradi and Kubly 1994). Sites at -4.1 mi (first sampled December 1994) and -9 mi (first sampled January 1994) were established to obtain additional data from habitats different (with respect to flow velocity, substrate and/or algal type) from those present at previously-established locations (-14 mi and -3.5 mi, first sampled May 1992). The Colorado River at -9mi is bifurcated by Duck Island, and transects were established in the main (river-side) and side (bank-side) channels. The following anecdotal descriptions present a brief outline of major features at each site:

-14 mi: Large cobbles abundant, forming a major portion of the substrata; very little silt; comparatively high biomass of *C. glomerata*, the predominant benthic alga; river bed slopes comparatively steeply; comparatively high flow velocity.

-9 mi: River-side--substrate predominantly silt and small stones; comparatively low biomass of benthic algae (little *C. glomerata*); river bed slopes gently over a broad, shallow zone; low flow velocity. Bank-side--slope of river bed, substrata and attached algae similar to -14 mi; low flow velocity.

-4.1 mi: Substrate predominantly small stones and silt; low biomass of benthic algae (little *C. glomerata)*; similar to -9 mi river side.

-3.5 mi: Depositional zone (silt, sand) with few, localized areas of small stone substrate; high algal biomass, predominantly *Chara sp.* and *Potamogeton sp.*; low flow velocity; river bed slopes comparatively steeply.

All analyses excluded, due to missing data from the 5,000 cfs flow elevation, samples from December 1992 (-4.1 mi) and January 1993 (-14 mi, -4.1 mi and -3.5 mi). . Density data were normalized using a sqrt(x+1)+sqrt(x) transformation (Sokal and Rohlf 1981) and analyzed using analysis of variance (ANOVA) with repeated measures. Density data from -14 mi and -3.5 mi were compared using a 2x2x20 design, density data from - 14 mi, -4.1 mi and -3.5 mi were compared using a 3x2x12 design and data from -14 mi, -9 mi (two sites), -4.1 mi and -3.5 mi were compared using a 5x2x3 design.

Biomass data were normalized using a sqrt(x+1)+sqrt (x) transformation and analyzed using ANOVA with repeated measures. Biomass data from -3.5 mi and -14 mi were compared using a 2x2x12 design, and data from -3.5 mi, -4.1 mi and -14 mi were compared using a 3x2x4 design.

Mature amphipod data were kurtotic and could not be normalized. Nonparametric tests would not provide needed comparisons. Therefore, ANOVA with repeated measures, using a 0.01 level of significance, was incorporated to analyze the data. In addition, this data set has a large sample size, which should minimize bias associated with the non-normal distribution. Mature amphipod density data from -3.5 mi and -14 mi were compared using a 2x2x12 ANOVA with repeated measures, and data from -3.5 mi, -4.1 mi and -14 mi were compared using a 3x2x4 design.

Female amphipod size and instantaneous death rate data were analyzed using ANOVA with repeated measures with a 2x2x12 design to compare data from -3.5 mi and -14 mi and analyzed using a 3x2x4 design to compare data from -3.5 mi, -4.1 mi and -14 mi. Data for number of eggs per female could not be normalized and were therefore analyzed using the Kruskal-Wallis ANOVA by ranks test.

RESULTS

Density

G. lacustris density was highest in the late summer-early fall at the 5000 cfs flow elevation (5000 cfs) at -3.5 mi ($p < 0.05$). Highest densities were found in the late summer and early fall at 5000 cfs at river miles -3.5, -4.1 and -14. Densities at 5000 cfs were two to six times higher than the 8000 cfs flow elevation (8000 cfs), depending on river mile and sampling period ($p < 0.05$). Densities at river -3.5 mi were higher than -14 mi during the first nine months of this study ($p < 0.05$).

Data set = River miles -3.5 and -14, May 1992 - July 1994 excluding January 1993.

G. lacustris density differed significantly between 5,000 cfs and 8,000 cfs. ($p < 0.01$) among river miles ($p < 0.05$), and among months ($p < 0.01$). Also, interaction was significant between river mile and flow elevation ($p < 0.05$), month and river mile ($p < 0.01$), month and flow elevation ($p < 0.01$), and between month, river mile and flow elevation ($p < 0.01$, Appendix 1 Table 2.4.5).

At 5000 cfs, seasonal density peaks were found in October 1992, 1993 and 1994 ($p < 0.05$, Figures 2.4.1 and 2.4.3). No seasonality was evident at 8000 cfs. Densities at 5000 cfs versus 8000 cfs elevation were seven times higher at -3.5 mi and four times higher at -14 mi

($p < 0.01$, Appendix 1 Table 2.4.5). At 5000 cfs, -3.5 mi had a significantly higher density than -14 mi ($p < 0.01$).

Data set = River miles -3.5, -4.1 and -14, February 1993 - July 1994.

Gammarus density differed significantly between 5,000 cfs and 8,000 cfs ($p < 0.01$) and among months ($p < 0.01$) but no significant differences were found between river miles. Also, interaction was significant between river mile and flow elevation ($p < 0.01$), month and river mile ($p < 0.01$), month and elevation ($p < 0.01$) and between month, river mile and elevation ($p < 0.01$, Appendix 1 Table 2.4.6).

Peaks in density at 5000 cfs occurred in October 1993 and 1994 at all three river miles (Figures 2.4.1 - 2.4.3). Peaks in density at 8000 cfs occurred in August - September 1993 at -3.5 mi and -4.1 mi and in September 1993 and April 1994 at -14 mi (Figures 2.4.1 - 2.4.3). Density at 5000 cfs was almost four times higher than at 8000 cfs ($p < 0.01$, Appendix 1 Table 2.4.6).

Data set = River miles -3.5, -4.1, -9 river side, -9 bank side and -14, January - July 1994.

G. lacustris density differed significantly between 5,000 cfs and 8,000 cfs ($p < 0.01$) among river miles ($p < 0.01$) and among months ($p < 0.01$). Also, interaction was significant between month and river mile ($p < 0.01$) and between month, river mile and flow elevation ($p < 0.01$, Appendix 1 Table 2.4.7).

Density at 5000 cfs was significantly higher than at 8000 cfs at all river miles except -14 mi ($p < 0.05$, Appendix 1 Table 2.4.7). At 5000 cfs, densities at -3.5 mi and -14 mi were significantly higher than at -4.1 mi and -9 mi bank and river sides ($p < 0.05$). In addition -9 mi river side and -4.1 mi were significantly higher than -9 mi bank side ($p < 0.05$). At 8000 cfs, densities at -14 mi were significantly higher than all other river miles and -4.1 mi was significantly higher than -9 mi river side ($p < 0.05$, Appendix 1 Table 2.4.7).

Biomass

No seasonal patterns in biomass were evident. *G. lacustris* biomass was higher at 5000 cfs versus 8000 cfs ($p < 0.05$). Biomass at 8000 cfs was higher at -3.5 mi than -14 mi, and at 5000 cfs, biomass was higher at -4.1 mi than -3.5 mi ($p < 0.05$).

Data set = River miles -3.5 and -14, May 1992 - May 1993 excluding January 1993.

G. lacustris biomass differed significantly between 5000 cfs and 8000 cfs ($p < 0.01$) among river miles ($p < 0.05$) and among months ($p < 0.01$). Also, interaction was significant between river mile and flow elevation ($p < 0.01$), month and river mile ($p < 0.01$) and between month and flow elevation ($p < 0.01$, Appendix 1 Table 2.4.8).

No seasonal pattern was evident at 5000 cfs (Figure 2.4.1 and 2.4.3). However, biomass peaks were found in August - September 1992 and January 1993 at -14 mile 8000 cfs and in January 1993 at -3.5 mile 8000 cfs (Figure 2.4.1 & 2.4.3). *G lacustris* biomass at 5000 cfs was significantly higher than at 8000 cfs at both river miles ($p < 0.01$, Appendix 1 Table 2.4.4). At 8000, cfs biomass was significantly higher at -3.5 mi than at -14 mi ($p < 0.01$), but no significant difference in biomass was found between the two river miles at 5000 cfs (Appendix 1 Table 2.4.8).

Data set = River miles -3.5, -4.1 and -14, February - May 1993.

G. lacustris biomass differed significantly between 5,000 cfs and 8,000 cfs ($p < 0.01$) among river miles ($p < 0.05$) and among months ($p < 0.01$). Also, interaction was significant between month and river mile ($p < 0.01$) and between month, river mile and flow elevation ($p < 0.01$, Appendix 1 Table 2.4.9).

G lacustris biomass at 5000 cfs was significantly higher than at 8000 cfs at all three river miles ($p < 0.01$, Appendix 1 Table 2.4.9). At 5000 cfs, biomass was significantly higher at -4.1 mi than at -3.5 mi ($p < 0.05$). All other river mile comparisons were not significant (Appendix 1 Table 2.4.9).

G. lacustris Size Distribution

At -3.5 Mile 5000 cfs, 2000 - 3400 1 mm *G. lacustris* / m^2 entered the population from August - December 1992 (Figure 2.4.4). Recruitment from 1 - 4 mm was evident from October - December 1992, but recruitment into the larger size categories was limited. In June and July 1992, recruitment into the 3 - 6 mm size range occurred followed by recruitment into the 7 mm and larger size class in July - October 1992.

From July - October 1992 at -3.5 Mile 8000 cfs, 300 - 1700 1 mm size *G. lacustris* / m^2 entered the population (Figure 2.4.5). Recruitment of these small *G. lacustris* into the 3 - 6 mm size category was minimal, but recruitment into the >6 mm size category occurred from July - October 1992. No recruitment into the 1-2 mm size class was found in May 1993.

Limited data from -4.1 Mile 5000 & 8000 cfs indicated 300-400 1 mm size *G. lacustris* entering into the population in December and January 1993 at 8000 cfs. Recruitment into the 2-3 mm size category was found in February and March 1993 at 5000 cfs and in December - February at 8000 cfs (Figures 2.4.6 & 2.4.7).

At -14 Mile 5000 cfs, 400 - 3700 1 mm *G. lacustris* / m^2 entered the population from May - November 1992, with the greatest numbers occurring in September (Figure 2.4.8). Recruitment into the 2-3 mm size class was substantial during this same time period. Recruitment into the 3 mm and greater size classes was highest in June and September - December 1992.

At -14 mile 8000 cfs only 100 - 400 1 mm *G. lacustris* / m^2 entered into the population from July 1992 - January 1993 (Figure 2.4.9). Most of these animals were recruited into the 2 mm size category. Recruitment into larger categories was higher on a percentage basis than was found at other locations but numerically lower.

Mature *G. lacustris* Density

Seasonal peaks in mature *G. lacustris* were found in August - October 1992 and January 1993. The 5000 cfs elevation had a significantly higher density of mature *G. lacustris* than did 8000 cfs ($p < 0.05$). At 5000 cfs, -3.5 mile had significantly higher numbers of mature *G. lacustris* than did -14 mi or -4.1 mi ($p < 0.01$). Male density was significantly higher than female density at 5000 cfs ($p < 0.01$), but no sex differences were found between river miles.

Data set = River miles -14 and -3.5, May 1992 - May 1993 excluding January 1993.

Mature *G. lacustris* density differed significantly between 5,000 cfs and 8,000 cfs ($p < 0.01$), between river miles ($p < 0.01$) and among months ($p < 0.01$) but not between sexs (Appendix 1 Table 2.4.10). Also, interaction was significant between river mile and elevation ($p < 0.05$) and river elevation and month ($p < 0.01$, Appendix 1 Table 2.4.10).

Seasonal peaks of mature *G. lacustris* were found in September and October 1992 at -3.5 mi 5000 cfs and in August and September 1992 and January 1993 at -3.5 mi 8000 cfs (Figures 2.4.10 & 2.4.11). Significantly higher numbers of mature *G. lacustris* were found at 5000 cfs, versus 8000 cfs ($p < 0.01$, Appendix 1 Table 2.4.10). At 5000 cfs a significantly higher number of mature *G. lacustris* were found at -3.5 mi versus -14 mi ($p < 0.01$, Appendix 1 Table 2.4.10, Figure 2.4.10).

Data set = River miles -3.5, 4.1 and -14, February - May 1993.

Mature *G. lacustris* density differed significantly between 5000 cfs and 8000 cfs ($p < 0.01$), among river miles ($p < 0.01$), between sexes ($p < 0.01$) and among months ($p < 0.01$, Appendix 1 Table 2.4.11). Also, interaction was significant between river mile and elevation ($p < 0.01$), river mile and month ($p < 0.01$), river elevation and month ($p < 0.01$), sex and month ($p < 0.01$), river mile, elevation and month ($p < 0.01$) and river elevation, sex and month ($p < 0.01$, Appendix 1 Table 2.4.11).

Significantly higher numbers of mature *G. lacustris* were found at 5000 cfs versus 8000 cfs ($p < 0.01$, Appendix 1 Table 2.4.11, Figures 2.4.10 & 2.4.11). At 5000 cfs, river mile -3.5 had significantly higher numbers of mature *G. lacustris* than river miles -4.1 and -14 ($p < 0.01$). Significantly higher numbers of males were found at 5000 cfs ($p < 0.01$, Appendix 1 Table 2.4.11). No significant difference in the number of males versus females was found at 8000 cfs, and no significant differences in male versus female density was found among river miles.

Adult Sex Ratio and Egg Number / Female

Sex ratios (Female / Male) ranged from 0.05 to 2.2 during this study. Seasonal highs occurred in June, and lows occurred in December at all river miles and flow level elevations (Table 2.4.1). Females with eggs ranged in size from slightly less than 7 mm to 14 mm. Males ranged in size from 7 - 22 mm. Mean number of eggs per female ranged from 5.75 for 6+ mm (6.6 - 6.99) females to 23.75 for 14 mm females (Table 2.4.2). Most of the egg bearing females were in the 7 - 11 mm range.

Table 2.4.1. Sex ratios female/male by river mile (-14, -4.1 and -3.5) and river elevations (5000 cfs and 8000 cfs), May 1992 - May 1993. ** = All female in sample, * = All male in sample.

