

The Response of Wetland Benthic Macroinvertebrates to Short-term Drawdown

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Abstract: Short-term effects of water drawdown on benthic macroinvertebrate communities of South Florida cypress systems were investigated. The time period and *in situ* mechanism of benthic response to drawdown conditions were of particular interest due to lack of data, as well as the increasing stress placed on wetland systems in proximity to high groundwater extraction areas. Microcosm experiments were conducted by subjecting soil cores collected from the field to varying time periods (3, 5, and 10 days) of drawdown. After each drawdown treatment, cores were sectioned, preserved, and processed to determine vertical distribution of macroinvertebrate populations. Cores were also subsampled for moisture and organic matter content, bulk density, and porosity. The prominent macroinvertebrate communities, annelids and dipterans, migrated down through the soil column over time reaching depths of 20-30cm. Chironomidae and Ceratopogonidae were the dominant dipteran families found. Macroinvertebrate response was evident between the third and fifth day of drawdown treatment. Vertical migration seems to be a viable drought response mechanism for benthos. Benthic migration, however, was not consistently correlated with organic matter content or total percent moisture content.

Introduction

Hydrology is a major environmental determinate of ecosystem character, influencing floral and faunal community structure by the frequency and duration of hydrological alterations. Wetland systems, by their very nature, experience dynamic hydrofluxes. In particular, cypress swamps and domes are naturally characterized by extreme hydrological fluctuations where severe drawdown of the system is likely to occur. Hydroperiods that drop the water table to greater than 150 cm below the soil surface for several months are not unusual (Duever 1975). The hydroperiodicity of cypress systems that are somewhat hydrologically isolated from the surrounding water table are regulated primarily by the factors of evaporation, precipitation, and groundwater recharge (Cutright 1974). If groundwater sources are depleted by withdrawal, in conjunction with minimal rainfall, normally unpredictable hydroperiods are further altered with deleterious effects to wetland ecosystems.

Intense hydrological change is occurring in South Florida, where exploding population growth and development has led to increased consumptive water use withdrawals. Active pumping of groundwater from municipal well fields is a prominent method for satisfying consumptive needs. Pumping has intensified the hydrological flux within cypress systems in close proximity to extraction areas through rapid drawdown of the surrounding water table and underlying aquifer. Long-term mechanical pumping of cypress swamps in and around Tampa, Florida has led to severe impacts including sinkhole development in susceptible areas and saltwater intrusion into underlying groundwater (Bradbury & Courser 1977, Fretwell 1988, Rochow 1985). Adverse changes in vegetation, wildlife, and soil composition have also been noted with rapid, extended drawdown (Biological Research Associates, Inc. 1988, Reddy & Patrick 1998,

Weller & Voigts 1983). Lowered water tables favor the development of woody versus herbaceous vegetation, decrease wetland species diversity, and encourage invasion of terrestrial and exotic species into wetland habitats, favoring succession to an upland system over time (Biological Research Associates, Inc. 1988, Taber 1982, Weller & Voigts 1983). In cypress systems, cypress tree growth decreases and mortality increases with prolonged water drawdown (Keeland et al. 1997, Taber 1982).

Wetland wildlife populations fluctuate with hydrology, particularly those depending solely on wetland habitats for survival, i.e. aquatic invertebrates and fish. With declines in these populations due to drawdown, higher vertebrates such as waterfowl, muskrats, bears, and alligators are deprived of valuable food sources, prompting species migration or extinction (Parker 1960, Weller & Voigts 1983). In addition to the biotic changes, prolonged dry conditions alter soil character in wetlands by promoting the oxidation, shrinkage and compaction of the usually well-developed organic layer (Parker 1960, Reddy & Patrick 1998). Dry wetlands are more susceptible to fire, which is another route of organic matter loss and vegetation change (Bradbury & Courser 1977, Parker 1960).

Wetland impacts have been documented in ecosystems within three hundred meters of active wells (Rochow 1985). Current regulations governing water withdrawals from wetland systems in Florida allow for a one foot or 0.30 meter drop in the surficial aquifer at the wetland edge over a ninety day period of no recharge before adverse impacts to wetland hydrology and functioning are expected (F.S. 1996). An attempt to evaluate this regulation scientifically through quantification of spatial and temporal impacts is needed.

It is crucial to determine the adaptations, both long and short-term, of aquatic species within wetlands undergoing ever increasing hydrological stress through pumping regimes. Specifically, the response of benthic invertebrates to drawdown is critical, as benthos are fundamental food web components and nutrient cyclers in cypress swamps and other wetlands (Mitsch & Gosselink 1986, Murkin & Kadlec 1986).

Macroinvertebrates have several mechanisms for surviving desiccation. Species can emigrate from the system as adults by timing their life cycle to avoid seasonal dry events (Batzer & Wissinger 1996, Mackay 1985, Tauber et al. 1998). This strategy is only viable under a fairly predictable wet-dry seasonality. Survival strategies *in situ* involve either the production of desiccation resistant structures or materials, or migration down through the soil towards moisture (Jackson & Mclachlan 1991, Wiggins et al. 1980, Mackay 1985). *In situ* survival mechanisms would be employed under unexpected and prolonged drought conditions, such as would occur with extreme consumptive pumping.

Previous studies have dealt with the long-term effects of natural drought on benthic turnover rates, biomass, and diversity during and after a drought event. Most have noted a high faunal turnover rate with drawdown, wet taxa being replaced by terrestrial taxa, and a rapid recovery of taxa richness and diversity following rewetting (Bataille & Baldassare 1993, Driver 1977, Jefferies 1994). While most research on invertebrates has been conducted in prairie potholes and reservoirs, Leslie et al. (1997) specifically looked at benthic community structure in Florida pondcypress swamps. The study found no significant change in wet taxa representation with drought, suggesting survival of benthos *in situ*.

Two studies have addressed the vertical migration through soil by benthos as a survival strategy to drought in a reservoir. Over a 100-day drawdown period, Paterson & Fernando (1969) found that oligochaete species burrowed downward (>20 cm) to avoid desiccation and winter freezing. Chironomid numbers remained stable at 3 to 6 cm below the surface, indicating that downward migration was not pronounced. In contrast, Kaster & Jacobi (1978) found that chironomid abundance was altered within 21 days of drought at depths from 2 to 8 cm below surface, and also discovered burrows deeper than 20 cm for both oligochaetes and chironomids. This study clearly demonstrated benthic migration to deeper soil depths to avoid the effects of drawdown. Although both studies looked at benthic migration depth, they sampled no further than 20 cm because of impenetrable, frozen ground.

Despite limited and conflicting data, little research has focused on the short-term response of wetland benthic invertebrates to rapid drawdown, particularly in cypress swamps (Bataille & Baldassare 1993, Driver 1977, Jefferies 1994, Leslie et al. 1997, Riley & Bookhout 1990). Examination of both benthic response time to drawdown and deep soil migration as a short-term drought escape mechanism is crucial to fully comprehend the temporal impacts of extended drawdown. Determining benthic drought tolerance is vital to understanding how benthos adapt to rapid, severe drawdown conditions initiated by unpredictable natural drought, as well as human-induced hydrologic alteration.

In order to investigate the vertical migration of benthic macroinvertebrates in response to water drawdown, this study employed drought simulation experiments

conducted on soil cores from a South Florida cypress ecosystem. These experiments assessed both response time and response mechanisms for benthic dessication survival.

Methods

Study Sites

The primary study sites were in cypress sloughs located within the Corkscrew Swamp Sanctuary in Collier County. The sanctuary comprises 4,275 hectares, with 300 hectares of virgin cypress. The sanctuary is adjacent to agriculture and residential development. The hydrology of the sanctuary is quite diverse, but hydroperiods of the sampling sites remain fairly constant between 150 and 300 days (Duever 1975). Sites were located 30 to 70 m into the swamp from the fringing marshland areas. Prior to the study, these sites went through prolonged natural drought, but sampling was confined to areas where water level never went below the soil surface. During the low water period (May 1999), samples were collected randomly from an open water slough area surrounded by *Taxodium distichum*. The macrophyte community included *Thalia geniculata*, *Pontederia cordata*, *Pistia stratiotes*, *Cladium jamaicense*, and *Cephalanthus occidentalis*. Sampling during flooded conditions (July and August 1999) occurred within 30-40 m of the swamp fringe, within the closed canopy area. This area was dominated by *Taxodium ascendens*, with an understory of *Acer rubrum*, *Limnobiium spongia*, *Pontederia cordata*, *Annona glabra*, *Sabal minor*, and numerous fern species.

Samples were also collected once from an inundated cypress dome (FP5) located in the Flint Pin Strand Management Area in Lee County, approximately thirty minutes from Corkscrew Swamp. The dome was approximately 60 m in diameter with an open-canopied water center comprised of floating macrophytes and peripherally ringed by

cypress. The original intent of the project was to sample exclusively from this dome system, but due to unforeseen logistical problems, only one sampling event took place and Corkscrew Swamp became the sampling focus. As a result of differences in the two systems, the FP5 sampling event will only be considered for gross comparisons of benthic communities between pre and post drought seasons.

Sampling Methods

To study the responses of benthic macroinvertebrates within cypress domes to rapid drawdown, three microcosm experiments were conducted. The microcosms were designed to simulate rapid drawdown conditions within wetland soils by subjecting soil cores to varying regimes of water loss. For each sampling event, one 40-m² area within the cypress canopy was delineated. Cores were randomly collected from the field down to a soil depth of 30 cm within this area based on water depth (at surface, but no greater than one meter deep) and organic matter depth (>15 cm). Cores were collected using an aluminum corer (1 m length) designed to reduce compression forces. The corer had an inside polycarbonate liner (9.3 cm ID) that remained stationary to hold roots, while the outside sleeve cut cleanly through the soil profile with sharp cutting teeth (patent pending). The corer was designed only for organic substrate. Each core was sealed on the bottom with a rubber stopper, left open on top for ventilation, and shielded from light with aluminum foil to decrease soil temperature fluctuation. All cores were allowed to dry out while in transport back to the lab, except those designated as controls, which were continuously maintained with water collected from the field.