	-14 MILE 5000 cfs	-14 MILE 8000 cfs	-4.1 MILE 5000 cfs	-4.1 MILE 8000 cfs	-3.5 MILE 5000 cfs	-3.5 MILE 8000 cfs
MAY 92	1.18	1.57			1.04	1.47
JUN 92	1.36	**			2.05	**
JUL 92	0.88	2.20			1.48	1.43
AUG 92	0.63	1.21			0.70	0.57
SEP 92	1.07	1.07			0.36	0.42
OCT 92	0.62	1.56			0.38	0.39
NOV 92	0.31	0.30			0.18	0.50
DEC 92	0.12	0.10		0.05	*	0.08
JAN 93		0.60		0.13		0.35
FEB 93	0.27	0.31	0.29	0.39	0.28	0.36
MAR 93	0.92	0.62	0.58	0.62	1.39	0.31
APR 93	1.00	1.11	1.29	0.86	1.55	1.26
MAY 93	1.49	1.35	0.60	1.50	0.75	1.04

Table 2.4.2. Mean egg number per female by female size.

Female Size mm	Mean egg #/ female	Standard Error	N		Female Size mm	Mean egg #/ female	Standard Error	N
6	5.75	0.51	24		11	12.39	1.03	163
7	7.33	0.32	184		12	19.14	2.08	58
8	7.80	0.24	516		13	10.40	3.10	15
9	8.15	0.32	660		14	23.75	4.48	4
10	11.65	0.57	344					

Data set = River miles -14 and -3.5, May 1992 - May 1993 excluding January 1993.

Egg number per female differed significantly on a monthly basis ($p < 0.01$, Appendix 1 Table 2.4.12). At -14 mi 5000 cfs, the seasonal maximum in egg number per female was in June and the minimum in February (Figure 2.4.12). At -3.5 mi 5000 cfs, the seasonal minimum was in November and December 1992 (Figure 2.4.12). Egg number per female was significantly higher at 5000 cfs versus 8000 cfs ($p < 0.05$) and at -14 mi versus -3.5 mi ($p < 0.01$, Appendix 1 Table 2.4.13 & 2.4.14)

Data set = River miles -3.5, 4.1 and -14, February - May 1993.

Egg number per female was significantly higher at 5000 cfs versus 8000 cfs ($p < 0.05$, Appendix 1 Table 2.4.15). River mile -14 had the highest egg number per female and -4.1 mi the lowest ($p < 0.01$, Appendix 1 Table 2.4.16).

Female Size

Data set = River miles -14 and -3.5, May 1992 - May 1993 excluding December 1992 and January 1993.

G. lacustris female size differed significantly between river miles ($p < 0.01$) and among months ($p < 0.01$, Appendix 1 Table 2.4.17). Also, interaction was significant between month and river mile ($p < 0.01$). Seasonal highs in female size were found during November or December 1992 at -14 mi 5000 cfs and 8000 cfs and -3.5 mi 8000 cfs (Figures 2.4.12 & 2.4.13). Seasonal lows in female size were found in August or September 1992 at both river miles and elevations (Figures 2.4.12 & 2.4.13). River mile -14 had significantly larger females than -3.5 mi ($p < 0.01$, Appendix 1 Table 2.4.17).

Data set = River miles -3.5, 4.1 and -14, February - May 1993.

G. lacustris female size differed significantly between river miles ($p < 0.01$, Appendix 1 Table 2.4.18). River miles -14 and -4.1 had significantly larger females than did -3.5 mi ($p < 0.05$), but female size at -14 mi versus -4.1 mi was not significantly different (Appendix 1 Table 2.4.18).

Instantaneous Death Rates

Mean monthly instantaneous death rates ranged from 0% to 28.54% for immature (<7 mm) *G. lacustris* and from 0% to 27.7% for mature *G. lacustris* during the study (Table 2.4.3). Seasonal highs in immature death rates were found in the summer and fall and lows in the spring. No seasonal pattern in mature death rates was evident. Death rates were significantly higher at 5000 cfs versus 8000 cfs ($p < 0.05$). At 8000 cfs, immature *G. lacustris* death rates were significantly higher at -14 mi versus -3.5 mi, but for mature *G. lacustris,* death rates were significantly higher at -3.5 mi.

Data set = River miles -14 and -3.5, May 1992 - May 1993 excluding January 1993.

Immature *G. lacustris*

Immature *G. lacustris* death rates differed significantly between 5,000 cfs and 8,000 cfs ($p < 0.01$), between river miles ($p < 0.05$) and among months ($p < 0.01$, Appendix 1 Table 2.4.19). Also, interaction was significant between month, river mile and elevation ($p < 0.01$, Appendix 1 Table 2.4.19).

Table 2.4.3. Mean instantaneous death rates for immature (< 7mm) and mature (≥7mm) *G. lacustris* by river mile (-3.5, -4.1 and -14 mile) and river elevation (5000 cfs and 8000 cfs). Mean ± SE.

Immature Gammarus < 7 mm	-14 MILE 5000 cfs	-14 MILE 8000 cfs	-4.1 MILE 5000 cfs	-4.1 MILE 8000 cfs	-3.5 MILE 5000 cfs	-3.5 MILE 8000 cfs
MONTH	MEAN ± SE		MEAN ± SE	MEAN ± SE	MEAN ± SE	MEAN ± SE
MAY 92	-0.1419 ± 0.0378	0.0130 ± 0.0383			-0.0058 ± 0.0648	0.0306 ± 0.0268
JUN 92	-0.1629 ± 0.0292	-0.0571 ± 0.0343			-0.0371 ± 0.0472	-0.0290 ± 0.0418
JUL 92	-0.2102 ± 0.0162	-0.2257 ± 0.0301			0.0033 ± 0.0109	-0.0842 ± 0.0312
AUG 92	-0.2605 ± 0.0169	-0.1365 ± 0.0210			-0.2134 ± 0.0234	-0.1193 ± 0.0870
SEP 92	-0.2455 ± 0.0142	-0.2461 ± 0.0296			-0.1669 ± 0.0193	-0.2081 ± 0.0193
OCT 92	-0.1764 ± 0.0483	-0.1159 ± 0.0224			-0.2346 ± 0.0472	-0.1035 ± 0.0251
NOV 92	-0.1212 ± 0.0358	-0.0597 ± 0.0422			-0.2854 ± 0.0193	0.1569 ± 0.1416
DEC 92	-0.1532 ± 0.0269	-0.1323 ± 0.0201		-0.2213 ± 0.0138	-0.1859 ± 0.0318	0.0087 ± 0.0166
JAN 93		-0.1464 ± 0.0363		-0.1747 ± 0.0258		0.0036 ± 0.0227
FEB 93	-0.1319 ± 0.0267	-0.0555 ± 0.0271	-0.0608 ± 0.0204	-0.0880 ± 0.0254	-0.1293 ± 0.0147	0.0263 ± 0.0341
MAR 93	-0.0608 ± 0.0345	0.0159 ± 0.1232	-0.0541 ± 0.0489	-0.0183 ± 0.0396	-0.0991 ± 0.0255	-0.0240 ± 0.0326
APR 93	-0.0215 ± 0.0323	-0.0314 ± 0.0283	-0.0228 ± 0.0344	0.0806 ± 0.1655	-0.0322 ± 0.0496	0.0641 ± 0.0414
MAY 93	0.0717 ± 0.0223	-0.0128 ± 0.0411	0.0727 ± 0.0262	0.1867 ± 0.0550	-0.0088 ± 0.0237	0.1391 ± 0.0474

Mature Gammarus ≥7mm	-14 MILE 5000 cfs	-14 MILE 8000 cfs	-4.1 MILE 5000 cfs	-4.1 MILE 8000 cfs	-3.5 MILE 5000 cfs	-3.5 MILE 8000 cfs
MONTH	MEAN ± SE	MEAN ± SE	MEAN ± SE	MEAN ± SE	MEAN ± SE	MEAN ± SE
MAY 92	-0.0738 ± 0.0098	-0.0605 ± 0.0375			-0.1482 ± 0.0259	-0.2770 ± 0.0680
JUN 92	-0.0834 ± 0.0135	0.1170 ± 0.1263			-0.1394 ± 0.0109	0.0776 ± 0.1351
JUL 92	-0.0357 ± 0.0135	-0.0014 ± 0.0286			-0.1950 ± 0.0185	-0.1447 ± 0.0133
AUG 92	-0.0532 ± 0.0121	0.0012 ± 0.0235			-0.1356 ± 0.0435	-0.1377 ± 0.0478
SEP 92	-0.0899 ± 0.0142	-0.0224 ± 0.0391			-0.1033 ± 0.022	-0.1092 ± 0.0183
OCT 92	-0.0883 ± 0.0251	-0.0634 ± 0.0319			-0.1118 ± 0.0219	-0.1884 ± 0.0156
NOV 92	-0.1196 ± 0.0169	0.0749 ± 0.1357			-0.0592 ± 0.0238	-0.0764 ± 0.0362
DEC 92	-0.0901 ± 0.0122	-0.0596 ± 0.0317		-0.0359 ± 0.0256	-0.0751 ± 0.0238	-0.1789 ± 0.0272
JAN 93		-0.0338 ± 0.0245		-0.0778 ± 0.0091		-0.0454 ± 0.0198
FEB 93	-0.0670 ± 0.0205	-0.0295 ± 0.0084	-0.0671 ± 0.0118	-0.0710 ± 0.0132	-0.0091 ± 0.0051	-0.1636 ± 0.0559
MAR 93	-0.1343 ± 0.0249	0.1446 ± 0.1426	-0.0840 ± 0.0213	-0.1099 ± 0.0264	-0.0875 ± 0.0261	0.0889 ± 0.1322
APR 93	-0.0916 ± 0.0144	-0.0889 ± 0.0347	-0.1740 ± 0.0165	0.0480 ± 0.1793	-0.0982 ± 0.0488	-0.1165 ± 0.0550
MAY 93	-0.0535 ± 0.0803	-0.0687 ± 0.0246	-0.1505 ± 0.0153	-0.1329 ± 0.0311	-0.1163 ± 0.0265	-0.0282 ± 0.0438

At -3.5 mi, seasonal highs in the death rate were found in August - December at 5000 cfs and in August - October at 8000 cfs (Table 2.4.3). Seasonal highs were found in July - September at -14 mi 5000 cfs and 8000 cfs. Seasonal lows in the death rate were found in April - July at -3.5 mi 5000 cfs and in November - June at 8000 cfs. At -14 mi, seasonal lows were found in March - May at both flow level elevations (Table 2.4.3). The death rate at 5000 cfs was significantly higher than at 8000 cfs ($p < 0.01$, Appendix 1 Table 2.4.19). At 8000 cfs, the death rate was significantly higher at -14 mi than at -3.5 mi ($p < 0.05$, Appendix 1 Table 2.4.19). No significant differences in death rate were found between the two river miles at 5000 cfs.

Mature *G. lacustris*

Mature *G. lacustris* death rates differed significantly between 5000 cfs and 8000 cfs ($p < 0.05$) and between river miles ($p < 0.01$, Appendix 1 Table 2.4.20). Also, interaction was significant between river mile and elevation ($p < 0.05$) and between month and river mile ($p < 0.05$, Appendix 1 Table 2.4.20).

No seasonality was apparent in the mature *G. lacustris* death rates (Table 2.4.3). Death rates were significantly higher at 5000 cfs versus 8000 cfs ($p < 0.05$, Appendix 1 Table 2.4.20). At 8000 cfs, death rates were significantly higher at river mile -3.5 mi than -14 mi ($p < 0.01$). No difference in death rate was found between river miles at 5000 cfs.

Data set = River miles -3.5, 4.1 and -14, February - May 1993.

Immature *G. lacustris*

Immature *G. lacustris* death rates differed significantly between 5000 cfs and 8000 cfs ($p < 0.01$) and among months ($p < 0.01$, Appendix 1 Table 2.4.21). Of the four months studied from this data set, February had the highest death rate except at -3.5 mi 8000 cfs, where the March death rate was highest (Table 2.4.3). No significant differences were found in death rate between river, miles but the death rate at 5000 cfs was significantly higher than at 8000 cfs ($p < 0.01$, Appendix 1 Table 2.4.21).

Mature *G. lacustris*

Mature *G. lacustris* death rates differed significantly only between 5000 cfs and 8000 cfs ($p < 0.05$), with mortality at the 5000 cfs being higher. All other comparisons were insignificant (Appendix 1 Table 2.4.22).

Flow velocity

Mean flow velocity ranged from 0.005 cm/sec at -9 mi river side 8000 cfs to 0.394 cm/sec at -14 mile 5000 cfs (Table 2.4.4.). River miles -4.1 and -9 river side had the lowest flow velocities and -14 mile the highest.

Table 2.4.4. Mean flow velocity (cm/sec) at river miles -3.5, -4.1, -9 bank side, -9 river side and -14 at 5000 cfs and 8000 cfs flow elevations. Mean ± SE.

	-3.5 mile	-4.1 mile	-9 mile bank	-9 mile river	-14 mile
5000 cfs	0.086 ± 0.020	0.006 ± 0.003	0.010 ± 0.007	0.0075 ± 0.005	0.394 ± 0.037
8000 cfs	0.057 ± 0.014	0.007 ± 0.003	0.020 ± 0.020	0.005 ± 0.005	0.360 ± 0.036

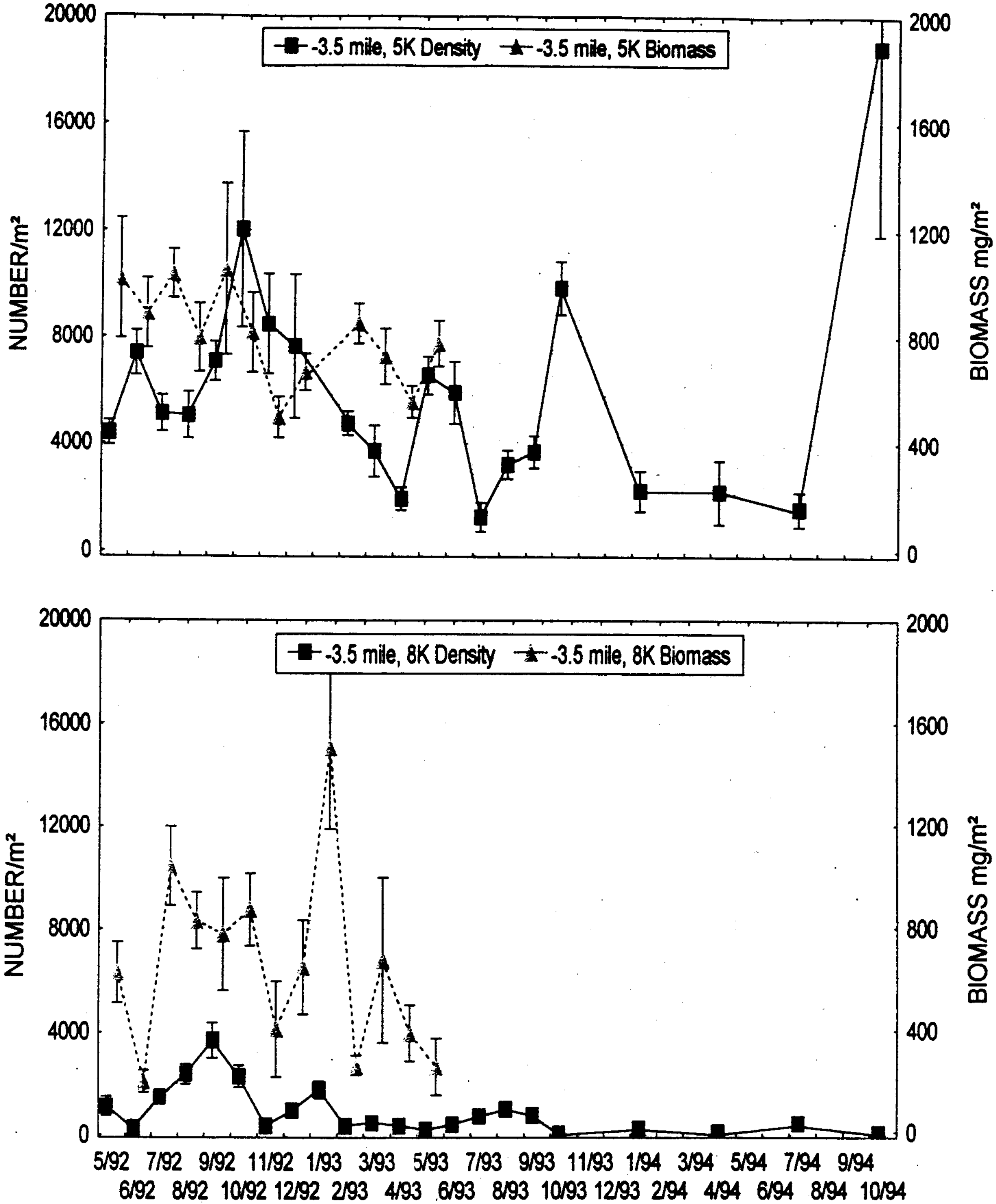

Figure 2.4.1. *G. lacustris* density and biomass at -3.5 mile, May 1992 - October 1994. Mean ± SE.

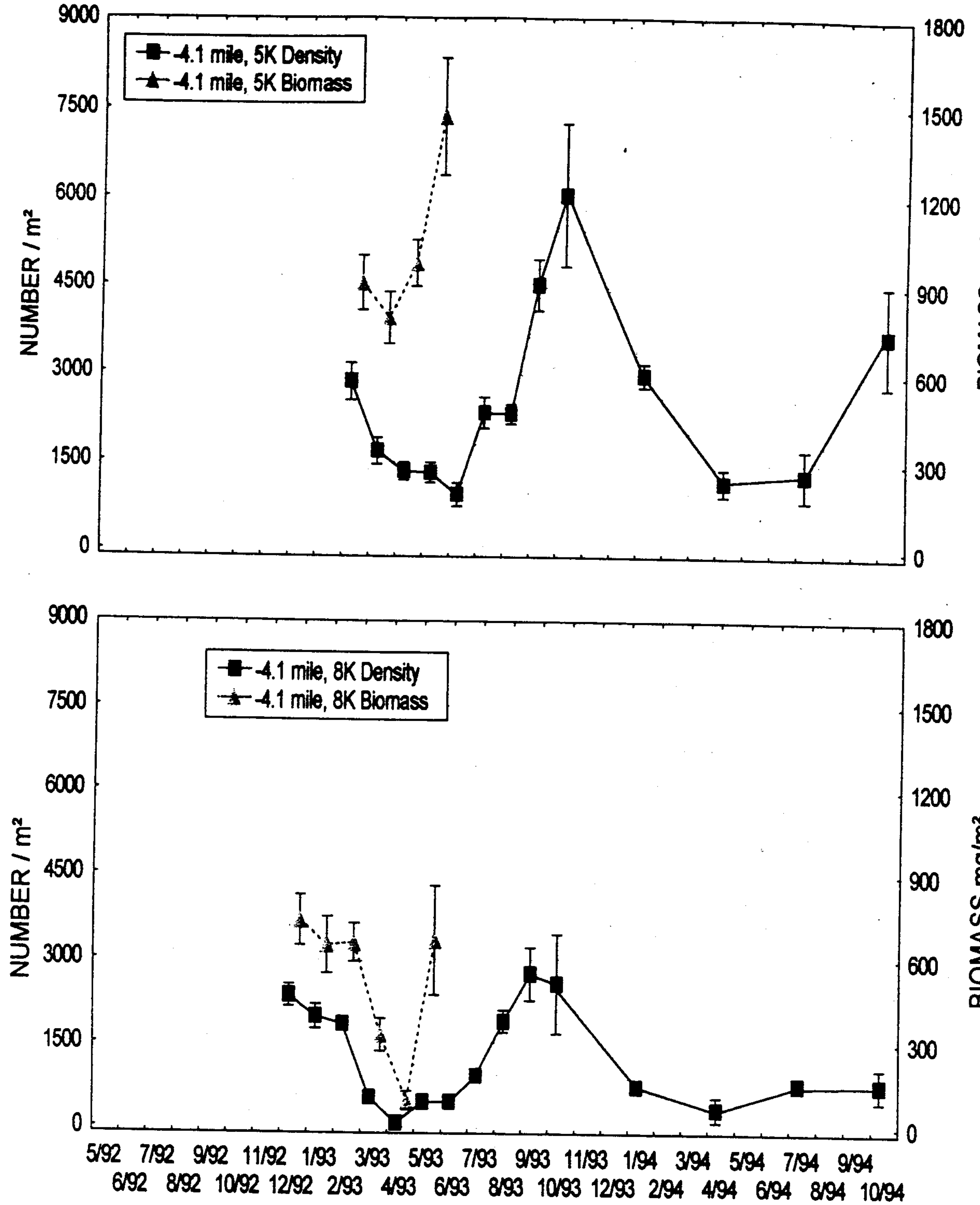

Figure 2.4.2. *G. lacustris* density and biomass at -4.1 mile, December 1992 - October 1994. Mean ± SE.

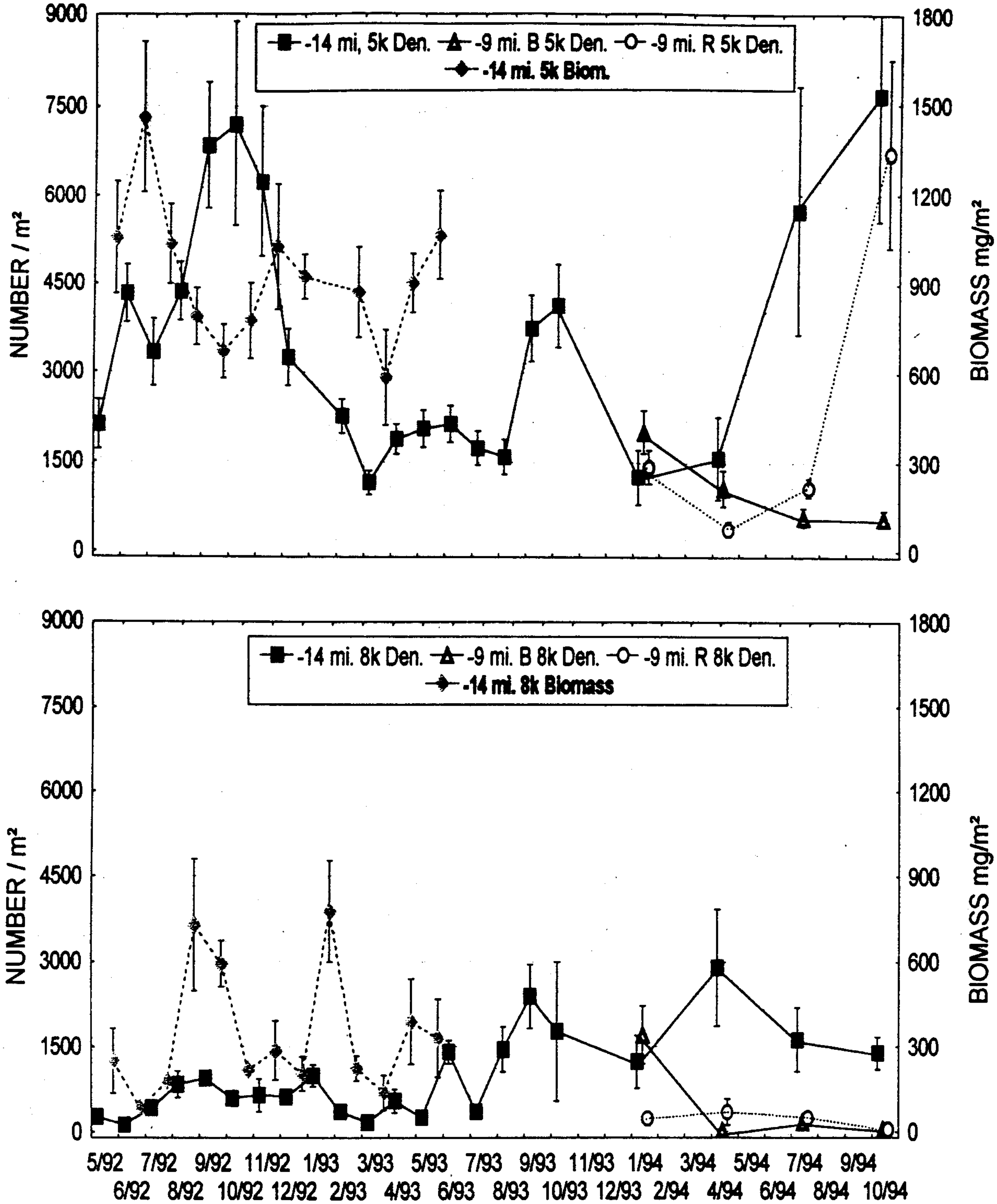

Figure 2.4.3. *G. lacustris* density and biomass at -14 mile and -9 mile bank (B) and river (R) side, May 1992 - October 1994. Mean ± SE.

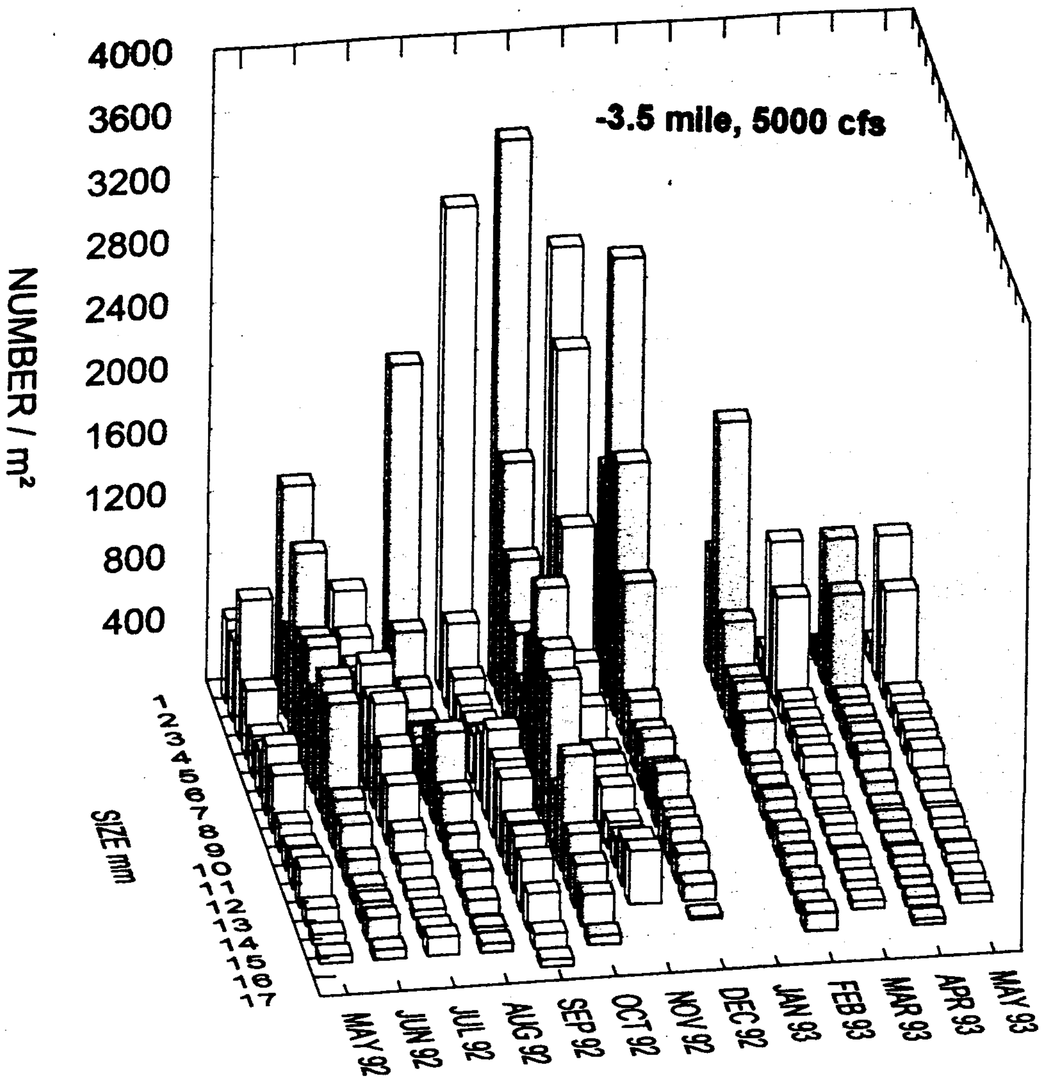

Figure 2.4.4. *G. lacustris* density by size at -3.5 mile, 5000 cfs May 1992 - May 1993.