In the field, water column DO, water temperature, and pH were measured from the middle of the water column and water depth was measured at each sampling site. These measurements were not collected in May, as there was insufficient surface water.

In the laboratory, soil cores were kept upright indoors under stable, ambient temperatures. Triplicate cores were subjected to one of four treatments: continuously saturated (control), or a drawdown period of three, five or ten days (time zero drought began on day of field collection). To simulate rapid drawdown, soil water was allowed to percolate down through the soil layers to drop the "water table" within the cores. At the end of the experimental drawdown period, soil cores were extracted using a metal rod tipped with a rubber stopper, and divided into 3 cm increments for the top 9 cm, and into 10 cm increments below. All soil increments were preserved with ethanol, stained with rose bengal, and passed through a U.S. Standard No. 30 sieve. Macroinvertebrates were hand picked from the retained fraction, identified to the lowest taxonomic level practical, and total numbers tallied. Representative invertebrate biomass values for dipterans and oligochaetes were based on published values for Florida (Brightman 1975).

Soil cores from the cypress dome in Flint Pin Strand were randomly collected by the same corer device along a transect line from dome center to edge, sectioned down to 30 cm in the same increments as described above, sieved in the field, and the preserved samples were returned to the lab for analysis of macroinvertebrates.

During core processing, the 3 cm and 10 cm increment samples were subsampled for moisture content. 2 cm³ and 6.5 cm³ subsamples from the 3 cm and 10 cm increments, respectively, were placed into pre-weighed bottles. Air and oven dry weight (100°C for at least 24 hours) for the subsamples were obtained to determine mass

moisture content. Organic matter was determined through loss on ignition (500°C for 1 hour) (APHA 1992). Dry weight bulk density and porosity also were calculated for the subsamples. In order to calculate porosity, particle density was estimated from the organic matter content according to the formula: $\text{particle density} = 2.65 - 0.02 * \% \text{ organic matter}$ (Bonneau & Souchier 1982).

Statistical Analysis

To compare total macroinvertebrate density, richness, and abundance relative to both length of drawdown and depth in the soil profile, data were pooled from each depth increment for the triplicates of each treatment. Density was reported as numbers per 3 cm³ interval. In order to normalize the intervals for comparison, the 10 cm increments were transformed by dividing the numbers by 3.3. A square root transformation of the data was performed to reduce high variances characteristic of low sample size. A one-way ANOVA test (SPSS version 9.0) compared macroinvertebrate biomass and density for each depth increment within a treatment to percent moisture, percent organic matter, porosity, and bulk density. P values less than 0.05 were considered significant. Two post hoc tests, Duncan and Tamhane, were applied to determine significant relationships. Pearson correlations were run between all parameters and compared at the level of the five soil depth intervals.

Results

Water Quality

Water depth at the FP5 cypress dome during the single February sampling event was approximately 74 cm in the center, and 11 to 23 cm at the edge. Dissolved oxygen

fluctuated between 0.05 to 0.65 mg/L along the transect from center to edge, respectively, with water temperatures ranging from 20.0 to 21.6 °C. pH was between 5.76 and 6.36.

Corkscrew Swamp had similarly low oxygen conditions, averaging 0.71 in July and 0.88 mg/L in August. Water temperatures in July and August ranged from 25.0 to 28.6 °C, respectively. pH remained fairly constant for both July and August (6.85 - 6.91). Water depth in July varied between 15 to 25 cm, and 28 to 31 cm at the August sampling. Water measurements were not taken for the May sampling period as there was less than 2 cm surface water.

Soil Parameters Within Microcosms

Percent organic matter decreased significantly with increasing core depth, in both the July and August microcosms (Table 1). Organic matter was fairly uniform in the top 9 cm of all soil cores at approximately 80% in the 0-3 cm increment and 40-60% by 7-9 cm (Figures 1-3). The July and August cores had sand lens starting at the 10 cm increment and organic content dropped to less than 30% at 21-30cm.

Bulk density of the soil generally increased with depth, particularly for the July and August cores containing the sand lens at 10 cm (Figures 4-6). Bulk density was not statistically affected by the length of drawdown (Table 1). Porosity did not alter over the course of the drawdown treatments, but was reduced significantly by the sand lens at 10 cm for July and August (Table 1, Figures 4-6). Porosity and bulk density were negatively correlated in July and August ($p < 0.01$) (Table 2). Porosity was positively correlated with percent organic matter and moisture for all three sets of experiments, while bulk density was negatively correlated with these parameters only during July and August.

Despite allowing cores to drain freely, percent moisture did not differ statistically relative to core depth or the temporal extent of draining during the May experiment (Table 1, Figure 1). Moisture differed significantly by depth in the July and August cores, where there was a significant decrease at the 10 cm level probably due to the presence of the sand lens (Figures 2-3). Moisture was positively correlated with percent organic matter in all experimental periods (Table 2).

Benthic Macroinvertebrates

Macroinvertebrate density was low for all sampling periods, ranging from 73 total individuals in the July experiment to 136 in August (Table 4), and decreased from the surface downward (Figures 7-10). Intra-treatment variance was high in all experiments. Most macroinvertebrates were found in the 0-3 cm and 4-6 cm depth intervals. For the February and May periods, 0-3 cm abundance was significantly different from all other depth levels ($p=0.05$ & $p=0.004$, respectively). In July, the 0-3cm was different from the 4-6cm and 21-30cm levels ($p=0.01$). The August experiment showed significant differences between 0-3 and 21-30 cm ($p=0.01$). Only the July experiment had significant differences among drawdown treatments for macroinvertebrate density (Table 3). The five-day drawdown treatment was different from all the other treatments and the control. Although August had the highest total abundance, the February experiment had the highest mean macroinvertebrate density and July had the lowest total abundance and mean density (Table 4, Figure 11).

drawdown within three to five days, whether due to increased mortality or vertical migration. Although inter-treatment differences were significant only in July, the other two experiments exhibited the same trend of declining numbers over the length of the drawdown period. While this could be a result of the core microcosm itself, control cores maintained macroinvertebrates (July & August only) and were not significantly different from the treatments. A precipitous drop in densities is to be expected with drawdown (Jefferies 1994, Kaster & Jacobi 1978, Paterson & Fernando 1969), and indeed, the February sampling event, which experienced no drawdown, exhibited higher mean densities than the microcosms.

Vertical migration within the soil seems to be a viable drought response for macroinvertebrates, as suggested by the current experiments. Macroinvertebrates from the February event were present predominantly in the top soil interval (0-3 cm). In the microcosms, most organisms were found in the upper soil layers (0-6 cm), but they also migrated downward in the cores as demonstrated by the lack of significant difference between the 0-3 cm layer and the next three consecutive soil layers (4-20 cm). Very few organisms were found at the 21-30 cm depth, suggesting a possible lower limit for vertical migration.

The specific mechanism prompting vertical migration is unclear. Macroinvertebrate densities were correlated with percent organic matter, percent moisture, and porosity. Organic matter content decreased throughout the depth profile in all three experiments, but was only correlated with densities during the May experiment. Macroinvertebrates exhibit food source preferences, requiring appropriate ingestible particle size and nutritional quality from organic matter (Gardiner 1972). However,

Mean macroinvertebrate biomass was highest during February (Figure 12). It decreased with soil depth, following the density trend, and displayed a significant depth relationship for the May and August experiments (Table 3).

Diptera and Oligochaeta were the dominant taxa in all experiments. Within Diptera, Chironomidae, Tipulidae, and Ceratopogonidae were the major genera. The Chironomidae were mostly composed of *Chironomus* spp. and *Polypedilum* spp.. In February, July, and August, Chironomidae and Oligochaeta accounted for 85% (February and July) and 82% (August) of total macroinvertebrate abundance (Table 4). Tipulidae and Ceratopogonidae dominated in May (47% and 30%). All were represented throughout the soil depths, with none showing preference in burrow depth (Figures 13-14). All genera decreased at the 4-6cm increments, with the exception of oligochaetes in the July microcosm (Figure 14). Dipteran species dominated in February and May, while Oligochaeta dominated July and August microcosms. Total species richness was highest for May, while the February and July experiments exhibited the lowest richness (Figure15).

Macroinvertebrate densities were positively correlated with decreasing organic matter content for May ($p=0.02$) and August ($p=0.05$), and moisture content ($p=0.02$) and porosity ($p=0.02$) for August (Table 2). There was no significant relationship between macroinvertebrate density and soil bulk density (Table 2).

Discussion

Macroinvertebrate densities in the study were very low overall, a product of both the limited number of core replicates, as well as the character of South Florida cypress

systems. Duever (1975) found low numbers of chironomid larvae and oligochaetes at Corkscrew Swamp, and sampling in recent years by Corkscrew biologists has yielded similarly low densities. The range of annual mean densities for cypress systems varies from 307 numbers/m² in an Everglades water conservation area (Rader 1994) to 4229 numbers/m² in Florida pondcypress swamps (Leslie et al. 1997). The mean densities for all experiments (February – August) ranged from 2 - 4 #/cm³ or approximately 0.02 - 0.04 #/m³. Low densities made statistical comparisons difficult, but still some trends of responses to drawdown were evident.

The macroinvertebrate communities of this study, dipterans and oligochaetes, were very indicative of drought conditions (Bataille & Baldassare 1993, Kaster & Jacobi 1978, Leslie et al 1997, Paterson & Fernando 1969). There were obvious seasonal differences, as the most abundant taxa in the spring months (February and May) were dipterans, while oligochaetes were dominant during summer (July and August). Within the Diptera, Ceratopogonidae and Tipulidae were most abundant in February and May, being replaced by Chironomidae in the latter months. The difference in species richness between May and the other experiments can be attributed to the onset of drought in May and its abatement in the July and August months. Higher diversity is expected with the initial days of drought, then decreasing during a prolonged drought period (Jefferies 1994).