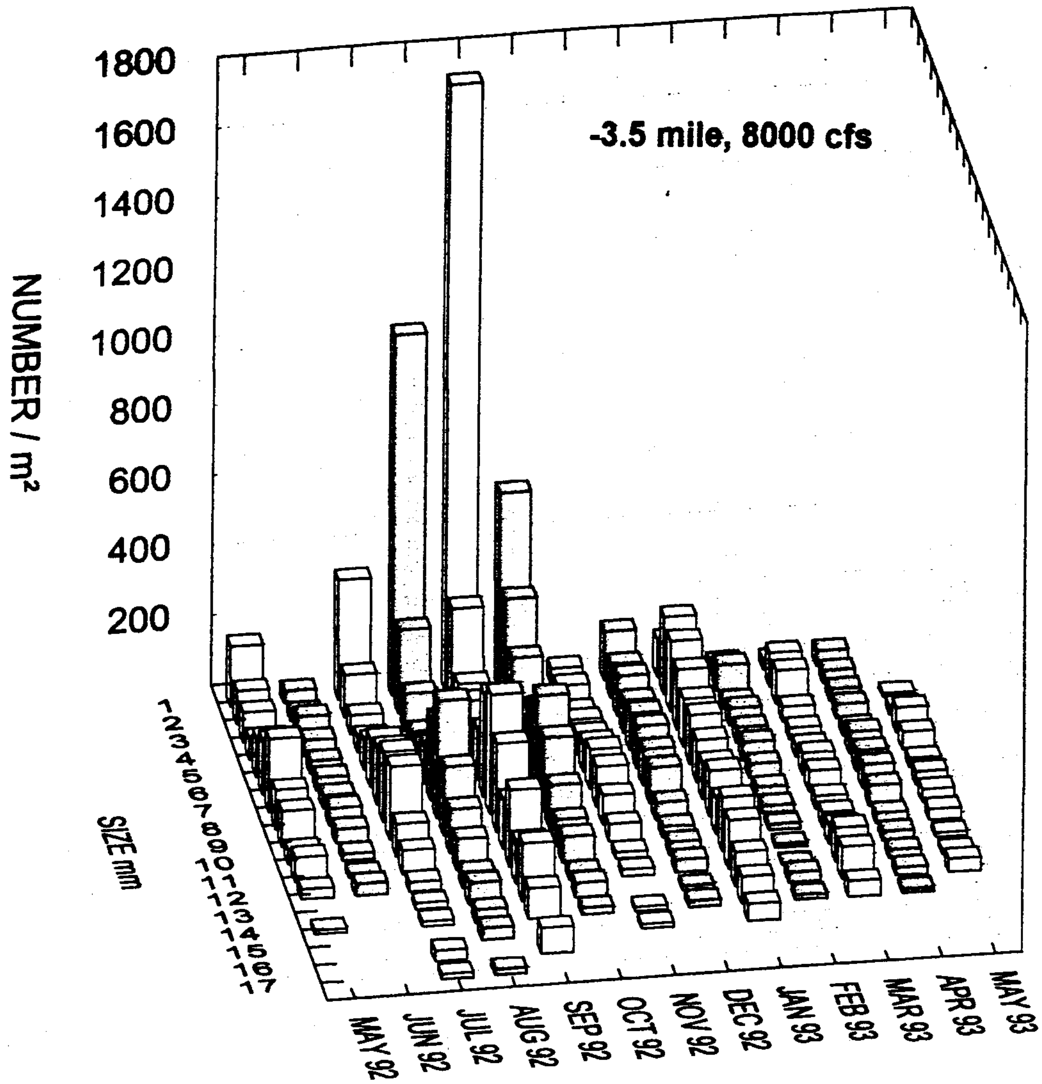

Figure 2.4.5. *G. lacustris* density by size at -3.5 mile, 8000 cfs May 1992 - May 1993.

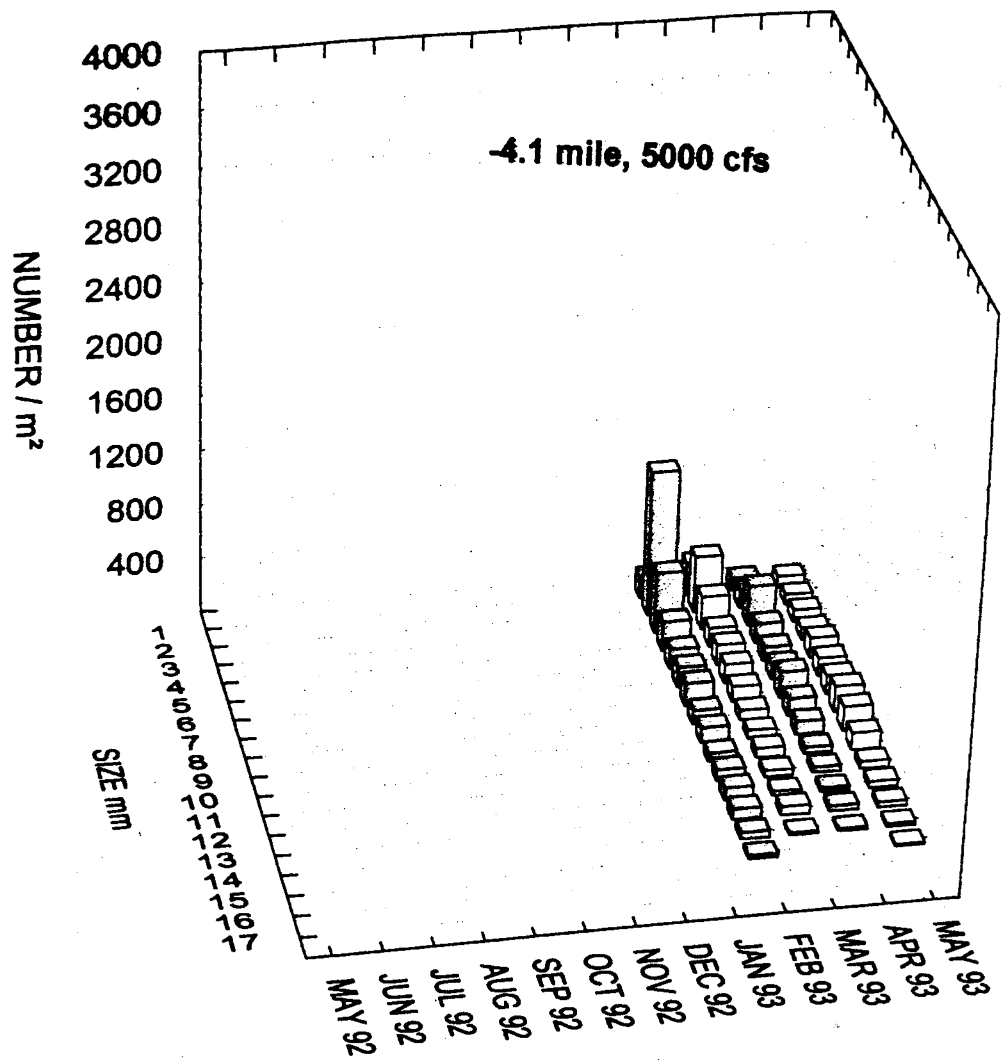

Figure 2.4.6. *G. lacustris* density by size at -4.1 mile, 5000 cfs May 1992 - May 1993.

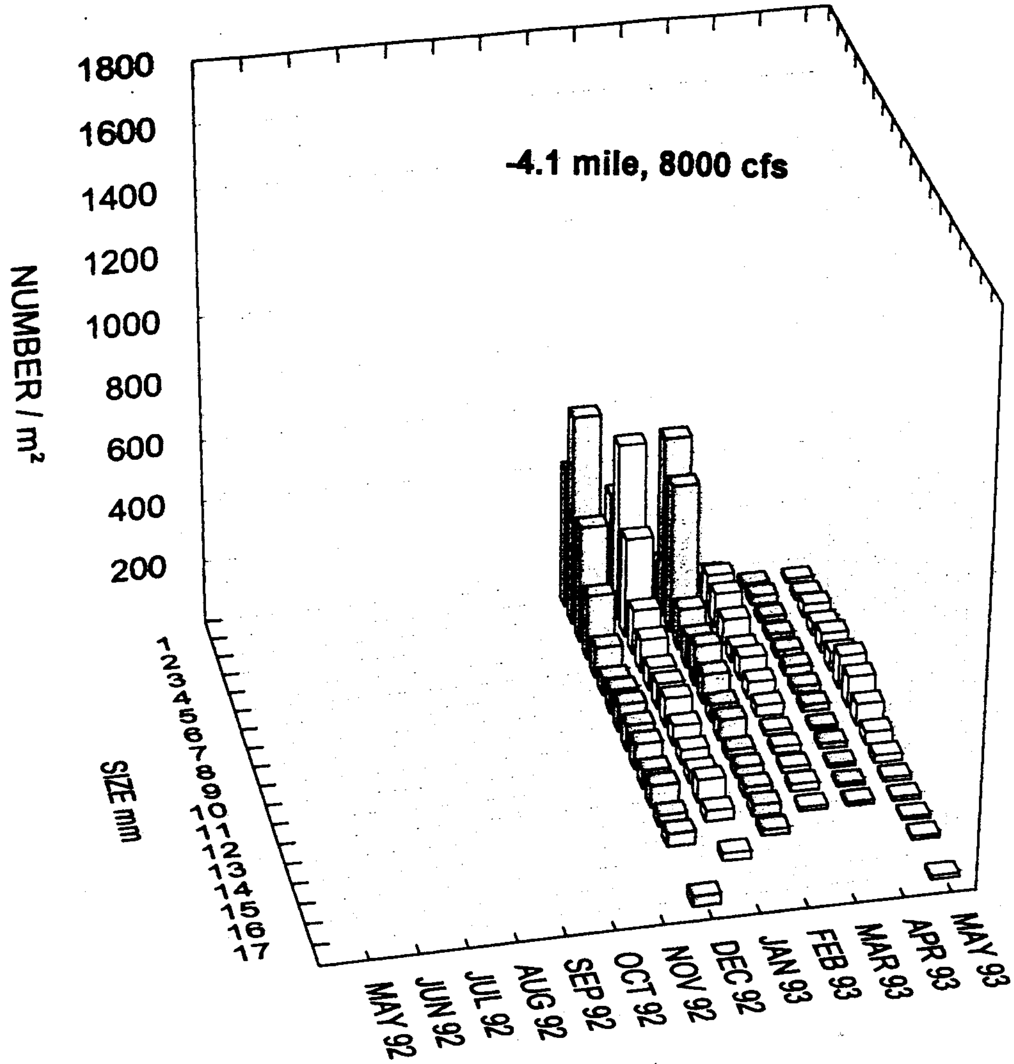

Figure 2.4.7. *G. lacustris* density by size at -4.1 mile, 8000 cfs May 1992 - May 1993.

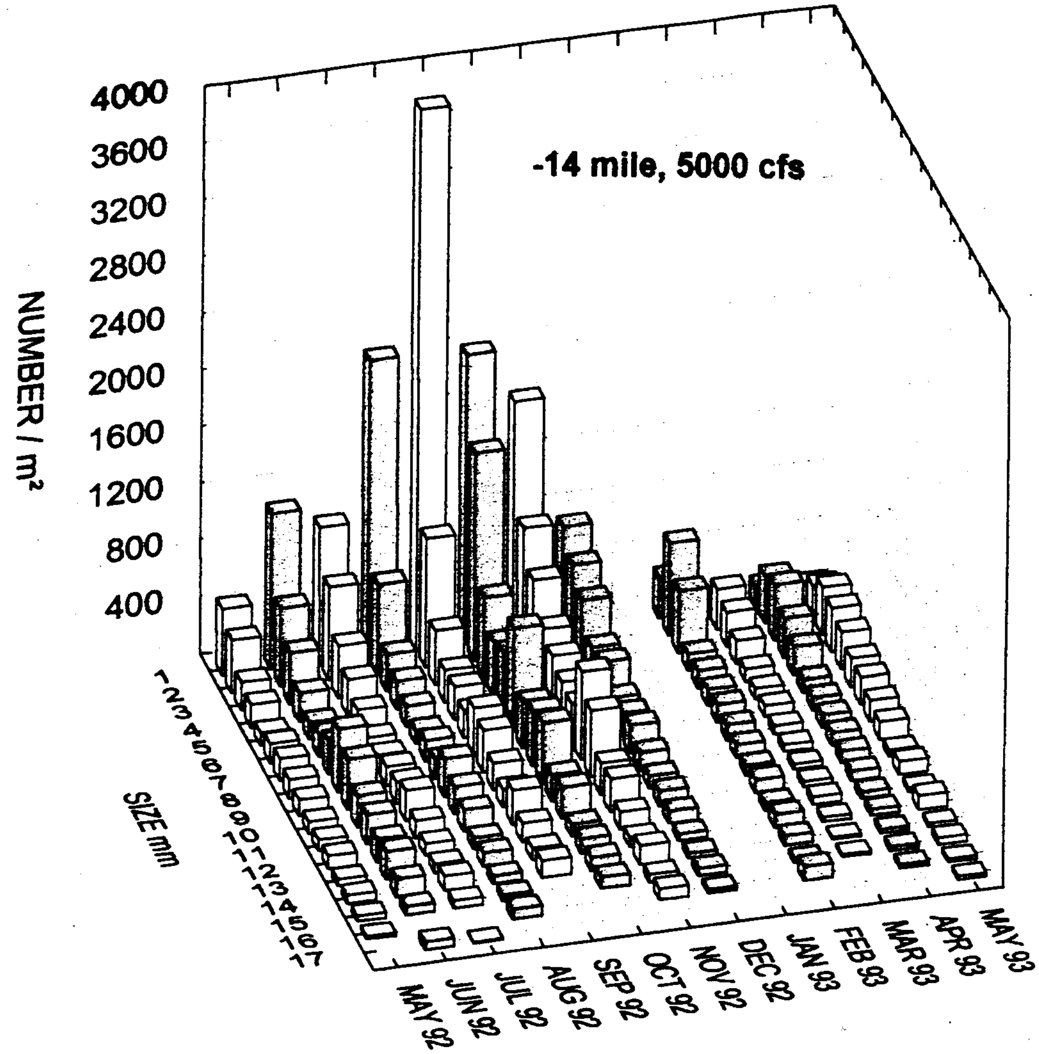

Figure 2.4.8. *G. lacustris* density by size at -14 mile, 5000 cfs May 1992 - May 1993.

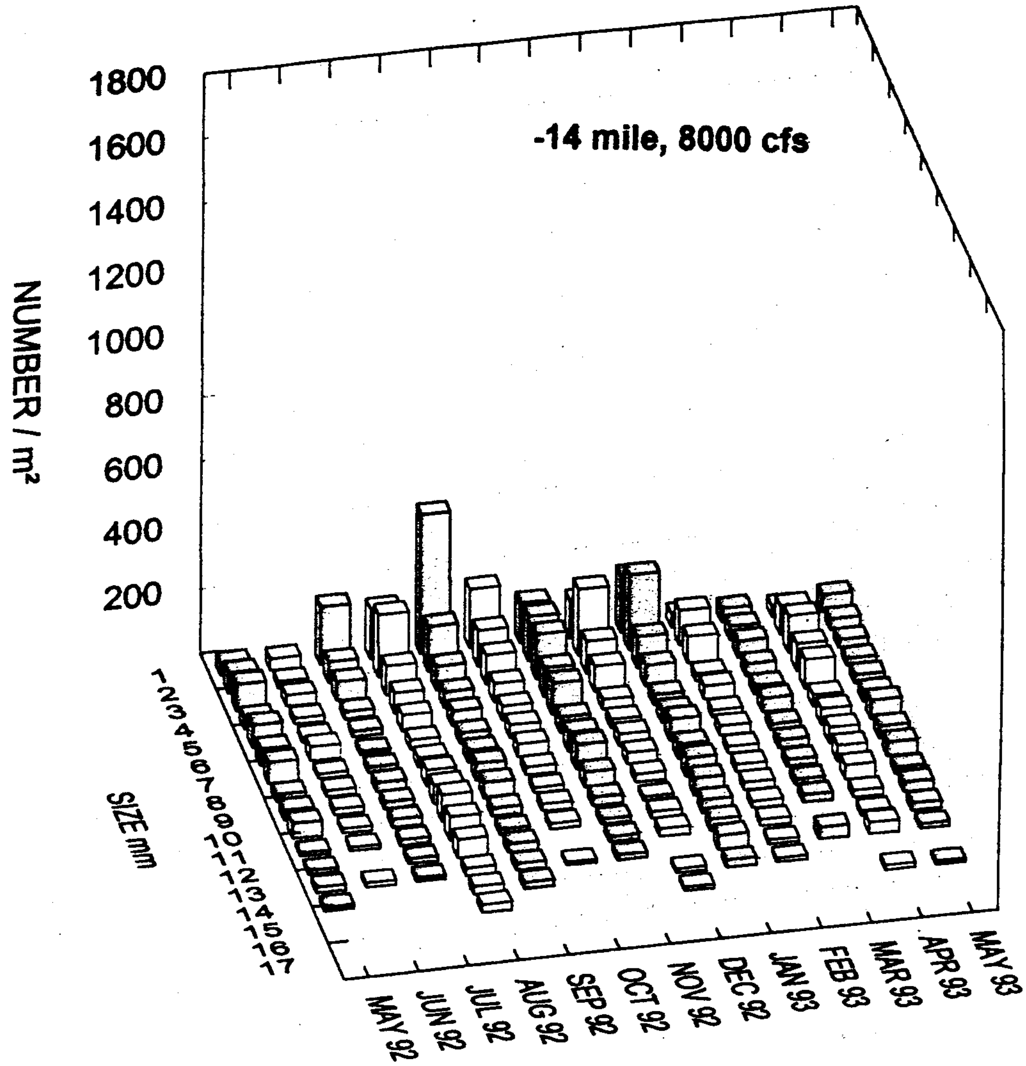

Figure 2.4.9. *G. lacustris* density by size at -14 mile, 8000 cfs May 1992 - May 1993.

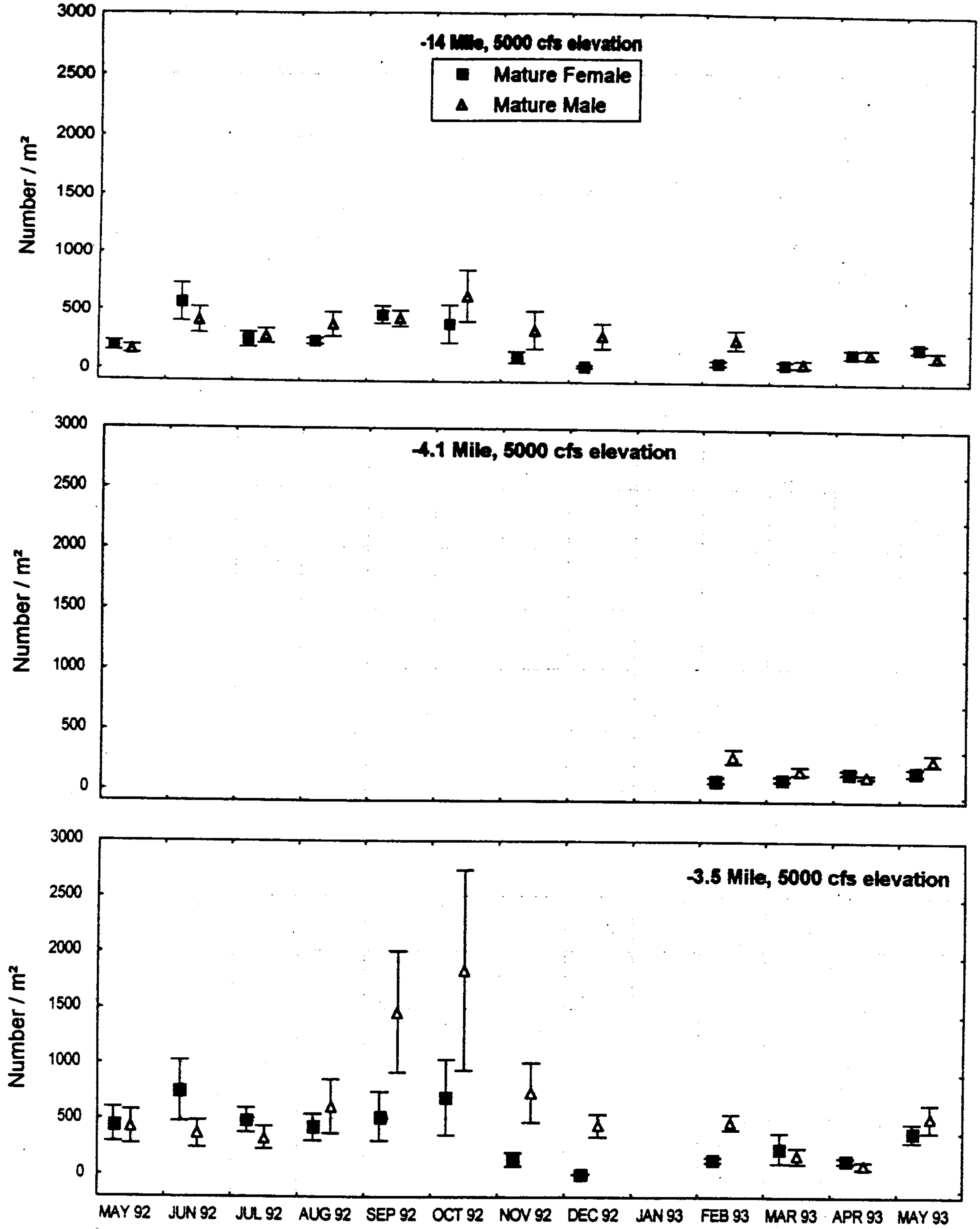

Figure 2.4.10. Density of mature male and mature female *G. lacustris* at -14, -4.1 and -3.5 mile, 5000 cfs elevation, May 1992 - May 1993. Mean ± SE.

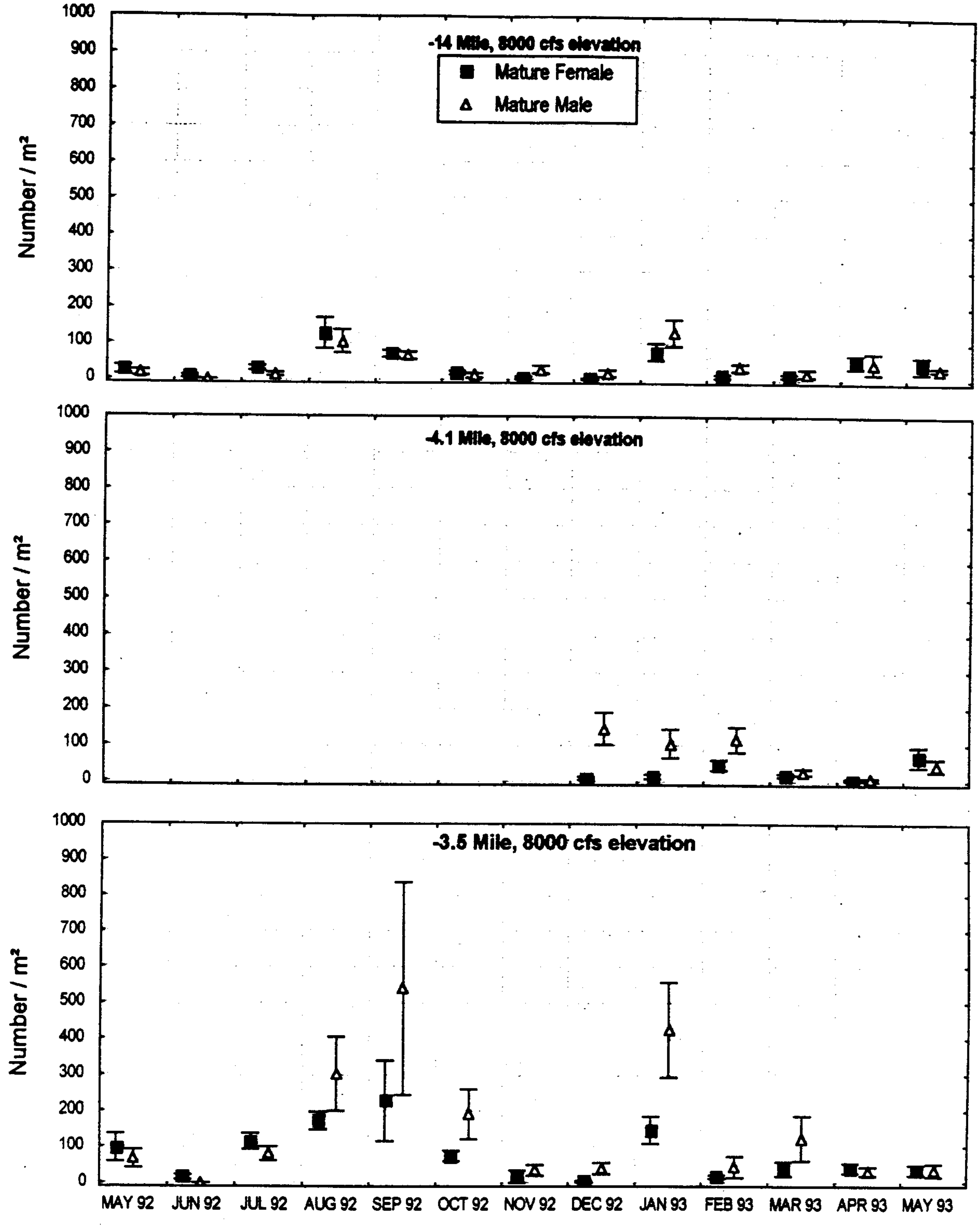

Figure 2.4.11. Density of mature male and mature female *G. lacustris* at -14, -4.1 and -3.5 mile, 8000 cfs elevation, May 1992 - May 1993. Mean ± SE.

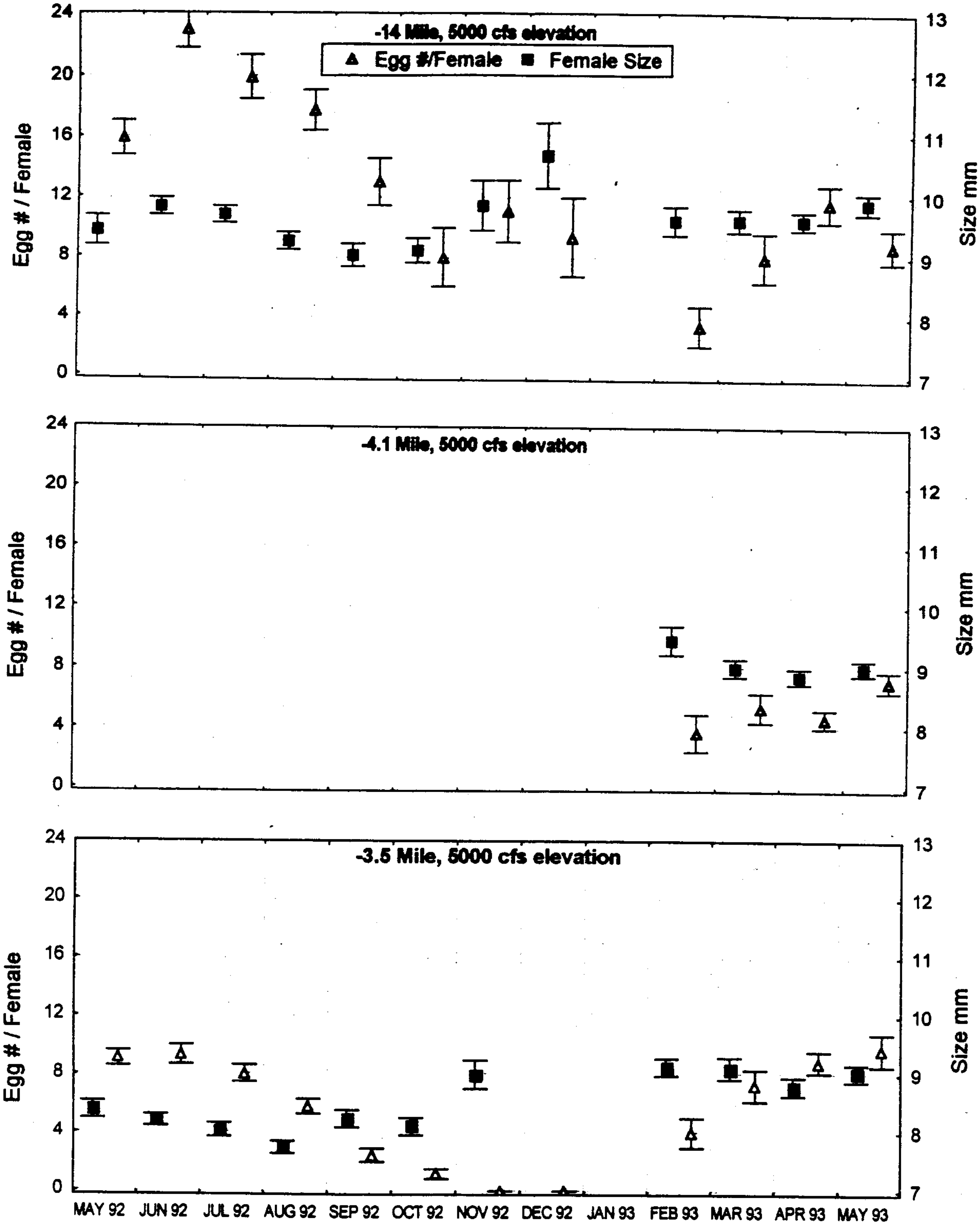

Figure 2.4.12. Number of eggs per female and female size at -14, -4.1 and -3.5 mile, 5000 cfs elevation, May 1992 - May 1993. Mean ± SE.