Many studies have shown that macroinvertebrates, especially dipterans and oligochaetes, can survive drought periods, but none have looked specifically at the response time within the soil. Only Kaster & Jacobi (1978) noted an initial response to drawdown onset for benthos (>7 days). Macroinvertebrates in our study responded to

organisms in this study appear to be migrating downward independent of organic matter content. Moisture content of the soil is undoubtedly critical to the organisms, as they require water to maintain osmotic balance and to facilitate oxygen adsorption through the integument (Gardiner 1972). Percent moisture decreased with soil depth, but did not change over the course of the drawdown time period. Although densities were correlated with moisture change down the core profile in August, the relationship was not apparent in either of the other microcosms or across drawdown treatments. Soil cores were analyzed for total moisture content, and no differentiation was made between pore water and water held in the interstitial spaces of the organic matter. These interstitial spaces may allow the persistence of humidity levels sufficient enough to supply adequate moisture to benthos. This subtle difference could influence benthic behavior, specifically migration patterns down a desiccating soil core.

The physical structure of the soil in terms of compaction and resistance may be important to organism movement. In July and August, porosity decreased drastically down the soil profile with an increase in bulk density and decrease in moisture content. The sand lens present in the July and August cores likely account for this shift. When soil columns lose water, they compact from the surface down within a few days, and porosity would be expected to be higher in the lower versus the upper sediments (EPA 1977). The well-compacted sand lens present in July and August experiments confounds the pattern of porosity change. The porosity decrease in August was slightly correlated with decreasing macroinvertebrate numbers, so organisms may be responding to the degree of soil compaction; however, this was not apparent in the other experiments.

The extent of vertical migration may be a constraint of burrow depth preference by different macroinvertebrate communities. Charbonneau and Hare (1998) found burrow depth to be very dependent upon species composition, particularly of Chironomidae assemblages. Three species of *Chironomus* burrowed to different depths and at different rates. The mean burrow depth of these *Chironomus* spp. was approximately 6 cm. A strong seasonal variability was also noted, as larvae migrated much further into the soil with a drop in temperature. Perhaps the lack of profound vertical migration within the current cores can be attributed to species variability and an under representation of taxa that migrate deeper. The species present might also need a more drastic change in water content to stimulate the vertical migration impulse.

Restrictions of the microcosm design should be taken into account when assessing study results. Container size and organism residence times have been shown to affect results in limnological microcosms (Stephenson et al. 1984). The core environment itself could have been a factor by inadvertently altering invertebrate behavior or mortality rates. Unfortunately, the amount of controls within the microcosms were inadequate to statistically determine this affect. Processing a replicate core before each drawdown treatment and prior to the advent of the experiments would have been optimal. Core effects on species assemblages would also have been better served by improvement of the controls. Large inter- and intra-variability was exhibited within the cores, which was unavoidable. Macroinvertebrate communities are naturally characterized by patchy distribution and as such, core to core variability is expected to be high (Leslie et al. 1997, Turner and Trexler 1997). Although the amount of cores required to significantly reduce

this variability is impractically large (Streever and Portier 1994), the study would be improved with more sample replicates.

Despite the limitations of the design, the microcosms were effective research tools as they allowed isolation of physical factors difficult to achieve in the field, and they have been widely used in studying microfaunal response to aquatic perturbations (Schratzberger & Warwick 1998, Warwick 1993). Of course, the results of these microcosms should be verified by field research. In addition to the above mentioned experimental design flaws, future research on macroinvertebrate drought response using microcosms should include several improvements. Further removal of confounding soil factors is necessary, perhaps by maintaining constant organic matter content and fluctuating the water table only. The addition of known macroinvertebrate assemblages and numbers to the cores would enable illumination of species soil migration preferences. Extending drawdown periods past ten days is crucial to determine the maximum desiccation tolerance limit for benthos. Core oxygen profile data, potentially ascertained from redox potential measurements, are needed as well, as oxygen limitations certainly affect benthic behavior.

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Table 1. Summary of ANOVA tests for differences between drawdown treatment (T) and soil depth (D) for physical soil parameters within each microcosm. Run for microcosms only.

Parameter	Microcosm					
	May		July		August	
	D	T	D	T	D	T
Percent Organic Matter	1.69	2.902	78.482*	0.424	65.45*	0.413
Percent Moisture	1.086	1.913	55.581*	0.131	64.068*	0.473
Porosity	0.591	1.619	50.4*	0.152	60.31*	0.184
Soil bulk density	0.287	0.874	89.522*	0.239	89.628*	0.221

* Significant at $p < 0.05$.

Table 2. Summary of Pearson correlations run between all parameters. Comparisons were made at the level of soil depth interval. Invertebrate numbers were analyzed using square root transformed data. Run for microcosms only. Pearson coefficients given.

Parameter	Microcosm																	
	May						July						August					
	D	OM	M	P	SB		D	OM	M	P	SB		D	OM	M	P	SB	
Macroinvertebrate Density (D)		0.370*													0.294*	0.302*		
Percent Organic Matter (OM)				0.611*						-0.946*					0.946*	0.847*	-0.938*	
Percent Moisture (M)		0.846*		0.902*			0.922*		0.929*	-0.955*						0.921*	-0.966*	
Porosity (P)									0.855*								-0.964*	
Soil bulk density (SB)									-0.964*									

* Significant at $p < 0.05$.

Table 3. Summary of ANOVA tests for differences between drawdown treatment (T) and soil depth (D) for biological parameters within each sampling event. Invertebrate numbers were analyzed using square root transformed data.

Parameter	Sampling Event							
	February		May		July		August	
	F Value		F Value		F Value		F Value	
Macroinvertebrate Density	D	T	D	T	D	T	D	T
	6.454*	-	4.746*	1.682	3.322*	2.658*	3.249*	0.48
Biomass	D	T	D	T	D	T	D	T
	5.258*	-	3.015*	-	1.415	-	2.178	-

* Significant at $p < 0.05$.

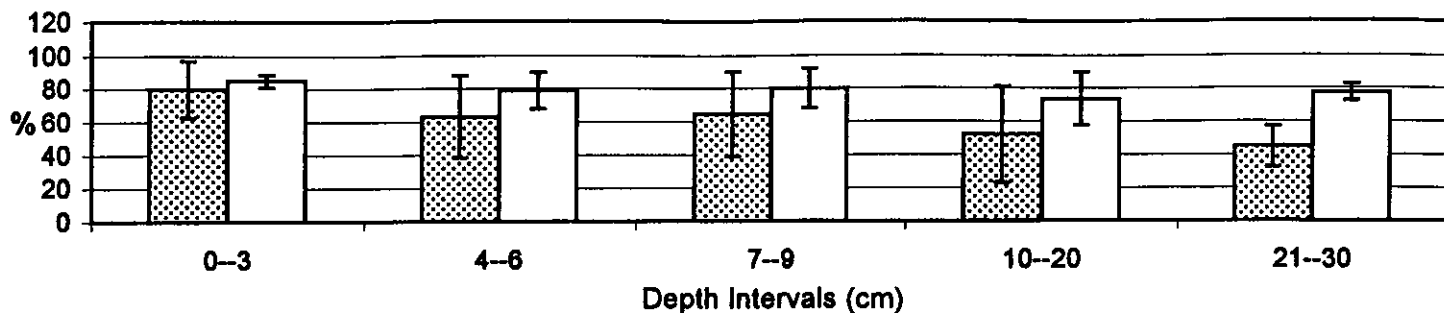
(-) Denotes no statistical analysis.

Table 4. Total and relative abundance of dominant taxa for each sample period. Total abundance pooled for all cores collected for each sampling event.

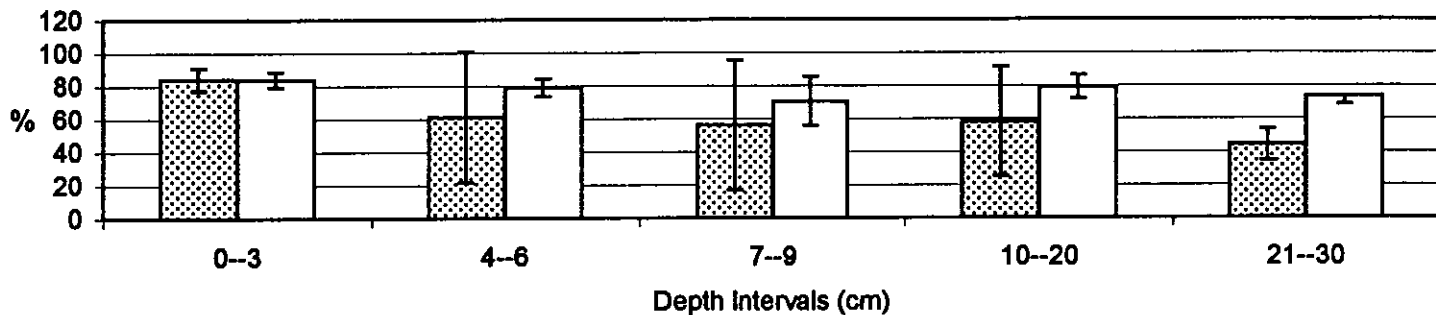
Sampling Event	Taxa	Total Abundance	Total Relative Abundance (%)
February	Oligochaeta	32	0.32
	Amphipoda	1	0.01
	Chironomidae	53	0.52
	Ceratopogonidae	9	0.09
	Coleoptera	6	0.06
	Total	101	
May	Oligochaeta	2	0.02
	Amphipoda	2	0.02
	Chironomidae	10	0.10
	Ceratopogonidae	29	0.30
	Collembola	6	0.06
	Coleoptera	2	0.02
	Tipulidae	46	0.47
Total	97		
July	Oligochaeta	53	0.73
	Amphipoda	8	0.11
	Chironomidae	9	0.12
	Ceratopogonidae	2	0.03
	Coleoptera	1	0.01
	Total	73	
August	Oligochaeta	72	0.53
	Amphipoda	17	0.13
	Chironomidae	39	0.29
	Ceratopogonidae	3	0.02
	Coleoptera	5	0.04
	Total	136	