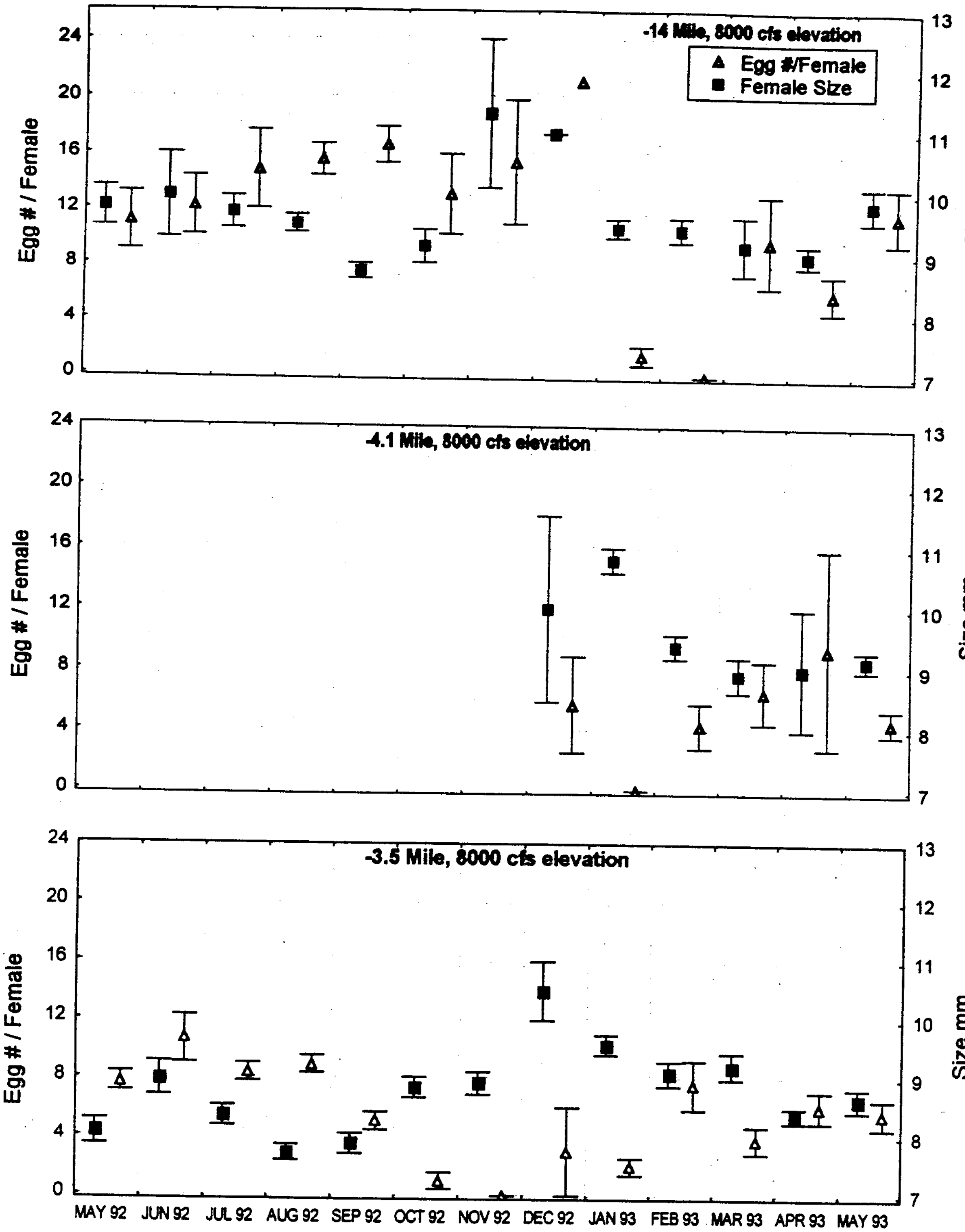

Figure 2.4.13. Number of eggs per female and female size at -14, -4.1 and -3.5 mile, 8000 cfs elevation, May 1992 - May 1993. Mean ± SE.

DISCUSSION

5000 cfs Flow elevation (Permanently-inundated Zone)

Although ambient air temperature in the Glen Canyon area may range from around 5°C (January) to 36°C (August), water releases from the hypolimnion of Lake Powell maintain temperature of dam tailwaters throughout the year at 7°C to 10°C (Stanford and Ward 1991). Waters within Glen Canyon (Lee's Ferry reach) thus provide a thermally stable environment that is near the lower winter temperatures within *G. lacustris*' range of geographic distribution (Hynes 1955, Hynes and Harper 1972, Marchant 1981).

Density and Biomass

Population density of *G. lacustris* increased during the spring and reached highest levels during the fall, lower levels during winter-early spring, conforming generally with the seasonal pattern in a small Minnesota stream (Waters 1964). Leibfried and Blinn (1987) also recorded higher densities during October 1985 at Lee's Ferry. However, biomass in the Glen Canyon tailwaters was about 8-10 times less than that observed in a small stream (Waters 1964). This is consistent with the tendency for small streams to have greater amphipod densities (Marchant 1981). Annual production of *G. lacustris* (in comparison to that of congeneric amphipods) at Lee's Ferry also was lower than in small lotic systems, but greater than in large river ecosystems (Blinn et al. 1994).

More specifically, peaks in total population density in the present study during September-November corresponded to maximum recruitment of the 1-2 mm size class and were associated with declining biomass of the population. Density of both male and female adults declined during mid-late summer in the present study, reflecting mortality following breeding (Hynes 1955). Further, sex ratios (females: males) varied seasonally and tended to be highest during spring-early summer, lowest during winter, indicating that males die before females (Hynes 1955).

Life History

Gravid females and 1-2 mm young were found during all months, indicating that *G. lacustris* reproduced throughout the year. Recruitment of young increased in spring, peaked during the fall and declined into winter. This sequence is in contrast to other studies, where the main season of production of young was briefer, occurred earlier in the year and was associated with a winter period of little or no recruitment (de March 1982, Hynes 1955, Hynes and Harper 1972, Marchant 1981). Hynes (1955) found the highest numbers of immature *G. lacustris* (in a shallow lake in England) during July and virtually none during September-March. In northern Ontario rivers, young were recruited into the population from July into September (Hynes and Harper 1972). However, field studies of *G. lacustris* have focused on freshwater systems that undergo major annual variations in temperature. Year-round reproduction by amphipods is unusual and may be related in the Lee's Ferry reach to relative thermal constancy (Dehdashti and

Blinn 1991). Notably, though, some populations of *G. pulex* have no definite resting period when minimum temperatures are around 6°-7° C, but breeding is reduced over winter (Marchant 1981).

Densities of ovigerous females tended to be higher during June-October in the Lee's Ferry reach. In contrast, Hynes (1955) found peak numbers of ovigerous females in March, none during August-November. Eggs per female declined (in the present study), while densities of ovigerous females increased over the period of increasing recruitment, supporting the hypothesis that it is density of ovigerous females rather than variation in clutch size that most influences recruitment (Marchant 1981).

The number of eggs per female in the present study was greatest during late spring-early summer, lowest during fall and winter. These findings correspond with other observations (Hynes 1955, Marchant 1981), where egg production is generally restricted to a period of highest water temperatures. However, constant water temperature throughout the year in the Lee's Ferry reach indicates that something other than water temperature (such as photoperiod) may be a major variable affecting onset of reproductive activity (de March 1982). If eggs of *G. lacustris* require at least 35-60 days to develop (Hynes 1955, Hynes and Harper 1972, Marchant 1981), breeding activity within the Glen Canyon Dam tailwaters may have begun during March-April and peaked during July-August. In this respect, Hynes and Harper (1972) observed breeding females only during May-August (peaking in July) in Ontario rivers.

The number of eggs per female in size classes greater than 7 mm was lower than previously observed (Hynes 1955, Hynes and Harper 1972, Marchant 1981). Water temperature and quantity/quality of food resources might influence the number of eggs per female (Marchant 1981). However, *C. glomerata*, *Chara sp.* and *Potamogeton sp.* within the Lee's Ferry reach host an abundant community of epiphytic diatoms (Ayers and McKinney 1996a, Blinn et al. 1994, Hardwick et al. 1992), providing a readily available food source for *G. lacustris* (Blinn et al. 1992, Moore 1977, Pinney 1991), indicating that food quantity likely was not a factor affecting fecundity. Also, we observed maximum adult sizes of 14 mm (female) and 22 mm (male), though few males exceeded 17 mm. These conform with previously observed maximum sizes (Hynes 1955), indicating that no suppression of growth occurred. However, water temperatures were well below the possible optimum (18° C) for reproduction by *G. lacustris* (Smith 1973), which might explain the lower number of eggs per female.

As reported by others (Blinn et al. 1994, Hynes 1955, Hynes and Harper 1972, Marchant 1981), sexual maturity of females was reached near 7 mm in size (few females in the 6-7 mm size range were gravid). Males also may become reproductively active at about 7 mm in length (Blinn et al. 1994), and both sexes may require about 1 yr to reach sexual maturity in Glen Canyon Dam tailwaters (D.W. Blinn, personal communication). All females 7 mm or more in size were ovigerous, except during November-January when we observed a few without eggs. Most ovigerous females were in the 7-11 mm size range. Also, number of eggs per female increased with female length, consistent with other findings (Hynes 1955, Hynes and Harper 1972, Marchant 1981). However, correspondence between eggs per female and mean female size in the population was apparent only during late spring and summer and deteriorated through the winter. Clutch size at a specific length may vary randomly during recruitment and between seasons (Hynes and Harper 1972, Marchant 1981).

Mortality rate of adults (7mm or greater in length) showed no clear seasonal pattern but was generally lower than that of immature (<7mm) size classes during late summer through midwinter, possibly due to a greater impact of seasonally higher tailwater flows on immature animals. During spring and early summer, however, adult mortality tended to be higher than that of immatures, reflecting increased survival of the younger size classes rather than increased adult mortality. Greater survival of immature animals during spring and early summer could result from lower flows during that time.

Habitat

Total amphipod density was higher (prior to 1993), as was density of adults, at -3.5 mi, as compared to the upstream cobble bar (-14 mi). These results are consistent with observed preference by *Gammarus* spp. for finer-particle substrate, low current velocity and macrophytes (Gee 1982, Marchant 1981, Rees 1972, Waters 1984). The upriver (-14 mi) and downriver (-9 mi, -4.1 mi and -3.5 mi) sites in the Lee's Ferry reach encompass a downstream trend toward slower current (Table 2.4.4) and smaller/finer substrate particles (Angradi and Kubly 1994). River mile -3.5 is a depositional zone (sand/silt substrate) dominated by *Chara sp.* and *Potamogeton sp.* rather than *C. glomerata* (Ayers and McKinney 1996b).

Peak seasonal recruitment and seasonal highs and lows in mortality of young (<7mm) in the downriver site at -3.5 mi tended to lag those upstream (-14 mi) by about one month, and the location downstream had greater recruitment of young during winter and spring. River mile -3.5 tended to reflect a similar seasonal pattern to that of -14 mile for number of eggs per female, but total eggs per female were lower at -3.5 mi, and mean size of ovigerous females tended to be smaller at -3.5 mi than at the other sites. The greater recruitment may have been due to sandy/silty substrate, lower flow and/or presence of *Chara sp.* and *Potamogeton sp.* The reason(s) for a lag in recruitment and mortality, lower eggs per female and smaller mean size of ovigerous females at -3.5 mi are unknown, but may be associated with algal phenology. Seasonal growth and abundance of *C. glomerata* is greatest during summer, while growth and abundance of *Chara sp.* and *Potamogeton sp.* is greatest during winter (Ayers and McKinney 1996b). Densities of diatoms epiphytic on *C. glomerata* also may tend to be greater during winter, lower during spring-summer (Ayers and McKinney 1996a). Our results indicate that substrate particle size (Gee 1992, Marchant 1981, Rees 1972, Waters 1984), algal composition and/or flow velocity may influence densities, fecundity, survival of young and the level and timing of reproductive performance of *G. lacustris* within the Glen Canyon Dam tailwater. The relative effects of these factors could not be determined, and further research is required to clarify possible interactions between the amphipod and its habitat and food resources.

8000 cfs Flow Elevation (Dewatered Zone)

Density, Biomass and Life History

Consistent with other findings (Angradi and Kubly 1993, Blinn et al. 1994, 1995), our results demonstrate clearly that standing crop, fecundity and reproductive performance of the amphipod within the zone of fluctuating flows in the Glen Canyon Dam tailwater were lowered in comparison to substrate not dewatered. Samples collected at the 8000 cfs flow elevation level in the present study were near the lower limits of dewatering and likely tended to minimize observed effects of daily fluctuation in flow. Total population density and biomass, density of mature females, egg numbers per female, recruitment of young and survival of both adults and young all were reduced in the dewatered zone. Size at sexual maturity was similar, and gravid females were present during all months in both flow zones. Also, average size of ovigerous females was comparable in both flow zones, reaching greater mean length during winter and lower mean length during late summer-early fall. Major seasonal recruitment of young was briefer and less pronounced (fewer young) in the dewatered zone, as well, consistent with reduced production by *G. lacustris* and lower biomass of eggs in brood pouches of females in the dewatered zone at Lee's Ferry (Blinn et al. 1994). Though seasonal patterns for parameters of amphipod reproductive performance tended to be similar in both flow zones, population density and biomass evidenced a clear seasonal pattern only in the permanently-inundated zone.