DAY 3

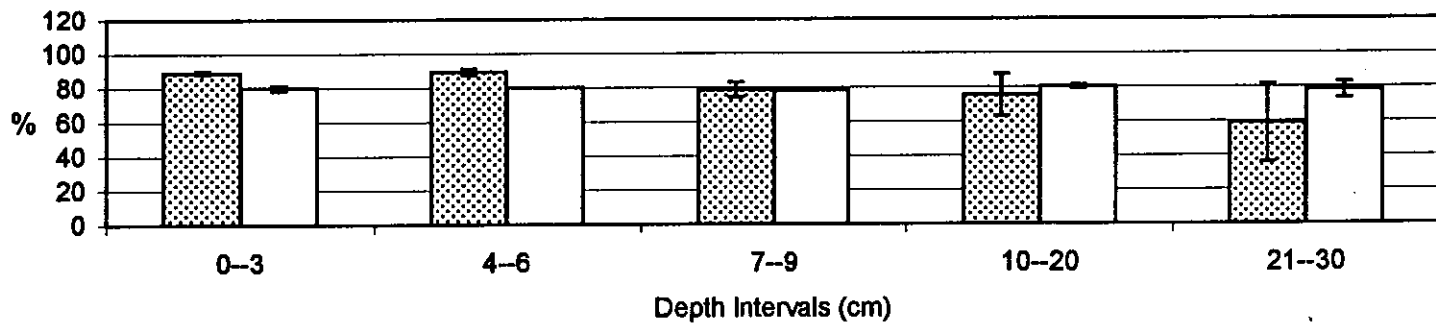
▨ % OM □ % MOISTURE



DAY 5



DAY 10



CONTROL

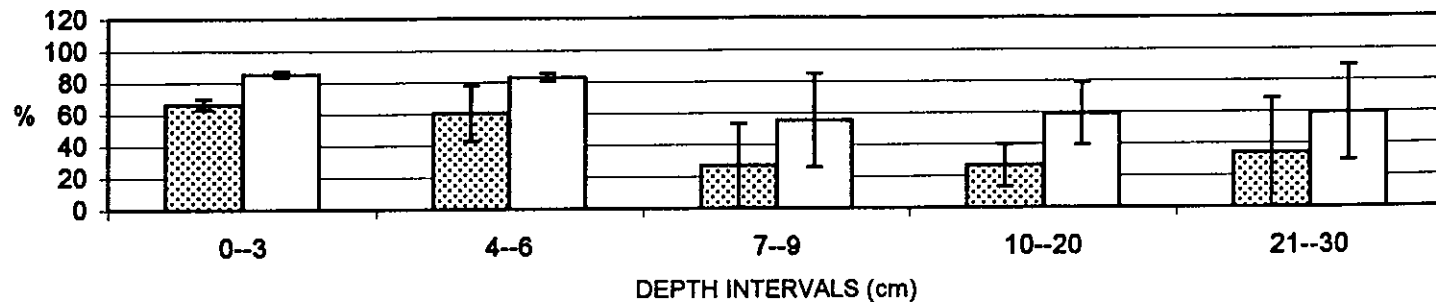
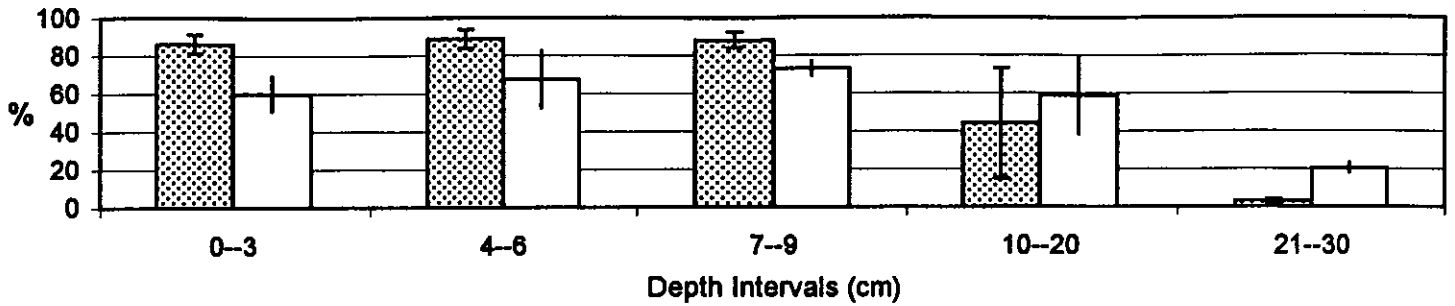


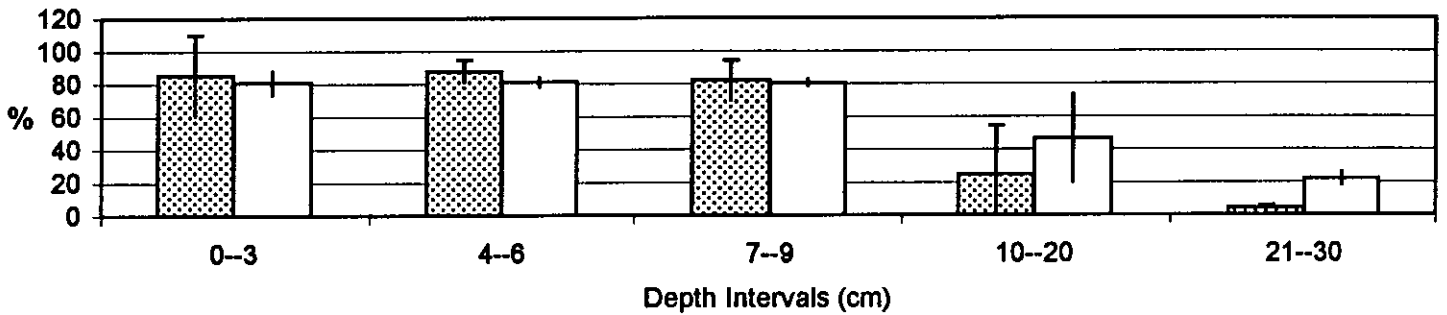
Figure 1. Mean percent organic matter and moisture for each drawdown treatment and control during the May 1999 microcosm experiment.

DAY 3

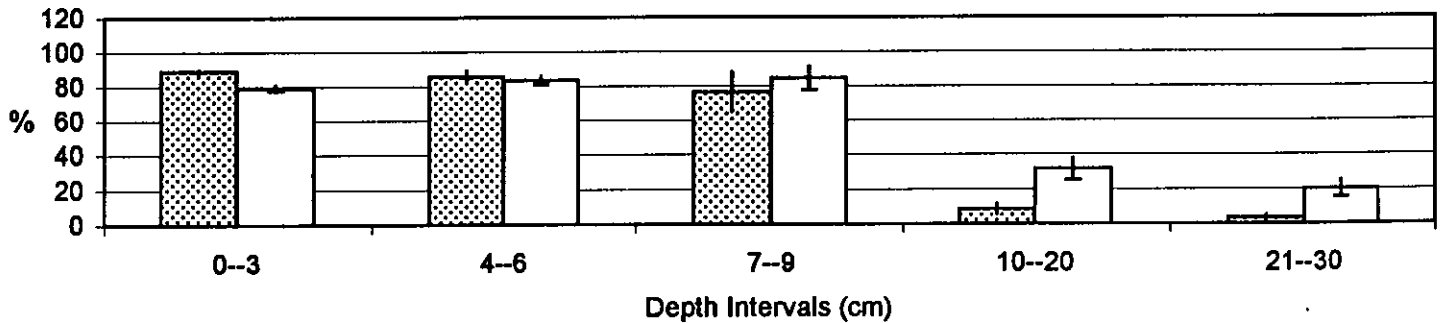
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DAY 5



DAY 10



CONTROL

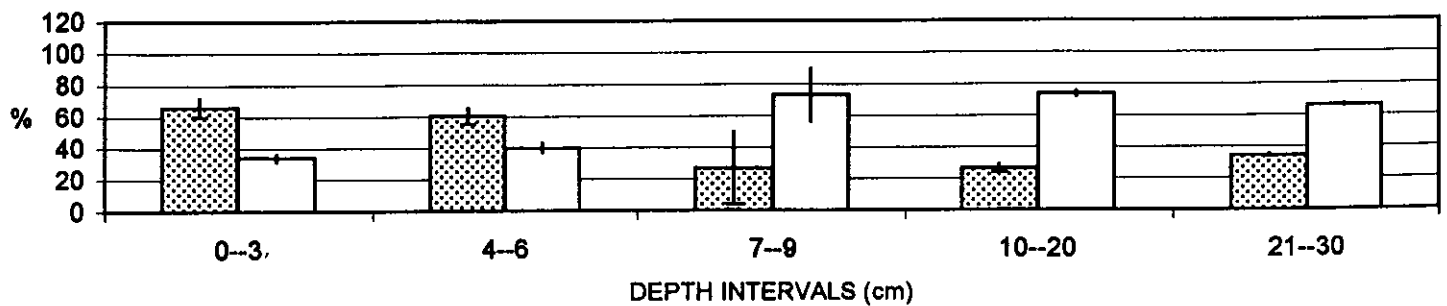
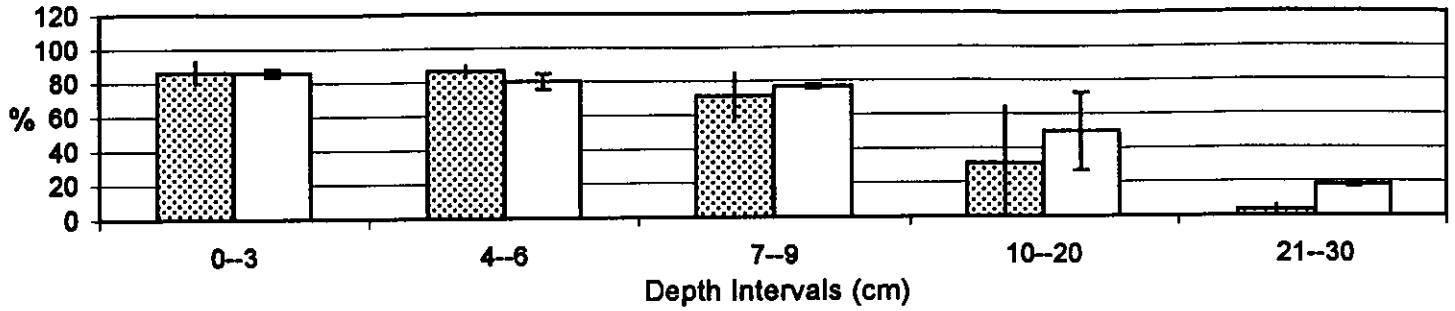


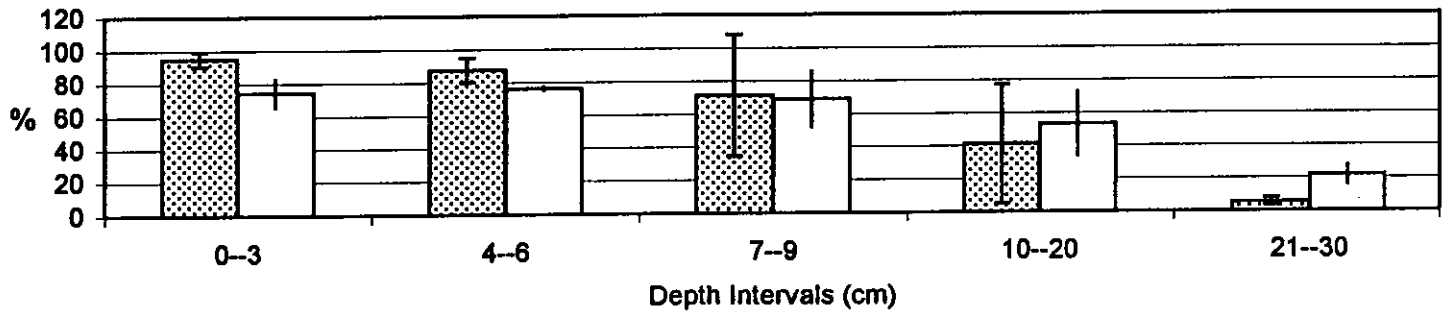
Figure 2. Mean percent organic matter and moisture for each drawdown treatment and control during the July 1999 microcosm experiment.

DAY 3

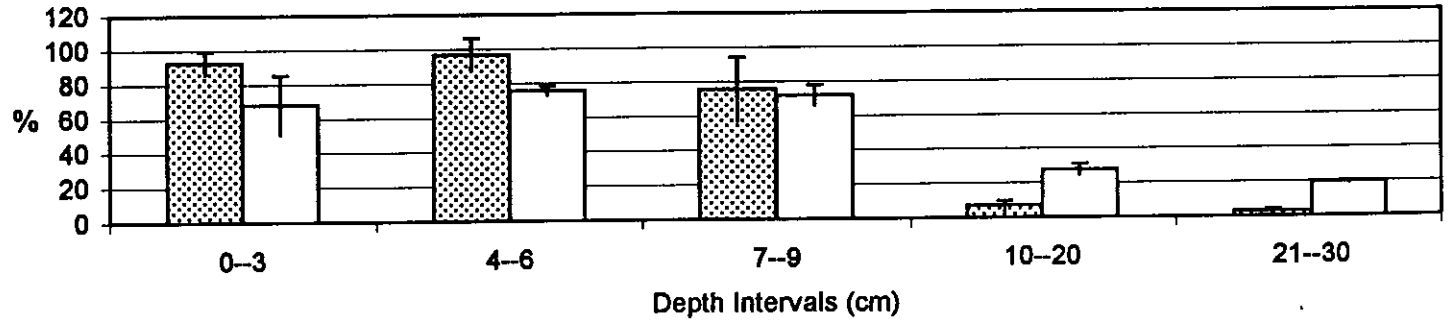
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DAY 5



DAY 10



CONTROL

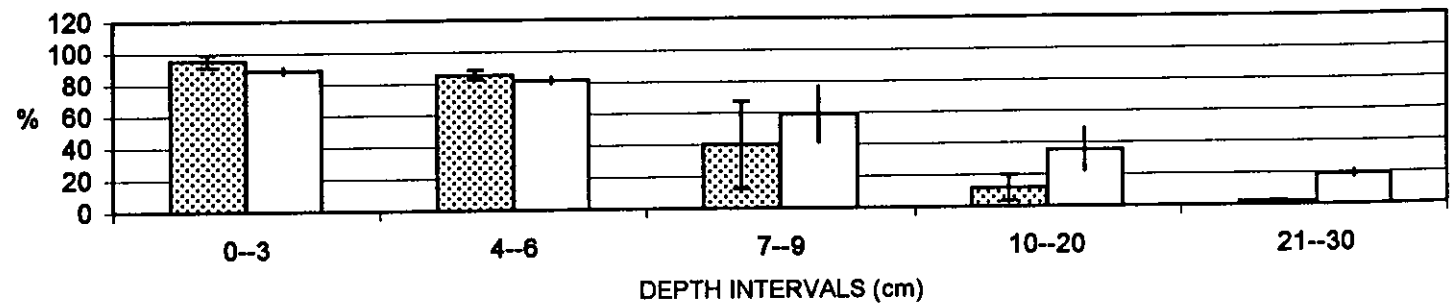
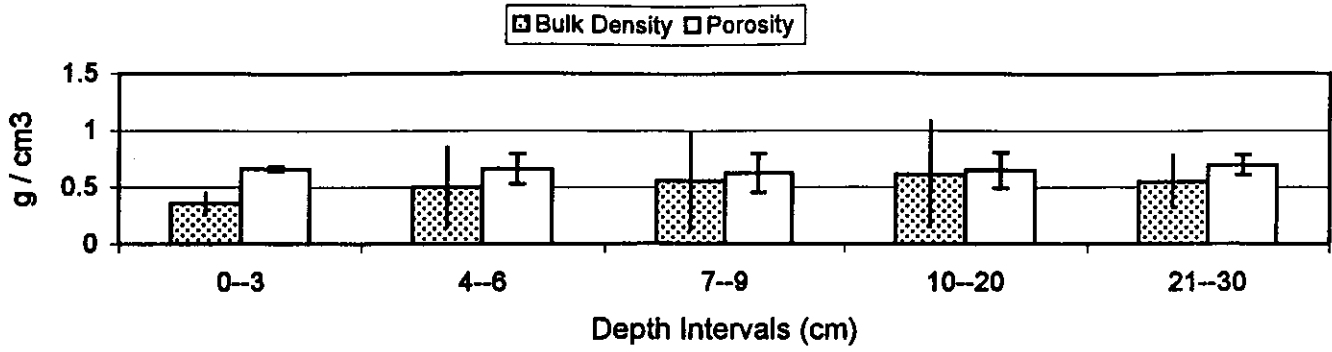
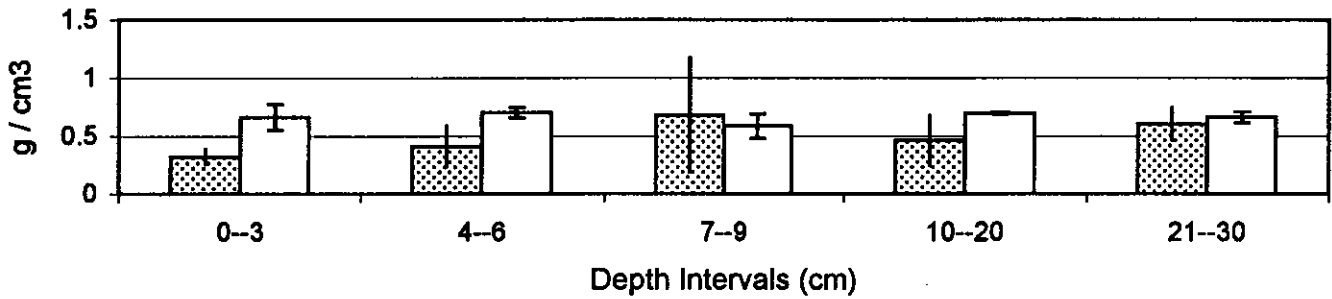


Figure 3. Mean percent organic matter and moisture for each drawdown treatment and control during the August 1999 microcosm experiment.