Fluctuating flow patterns may adversely affect algal beds required by benthic invertebrates, rendering them unsuitable even after rewetting (Fisher and LaVoy 1972, Trotzky and Gregory 1974). Atmospheric exposure may reduce biomass, chlorophyll a content and production of algae (Angradi and Kubly 1993, Blinn et al. 1994, 1995). Within the Lee's Ferry reach (through mid-1993), periphyton biomass and chlorophyll a were found to be lower at dewatered sites dominated by *C. glomerata*, and algal biomass was lower at the dewatered site dominated by *Chara sp.* and *Potamogeton sp.* (Ayers and McKinney 1996b). Recolonization by *G. lacustris* is slower on dewatered as compared to permanently-submerged cobble substrates (Blinn et al. 1994, 1995). However, recolonization of exposed substrata by the amphipod (and other macroinvertebrates) is faster than that by *C. glomerata*, possibly due to rapid recovery of epiphyton. Moreover, reduced quality/quantity of epiphytic diatoms in the dewatered zone (Ayers and McKinney 1996a, Blinn et al. 1994, 1995) may have contributed to lower amphipod reproductive performance. Thus, reduced forage and cover potentially decrease the carrying capacity of the dewatered zone. Stranding of *G. lacustris* is a possible source of loss from an area as substrate is dewatered and resubmerged. Amphipods in the dewatered zone may become dislodged daily and enter stream drift during the rising limb of the hydrograph (Blinn et al. 1994, Perry and Perry 1986). But stranding was not observed at -3.5 mi and therefore likely was not a factor affecting differences in *G. lacustris* densities between flow zones. At other sites (-4.1 mi & -14 mi), stranding was associated with comparatively low in situ mortality (from 0 to about 20%) during exposure (while flow elevation was at the daily low) in winter, spring and early summer (Ayers and McKinney, unpublished data).

Habitat

In comparison to the permanently-inundated zone, fewer differences in amphipod population and reproductive parameters were found among dewatered sites corresponding to flow rate, substrate particle size and/or dominant algal type. However, prior to 1993, at the -14 mi site (dominated by *C. glomerata* and having a comparatively higher mean flow rate), amphipod biomass and survival of young (<7mm) were lower, but survival of adults was greater, than at downstream dewatered sites. Mean flow rate at -14 mi (both flow zones) was greater than that previously associated with highest numbers of *G. pseudolimnaeus* but lower than the maximum velocity (about 58 cm^{s-1}) where individuals were found by Rees (1972). A tendency toward greater survival of young *G. lacustris* (versus adults) during spring in the permanently-inundated zone also was observed in the dewatered zone at -14 mi, but not at dewatered sites downstream. Indeed, survival of young exceeded that of adults throughout the year in the dewatered zone only in habitat dominated by *Chara sp.* and *Potamogeton sp.* (-3.5 mi), reflecting perhaps differences related to substrate particle size, algal composition, slower current and/or the food resource.

Prior to inception of the interim flows, river surface elevations fluctuated daily with greater high/low flow extremes, potentially exacerbating effects of exposure of biota within the dewatered zone. Algal biomass and chlorophyll *a* were reduced within the dewatered zone until about mid-1993, but differences between flow elevation zones have diminished after that time. Algal biomass in the dewatered zone at -3.5 mi and -14 mi trended higher after 1991 (Ayers and McKinney 1996b). Total amphipod density (permanently-inundated zone), biomass and survival of young and adults (dewatered zone) also were statistically similar between -3.5 mi and -14 mi sites after mid-1993 (Ayers and McKinney 1996b). These changes appear to reflect favorable influence of the interim flow regime on primary and secondary trophic levels.

Conclusions and Management Considerations

Recruitment of young by *G. lacustris* in the Glen Canyon Dam tailwaters occurred throughout the year in both the dewatered and permanently-inundated zones, increasing from spring to fall and declining into winter. The period of major reproductive activity was more extended and recruitment peaked later in the year than has been observed in other freshwater systems which experience seasonal change in water temperatures. Within the permanently-inundated zone, habitat-related differences were apparent. Seasonal trends in amphipod density, biomass and reproductive parameters within the zone generally were similar at different sites. During mid-1992 to mid-1993, higher standing crop, greater recruitment of young, fewer eggs per female and smaller size of ovigerous females were found in areas with lower mean flow velocity, finer substrate particle size, and in association with *Chara sp.* and *Potamogeton sp.*

Within the dewatered zone (as compared to the permanently-inundated zone) of the Lee's Ferry reach, however, seasonal recruitment of young was briefer, fewer young were recruited, and no clear seasonal pattern of amphipod density (as was seen in the permanently-inundated zone) occurred. Moreover, population density, biomass, density of ovigerous females, number of eggs per female and survival of both adult and immature amphipods were lower in the dewatered zone. Habitat-related differences were evident only in higher biomass and greater survival of young, but lower survival of adults, at the depositional site (-3.5 mi) dominated by *Chara sp.* and *Potamogeton sp.*

Benthic flora and epiphytic diatoms provide refuge (habitat) and food for *G. lacustris* within the Lee's Ferry reach (Ayers and McKinney 1996a, 1996b, Blinn et al. 1992, 1994, 1995, Pinney 1991, Shannon et al. 1994). If implemented, selective withdrawal of water from upper levels of Lake Powell during spring-summer (Anonymous 1995) potentially will impact the tailwater ecosystem (e.g., Petts 1984). Elevated tailwater temperatures may reduce the standing crop of *C. glomerata* (Dodds and Gudder 1992, Whitton 1970) and epiphytic diatoms (Blinn et al. 1989) Distribution and abundance of *Chara sp.* and *Potamogeton sp.* have increased in the Glen Canyon tailwater during interim flows (Ayers and McKinney unpublished data, Blinn et al. 1994), but possible effects of elevated tailwater temperatures on distribution/abundance of *Chara sp.* and *Potamogeton sp.* and associated epiphytic diatoms presently are not known. Potentially negative influence of higher tailwater temperatures in spring-summer on food/habitat during major reproduction by *G. lacustris* may adversely impact upon annual production and standing crops of the amphipod. Reduced amphipod production and standing crops would likely contribute to lower ecosystem energy (from this source) (Blinn et al. 1992) and possibly to reduced food availability for tailwater fish populations (Angradi 1994, Angradi et al. 1992, Blinn and Cole 1991, Leibfried 1988). Conversely, higher water temperatures may increase the reproductive potential of *G. lacustris* populations (Marchant 1981, Smith 1973), possibly offsetting (to unknown extent) potential losses of food resources and/or habitat. Further research is necessary to determine possible effects of elevated temperatures in the tailwater on *Chara sp.* and *Potamogeton sp.*, their epiphytic diatoms and on amphipod production.

We recommend consideration of the following (as related to dam operations) regarding future monitoring and research of *G. lacustris* in the Glen Canyon Dam tailwaters:

1) Continue seasonal monitoring of densities in the permanently-inundated zone. Increase monitoring effort in habitat dominated by *Chara sp.* and *Potamogeton sp.* to incorporate a site(s) in the region of -14 mi.

2) Monitor distribution of habitat dominated by *Chara sp.* and *Potamogeton sp.* versus *C. glomerata.*

3) Initiate studies to determine and monitor relationships between amphipod densities, biomass of *Chara sp.*, *Potamogeton sp.* and *C. glomerata* and composition/densities of epiphytic diatoms on these benthic flora.

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APPENDIX 1

Table 2.4.5. Analysis of variance and Duncan's multiple range test results of *G lacustris* density by river mile (-3.5 and -14) and elevation (5000 cfs and 8000 cfs), May 1992 - December 1992 and February 1993 - October 1994.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	372538.3	8	454.6485	819.3984	0.000000
River mile	1	10411.4	8	454.6485	22.9000	0.001381
Month	20	6649.1	160	996.0869	6.6752	0.000000
River mile x elev.	1	16468.9	8	454.6485	36.2234	0.000317
Month x River mi.	20	2592.6	160	996.0869	2.6028	0.000497
Month x elevation	20	5793.6	160	996.0869	5.8163	0.000000
Month x mile x elev.	20	2196.0	160	996.0869	2.2047	0.003652

	5000 cfs elevation	8000 cfs elevation
Mean # / m²	4842	884

Comparison	p-level
5000 cfs elevation X 8000 cfs elevation	0.000223

	-3.5 mi, 5000 cfs	-3.5 mi, 8000 cfs	-14 mi, 5000 cfs	-14 mi, 8000 cfs
Mean # / m²	6126	878	3557	890

Comparison	p-level
-3.5 mile, 5000 cfs X -3.5 mile 8000 cfs	0.00008
-14 mile, 5000 cfs X -14 mile, 8000 cfs	0.00022
-3.5 mile, 5000 cfs X -14 mile, 5000 cfs	0.00026

Table 2.4.6. Analysis of variance and Duncan's multiple range test results of *G lacustris* density by river mile (-3.5, -4.1 and -14) and elevation (5000 cfs and 8000 cfs), February 1993 - October 1994.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	177208.7	12	652.6028	271.5414	.000000
River mile	2	632.2	12	652.6028	0.9687	.407365
Month	12	7158.9	144	769.2052	9.3069	.000000
River mile x elev.	2	15019.0	12	652.6028	23.0140	.000078
Month x River mi.	24	1906.9	144	769.2052	2.4790	.000506
Month x elevation	12	5367.2	144	769.2052	6.9775	.000000
Month x mile x elev.	24	2274.5	144	769.2052	2.9569	.000034

Table 2.4.6 Continued.

	5000 cfs elevation	8000 cfs elevation
Mean # / m²	3478	884

Comparison	p-level
5000 cfs elevation X 8000 cfs elevation	0.000172

Table 2.4.7. Analysis of variance and Duncan's multiple range test results of *G. lacustris* density by river mile (-3.5, -4.1, -9 R, -9B and -14) and elevation (5000 cfs and 8000 cfs), January 1994 - October 1994.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	86161.09	20	451.8096	190.7022	0.000000
River mile	4	9557.17	20	451.8096	21.1531	0.000001
Month	3	8551.75	60	854.3987	10.0091	0.000019
River mile x elev.	4	4991.69	20	451.8096	11.0482	0.000068
Month x River mi.	12	3352.65	60	854.3987	3.9240	0.000188
Month x elevation	3	14485.25	60	854.3987	16.9537	0.000000
Month x mile x elev.	12	3153.57	60	854.3987	3.6910	0.000354

	5000 cfs elevation	8000 cfs elevation
Mean # / m²	3200	672

Comparison	p-level
5000 cfs elevation X 8000 cfs elevation	0.000151

Mean # / m²									
-3.5 mi, 5000 cfs	-3.5 mi, 8000 cfs	-4.1 mi, 5000 cfs	-4.1 mi, 8000 cfs	-9 mi R, 5000 cfs	-9 mi R, 8000 cfs	-9 mi B, 5000 cfs	-9 mi B, 8000 cfs	-14 mi, 5000 cfs	-14 mi, 8000 cfs
6220	214	2289	644	2387	224	1057	493	4047	1786

Comparisons	p-level	Comparisons	p-level
-3.5 mile, 5000 cfs X 8000 cfs	0.00002	At 5000 cfs	
-4.1 mile, 5000 cfs X 8000 cfs	0.00018	-3.5 mile X -4.1 mile	0.00076
-9 mile R, 5000 cfs X 8000 cfs	0.00003	-3.5 mile X -9 mile R	0.00018
-9 mile B, 5000 cfs X 8000 cfs	0.00325	-3.5 mile X -9 mile B	0.00003
At 8000 cfs		-14 mile X -4.1 mile	0.01383
-14 mile X -3.5 mile	0.00004	-14 mile X -9 mile R	0.00296
-14 mile X -4.1 mile	0.01827	-14 mile X -9 mile B	0.00004
-14 mile X -9 mile R	0.00004	-9 mile R X -9 mile B	0.02075
-14 mile X -9 mile B	0.00008	-4.1 mile X -9 mile B	0.00423
-4.1 mile X -9 mile R	0.02526		

Table 2.4.8. Analysis of variance and Duncan's multiple range test results of *G. lacustris* biomass by river mile (-3.5 and -14) and elevation (5000 cfs and 8000 cfs), May 1992 - May 1993 excluding January 1993.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	30021.33	21	237.2342	126.5472	0.000000
River mile	1	1162.83	21	237.2342	4.9016	0.038030
Month	11	737.61	231	212.3198	3.4741	0.000167
River mile x elev.	1	3224.36	21	237.2342	13.5915	0.001371
Month x River mi.	11	619.92	231	212.3198	2.9197	0.001252
Month x elevation	11	767.95	231	212.3198	3.6170	0.000098
Month x mile x elev.	11	321.81	231	212.3198	1.5157	0.126626

	5000 cfs elevation	8000 cfs elevation
Mean mg / m²	854.8182	424.3596

Comparison	p-level
5000 cfs elevation X 8000 cfs elevation	0.000147

	-3.5 mi, 5000 cfs	-3.5 mi, 8000 cfs	-14 mi, 5000 cfs	-14 mi, 8000 cfs
Mean mg/m²	814.9	540.0	834.8	308.7

Comparison	p-level
-3.5 mile, 8000 cfs X -14 mile, 8000 cfs	0.000569
-3.5 mile, 5000 cfs X -3.5 mile, 8000 cfs	0.000168
-14 mile, 5000 cfs X -14 mile, 8000 cfs	0.000057

Table 2.4.9. Analysis of variance and Duncan's multiple range test results of *G lacustris* biomass by river mile (-3.5, -4.1 and -14) and elevation (5000 cfs and 8000 cfs), February - May 1993.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	28426.71	39	239.7474	118.5695	0.000000
River mile	2	1127.23	39	239.7474	4.7017	0.014814
Month	3	853.21	117	159.5874	5.3464	0.001738
River mile x elev.	2	50.86	39	239.7474	.2121	0.809789
Month x River mi.	6	747.94	117	159.5874	4.6867	0.000262
Month x elevation	3	215.33	117	159.5874	1.3493	0.261861
Month x mile x elev.	6	506.99	117	159.5874	3.1769	0.006344

Table 2.4.9. Continued.