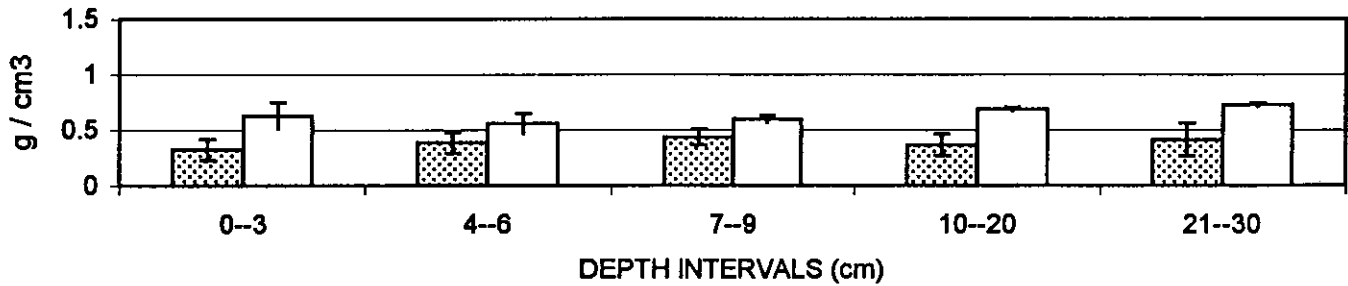
DAY 3



DAY 5



DAY 10



CONTROL

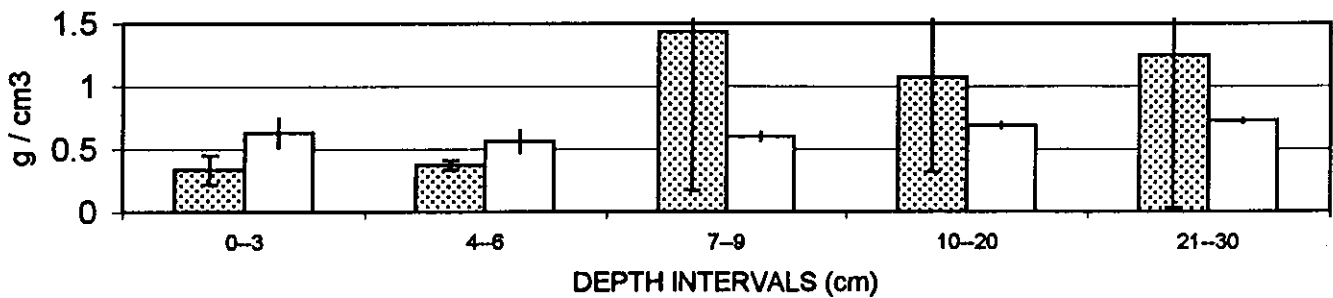
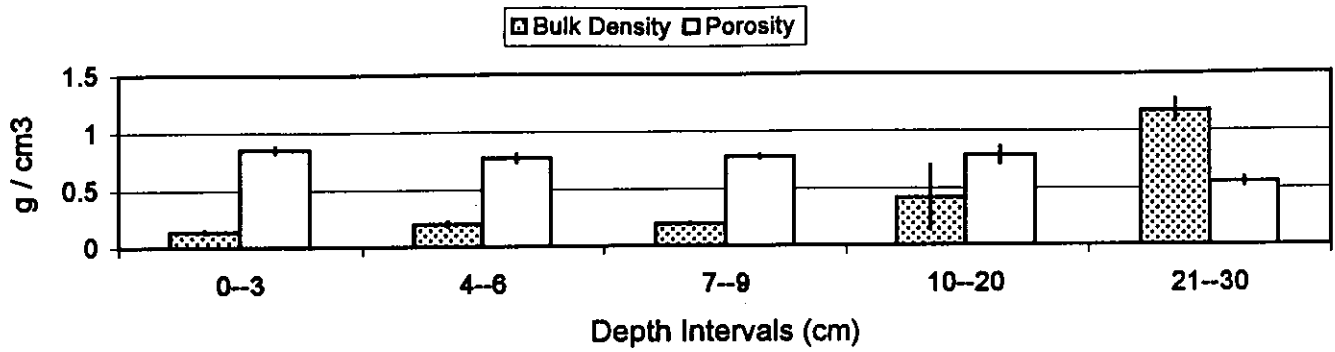
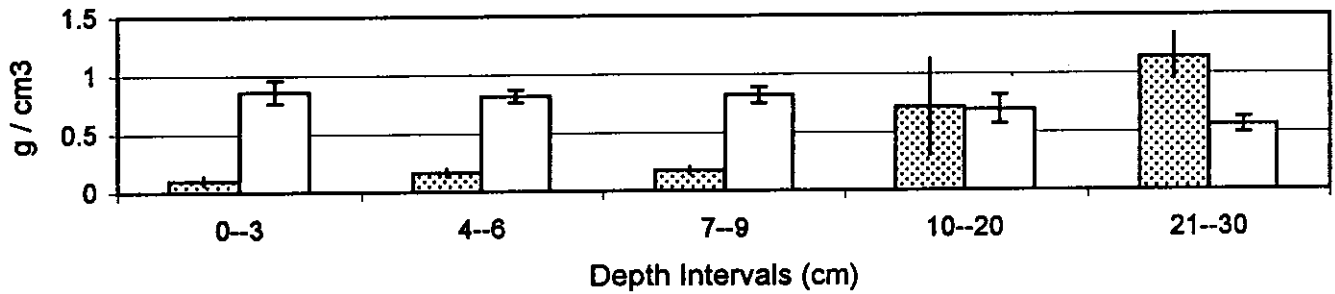


Figure 4. Mean bulk density and porosity for each drawdown treatment and control during the May 1999 microcosm experiment. Although porosity is scaled the same as bulk density on the graphs, it is unitless.

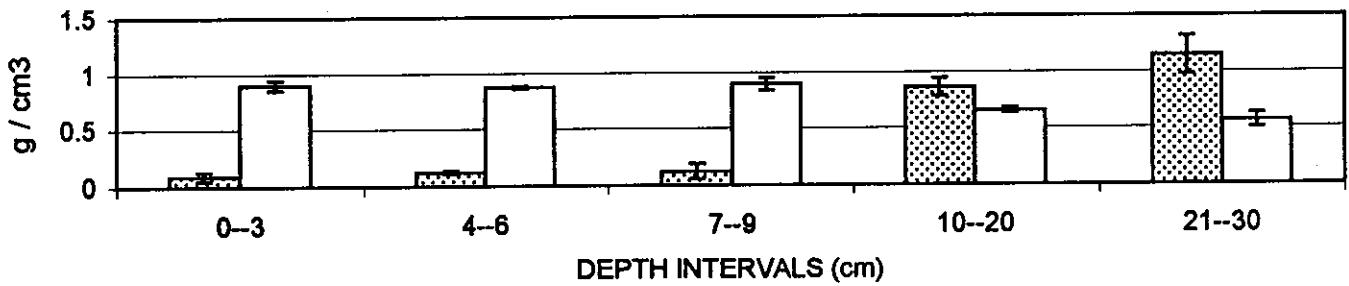
DAY 3



DAY 5



DAY 10



CONTROL

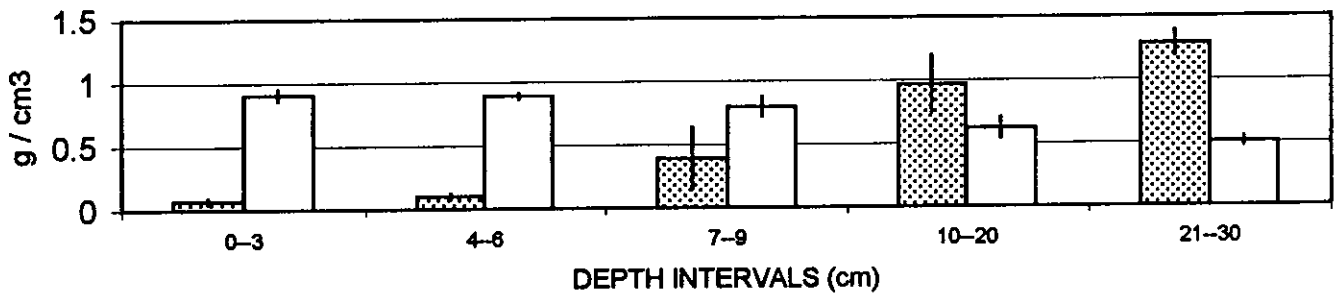
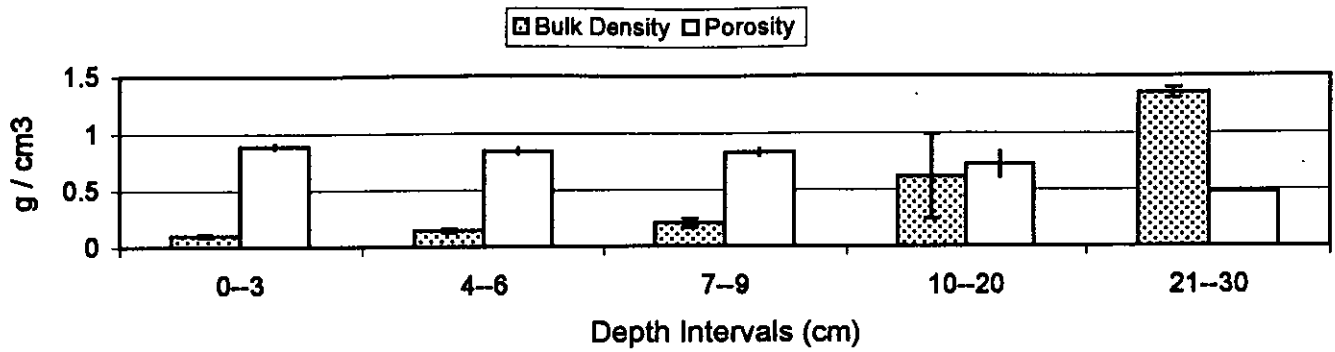
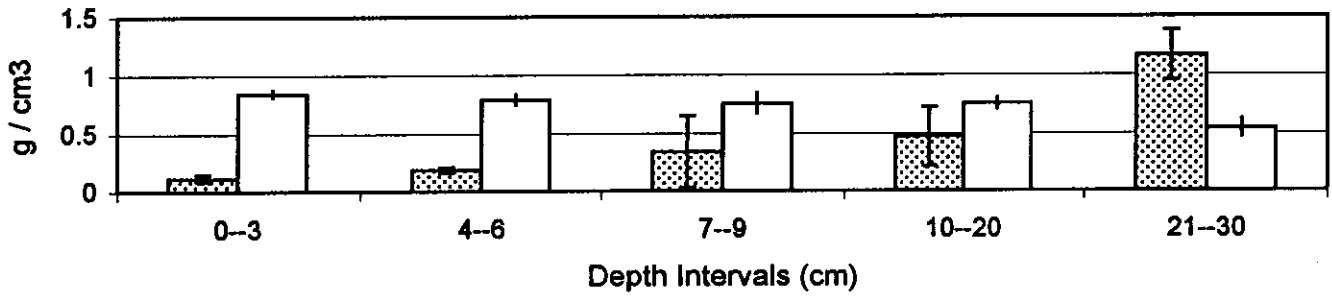


Figure 5. Mean bulk density and porosity for each drawdown treatment and control during the July 1999 microcosm experiment. Although porosity is scaled the same as bulk density on the graphs, it is unitless.