	5000 cfs elevation	8000 cfs elevation
Mean mg / m²	880.89	340.59
Comparison		p-level
5000 cfs elevation X 8000 cfs elevation		0.000117

	-3.5 mi, 5000 cfs	-3.5 mi, 8000 cfs	-4.1 mile, 5000 cfs	-4.1 mile, 8000 cfs	-14 mi, 5000 cfs	-14 mi, 8000 cfs
Mean mg/m²	743.8	300.5	1040.5	434.7	858.4	286.6
Comparison					p-level	
-3.5 mile, 5000 cfs X -4.1 mile, 5000 cfs					0.030172	
-3.5 mile, 5000 cfs X -3.5 mile, 8000 cfs					0.000062	
-4.1 mile, 5000 cfs X -4.1 mile, 8000 cfs					0.000055	
-14 mile, 5000 cfs X -14 mile, 8000 cfs					0.000032	

Table 2.4.10. Analysis of variance and Duncan's multiple range test results of **mature** *G. lacustris* density by river mile (-3.5 and -14) elevation (5000 cfs and 8000 cfs) and sex, May 1992 - May 1993 excluding January 1993.

Source	d.f. Effect	MS Effect	d.f. Erro r	MS Error	F	p-level
River mile	1	4400017.	42	362115.4	12.15087	.001163
River elevation	1	13676775.	42	362115.4	37.76910	.000000
Sex	1	1372701.	42	362115.4	3.79078	.058243
Month	11	1027781.	462	176864.3	5.81113	.000000
River mile x elev.	1	1693507.	42	362115.4	4.67671	.036317
River mile x sex	1	602803.	42	362115.4	1.66467	.204032
River elev. x sex	1	672724.	42	362115.4	1.85776	.180147
River mi. x month	11	301836.	462	176864.3	1.70660	.069074
River elev. x month	11	570903.	462	176864.3	3.22791	.000295
Sex x month	11	299250.	462	176864.3	1.69198	.072263
River mi. x elev. x sex	1	174177.	42	362115.4	.48100	.491788
River mi. x elev. x month	11	124690.	462	176864.3	.70500	.734161
River mi. x sex x month	11	180336.	462	176864.3	1.01963	.427535
River elev. x sex x month	11	179582.	462	176864.3	1.01537	.431346
River mi. x elev. x sex x month	11	89615.	462	176864.3	.50669	.899035

	5000 cfs elevation	8000 cfs elevation
Mean # / m²	376.6	65.6
Comparison		p-level
5000 cfs elevation X 8000 cfs elevation		0.000118

Table 2.4.10. Continued.

	-3.5 mi, 5000 cfs	-3.5 mi, 8000 cfs	-14 mi, 5000 cfs	-14 mi, 8000 cfs
Means #/m²	519.4	99.1	233.7	32.2
Comparison				p-level
-3.5 mile, 5000 cfs X -3.5 mile, 8000 cfs				0.00006
-14 mile, 5000 cfs X -14 mile, 8000 cfs				0.00998
-3.5 mile, 5000 cfs X -14 mile, 5000 cfs				0.00036

Table 2.4.11. Analysis of variance and Duncan's multiple range test results of **mature** *G. lacustris* density by river mile (-3.5, -4.1 and -14) elevation (5000 cfs and 8000 cfs) and sex, February 1993 - May 1993.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River mile	2	161950.	78	14440.38	11.2151	.000052
River elevation	1	2019960.	78	14440.38	139.8827	.000000
Sex	1	152075.	78	14440.38	10.5312	.001730
Month	3	125803.	234	14158.82	8.8851	.000013
River mile x elev.	2	119007.	78	14440.38	8.2413	.000566
River mile x sex	2	10664.	78	14440.38	.7385	.481162
River elev. x sex	1	59761.	78	14440.38	4.1385	.045318
River mi. x month	6	48544.	234	14158.82	3.4285	.002905
River elev. x month	3	91957.	234	14158.82	6.4947	.000307
Sex x month	3	112575.	234	14158.82	7.9508	.000045
River mi. x elev. x sex	2	2638.	78	14440.38	.1827	.833360
River mi. x elev. x month	6	54643.	234	14158.82	3.8593	.001083
River mi. x sex x month	6	8025.	234	14158.82	.5668	.756579
River elev. x sex x month	3	66165.	234	14158.82	4.6730	.003432
River mi. x elev. x sex x month	6	19907.	234	14158.82	1.4060	.213037

	5000 cfs elevation	8000 cfs elevation
Mean # / m²	190.5	40.4
Comparison		p-level
5000 cfs elevation X 8000 cfs elevation		0.000114

	-3.5 mi, 5000 cfs	-3.5 mi, 8000 cfs	-4.1 mile, 5000 cfs	-4.1 mile, 8000 cfs	-14 mi, 5000 cfs	-14 mi, 8000 cfs
Mean #/m²	268.6	45.6	159.9	43.6	143.0	31.8
Comparison						p-level
-3.5 mile, 5000 cfs X -4.1 mile, 5000 cfs						0.000117
-3.5 mile, 5000 cfs X -14 mile, 5000 cfs						0.000055

Table 2.4.11. Continued

	5000 cfs, Female	5000 cfs, Male	8000 cfs, Female	8000 cfs, Male
Mean # / m²	156.99	224.01	32.67	48.04
Comparisons				p-level
Female @ 5000 cfs vs Male @ 5000 cfs				0.00046
Female @ 5000 cfs vs Female @ 8000 cfs				0.00006
Male @ 5000 cfs vs Male @ 8000 cfs				0.00006

Table 2.4.12. Kruskal-Wallis ANOVA by ranks test for egg number per female by month, May 1992 - May 1993 excluding January 1993.

Kruskal-Wallis test: H (11,N =1648) = 230.02, p = 0.0000			
Month	Valid N	Mean	Mean Rank
May 92	203	11.08	917.21
Jun 92	182	16.63	1109.47
Jul 92	203	12.09	931.23
Aug 92	232	11.79	932.58
Sep 92	176	9.20	768.39
Oct 92	100	4.20	459.78
Nov 92	42	5.05	521.70
Dec 92	12	9.52	807.88
Feb 93	65	3.95	467.72
Mar 93	97	6.81	652.34
Apr 93	170	8.95	780.65
May 93	166	8.91	759.33

Table 2.4.13. Kruskal-Wallis ANOVA by ranks test for egg number per female by flow elevation (5000 & 8000 cfs), May 1992 - May 1993 excluding January 1993 at river miles -14 and -3.5.

Kruskal-Wallis test: H (1,N = 1648) = 4.6831, p = 0.0305			
Flow Elevation	Valid N	Mean	Mean Rank
5000 cfs	1098	10.67	842.34
8000 cfs	550	9.14	788.88

Table 2.4.14. Kruskal-Wallis ANOVA by ranks test for egg number per female by river mile (-3.5 mile and -14 mile), May 1992 - May 1993 excluding January 1993.

Kruskal-Wallis test: H (1,N = 1648) = 195.1039, p = 0.000			
River Mile	Valid N	Mean	Mean Rank
-3.5 mile	860	6.692	668.75
-14 mile	788	13.948	994.48

Table 2.4.15. Kruskal-Wallis ANOVA by ranks test for egg number per female by flow elevation (5000 & 8000 cfs), February - May 1993 at river miles -3.5, -4.1 and -14.

Kruskal-Wallis test: H (1,N = 798) = 4.1773, p = 0.0410			
Flow Elevation	Valid N	Mean	Mean Rank
5000 cfs	571	7.329	409.64
8000 cfs	227	5.916	374.00

Table 2.4.16. Kruskal-Wallis ANOVA by ranks test for egg number per female by river mile (-3.5, -4.1 and -14 mile), February - May 1993.

Kruskal-Wallis test: H (2,N =798) =16.6276 , p = 0.0002			
River Mile	Valid N	Mean	Mean Rank
-3.5 mile	230	7.026	421.09
-4.1 mile	300	5.363	358.28
-14 mile	268	8.593	427.11

Table 2.4.17. Analysis of variance and Duncan's multiple range test results of female *G. lacustris* size by river elevation (5000 cfs and 8000 cfs) and river mile (-3.5 and -14), May 1992 - May 1993 excluding December 1992 and January 1993.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	2.86435	35	1.086248	2.63692	0.113379
River mile	1	96.90343	35	1.086248	89.20929	0.000000
Month	10	4.78756	350	1.417042	3.37856	0.000316
River mile x elev.	1	2.37270	35	1.086248	2.18431	0.148367
Month x River mi.	10	3.93874	350	1.417042	2.77955	0.002557
Month x elevation	10	2.11149	350	1.417042	1.49007	0.141138
Month x mile x elev.	10	1.28714	350	1.417042	0.90833	0.525532

	-3.5 Mile	-14 Mile
Mean size mm	8.58	9.72

Comparison	p-level
-3.5 mile X -14 mile	0.000122

Table 2.4.18. Analysis of variance and Duncan's multiple range test results of female *G. lacustris* size by river elevation (5000 cfs and 8000 cfs) and river mile (-3.5, -4.1 and -14), February - May 1993.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	0.543098	81	0.994649	0.546020	0.462084
River mile	2	6.267340	81	0.994649	6.301057	0.002861
Month	3	1.702433	243	0.986577	1.725596	0.162319
River mile x elev.	2	0.579630	81	0.994649	0.582749	0.560685
Month x River mi.	6	0.510588	243	0.986577	0.517535	0.794813
Month x elevation	3	0.851604	243	0.986577	0.863191	0.460802
Month x mile x elev.	6	1.414673	243	0.986577	1.433920	0.202176

	-3.5 Mile	-4.1 Mile	-14 Mile
Mean size mm	8.85	9.13	9.37

Comparison	p-level
-3.5 mile X -4.1 mile	0.037287
-3.5 mile X -14 mile	0.000376

Table 2.4.19. Analysis of variance and Duncan's multiple range test results of instantaneous death rates for **immature** (size 1-6 mm) *G. lacustris* by elevation (5000 cfs and 8000 cfs) and river mile (-3.5 and -14), May 1992 - May 1993 excluding January 1993.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	.357483	19	.022481	15.90135	.000788
River mile	1	.125986	19	.022481	5.60405	.028688
Month	11	.149942	209	.014374	10.43153	.000000
River mile x elev.	1	.060656	19	.022481	2.69806	.116918
Month x River mi.	11	.025671	209	.014374	1.78596	.058015
Month x elevation	11	.025337	209	.014374	1.76271	.062241
Month x mile x elev.	11	.042809	209	.014374	2.97822	.001071

	5000 cfs elevation	8000 cfs elevation
Mean instantaneous death rate	-0.119463	-0.045441

Comparison	p-level
5000 cfs elevation X 8000 cfs elevation	.00075

	-3.5 mi, 5000 cfs	-3.5 mi, 8000 cfs	-14 mi, 5000 cfs	-14 mi, 8000 cfs
Mean death rates	-0.112737	-0.008224	-0.126190	-0.082658

Comparison	p-level
-3.5 mile, 8000 cfs X -14 mile, 8000 cfs	0.0107

Table 2.4.20. Analysis of variance and Duncan's multiple range test results of instantanious death rates for **mature** (size 7 - 17 mm) *G. lacustris* by elevation (5000 cfs and 8000 cfs) and river mile (-3.5 and -14), May 1992 - May 1993 excluding January 1993.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	.108649	19	.023389	4.64535	.044173
River mile	1	.253576	19	.023389	10.84175	.003828
Month	11	.029661	209	.019734	1.50305	.132071
River mile x elev.	1	.105447	19	.023389	4.50842	.047085
Month x River mi.	11	.044800	209	.019734	2.27022	.012358
Month x elevation	11	.013805	209	.019734	.69956	.738297
Month x mile x elev.	11	.015446	209	.019734	.78273	.657146

Table 2.4.20. Continued.

	5000 cfs elevation	8000 cfs elevation
Mean instantaneous death rate	-0.09193	-0.05112
Comparison		p-level
5000 cfs elevation X 8000 cfs elevation		0.0393

	-3.5 mi, 5000 cfs	-3.5 mi, 8000 cfs	-14 mi, 5000 cfs	-14 mi, 8000 cfs
Mean death rates	-0.10300	-0.1024	-0.08086	0.00015
Comparison				p-level
-3.5 mile, 8000 cfs X -14 mile, 8000 cfs				0.0016

Table 2.4.21. Analysis of variance and Duncan's multiple range test results of instantanious death rates for imature (size 1-6 mm) *G. lacustris* by elevation (5000 cfs and 8000 cfs) and river mile (-3.5, -4.1 and -14), February 1993 - May 1993.

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	.171744	39	.016547	10.37927	.002573
River mile	2	.021346	39	.016547	1.29003	.286749
Month	3	.194610	117	.021848	8.90727	.000023
River mile x elev.	2	.040201	39	.016547	2.42954	.101298
Month x River mi.	3	.000384	117	.021848	.01756	.996816
Month x elevation	6	.013953	117	.021848	.63861	.699109
Month x mile x elev.	6	.022602	117	.021848	1.03449	.406572

	5000 cfs elevation	8000 cfs elevation
Mean instantaneous death rate	-0.03948	0.02243
Comparison		p-level
5000 cfs elevation X 8000 cfs elevation		0.0026

Table 2.4.22. **Analysis of variance and Duncan's multiple range test results of instantanious death rates for mature (size 7 - 17 mm) *G. lacustris* by elevation (5000 cfs and 8000 cfs) and river mile (-3.5, -4.1 and -14), February 1993 - May 1993.**

Source	d.f. Effect	MS Effect	d.f. Error	MS Error	F	p-level
River elevation	1	.110784	39	.023103	4.795138	.034587
River mile	2	.026831	39	.023103	1.161364	.323649
Month	3	.033751	117	.030699	1.099413	.352343
River mile x elev.	2	.012941	39	.023103	.560131	.575661
Month x River mi.	3	.062729	117	.030699	2.043364	.111599
Month x elevation	6	.019407	117	.030699	.632181	.704236
Month x mile x elev.	6	.065537	117	.030699	2.134845	.054402

	5000 cfs elevation	8000 cfs elevation
Mean instantaneous death rate	-0.09263	-0.04290

Comparison	p-level
5000 cfs elevation X 8000 cfs elevation	0.03436