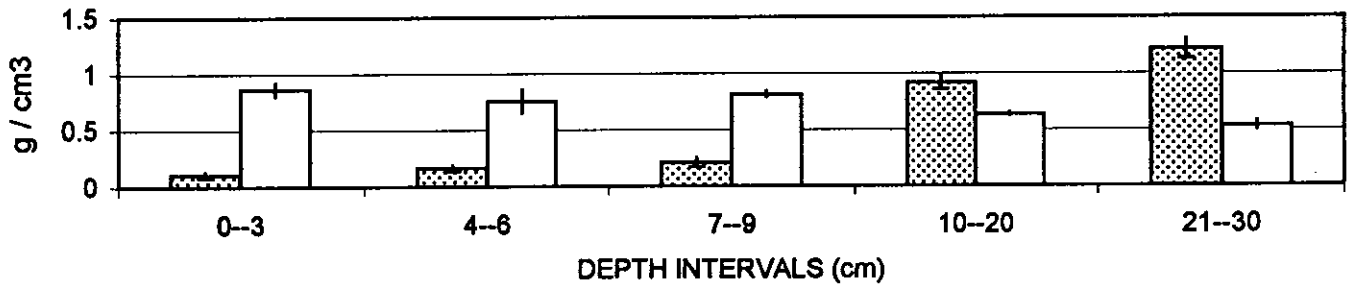
DAY 3



DAY 5



DAY 10



CONTROL

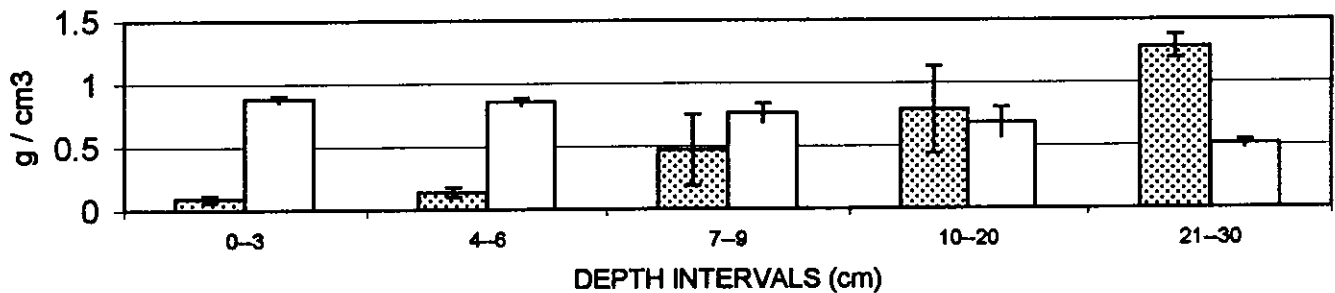


Figure 6. Mean bulk density and porosity for each drawdown treatment and control during the August 1999 microcosm experiment. Although porosity is scaled the same as bulk density on the graphs, it is unitless.

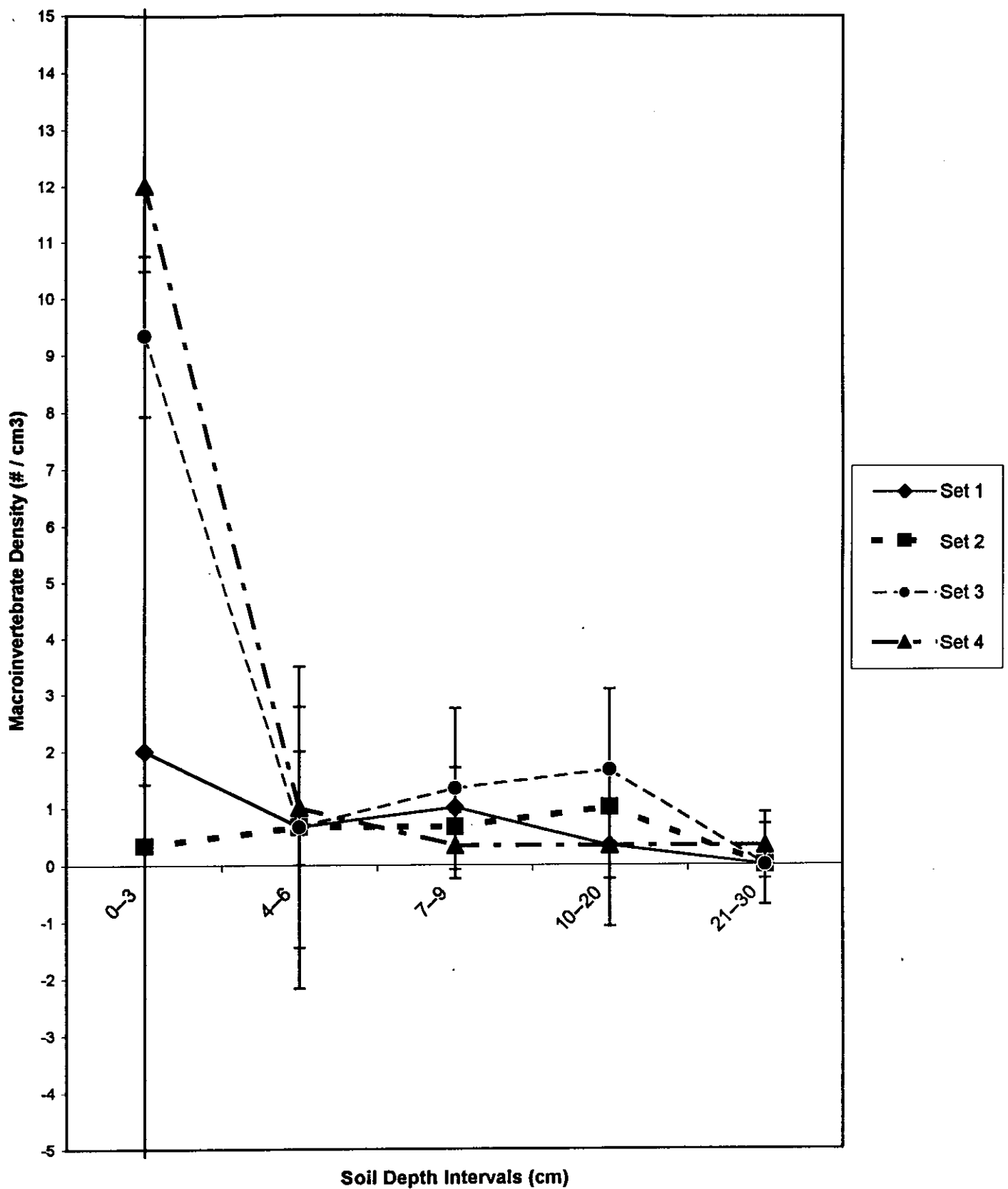


Figure 7. Mean macroinvertebrate density (+SE) for February sampling. Data pooled for each set of triplicate cores collected.

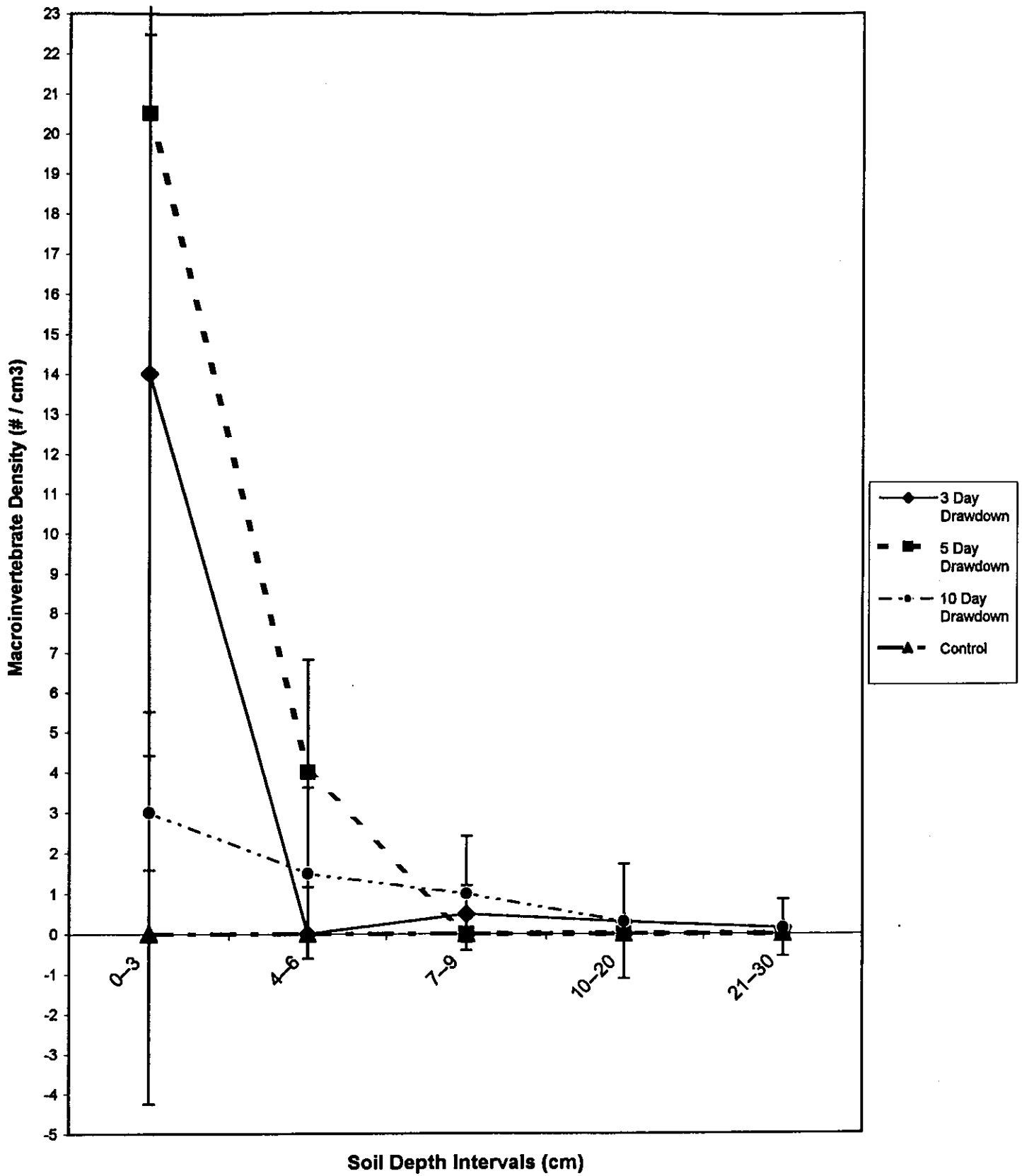


Figure 8. Mean macroinvertebrate density (+SE) compared to soil depth increment for May.

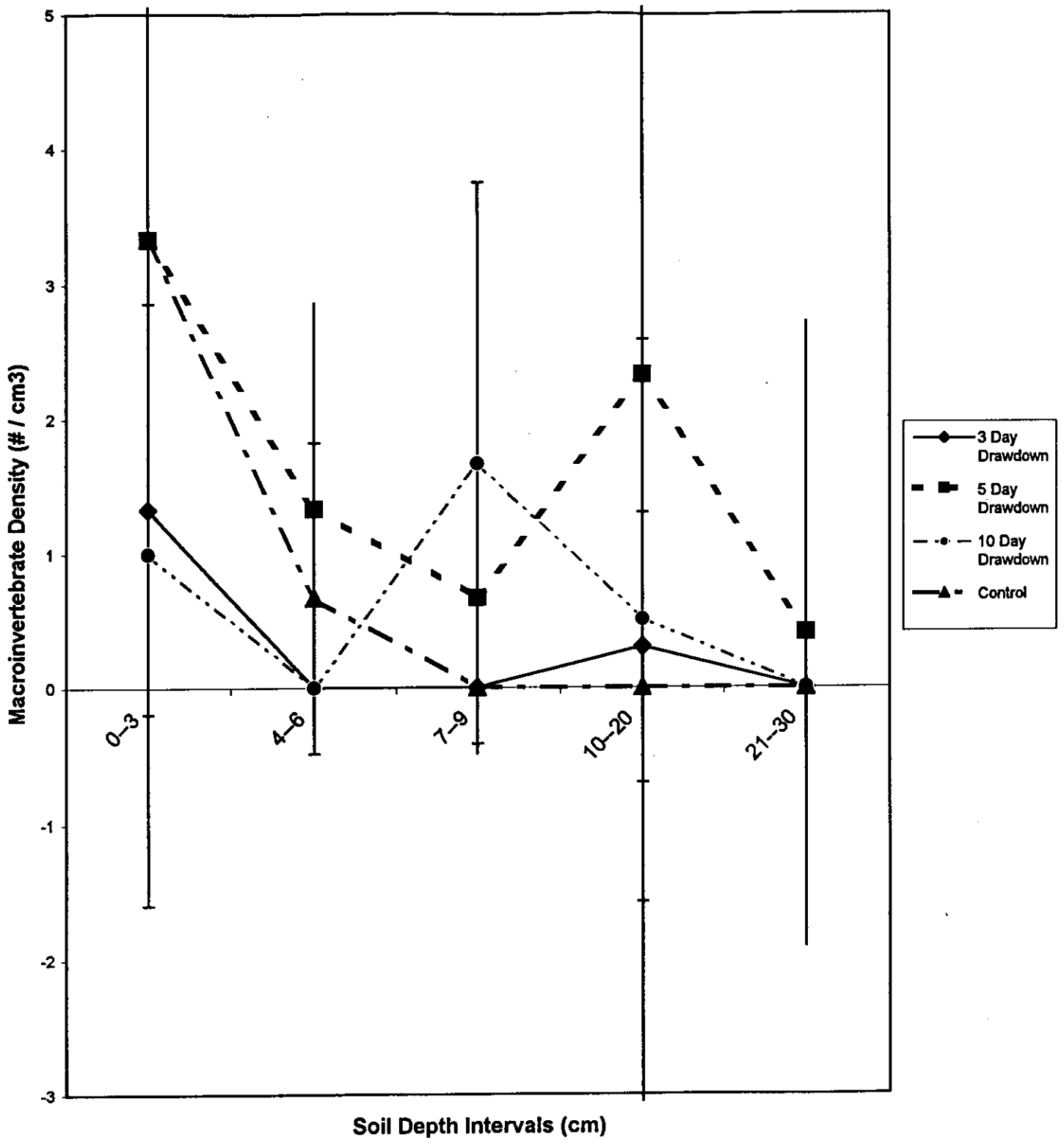


Figure 9. Mean macroinvertebrate density (+SE) compared to soil depth increment for July.

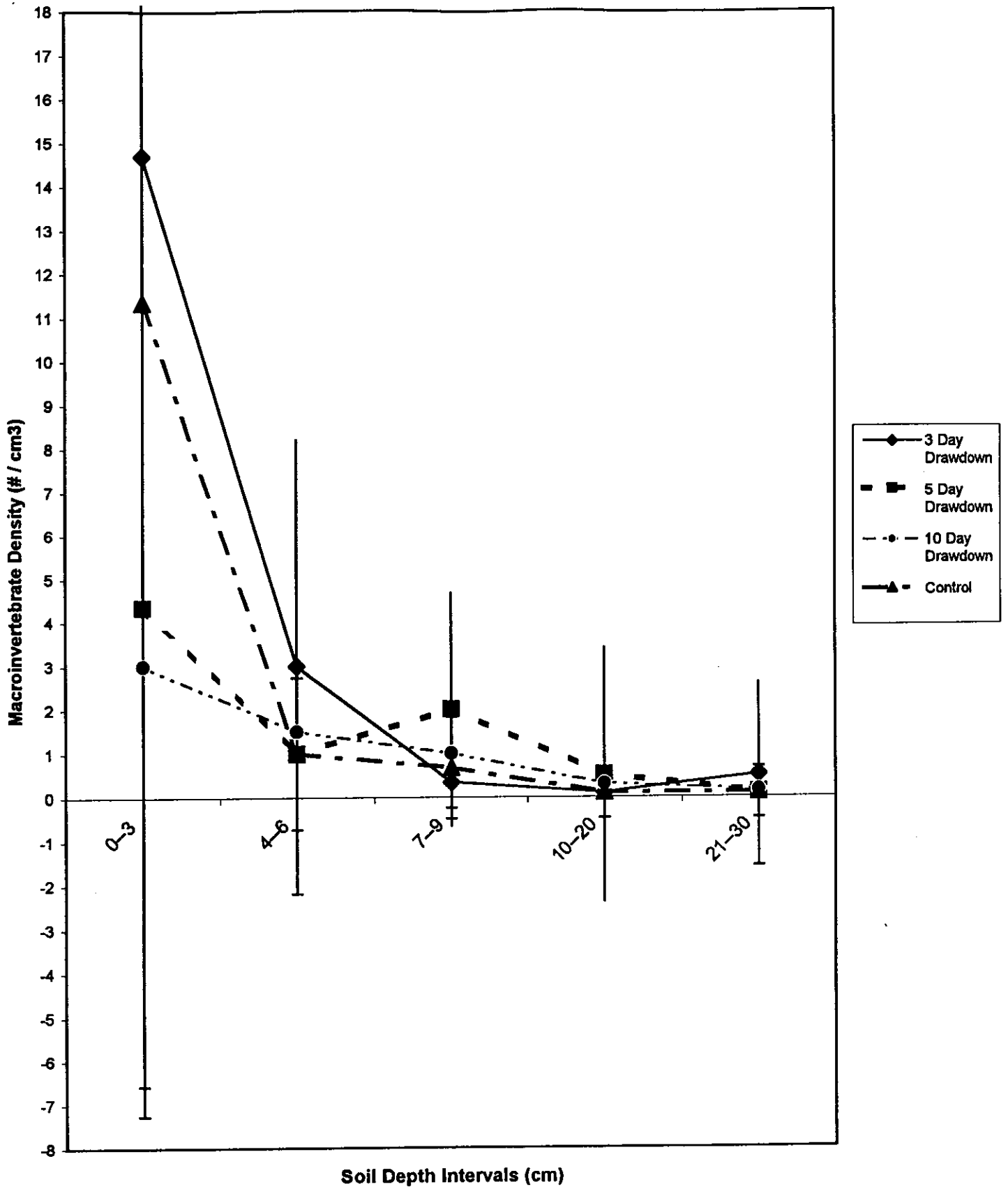


Figure 10. Mean macroinvertebrate density (+SE) compared to soil depth increment for August.

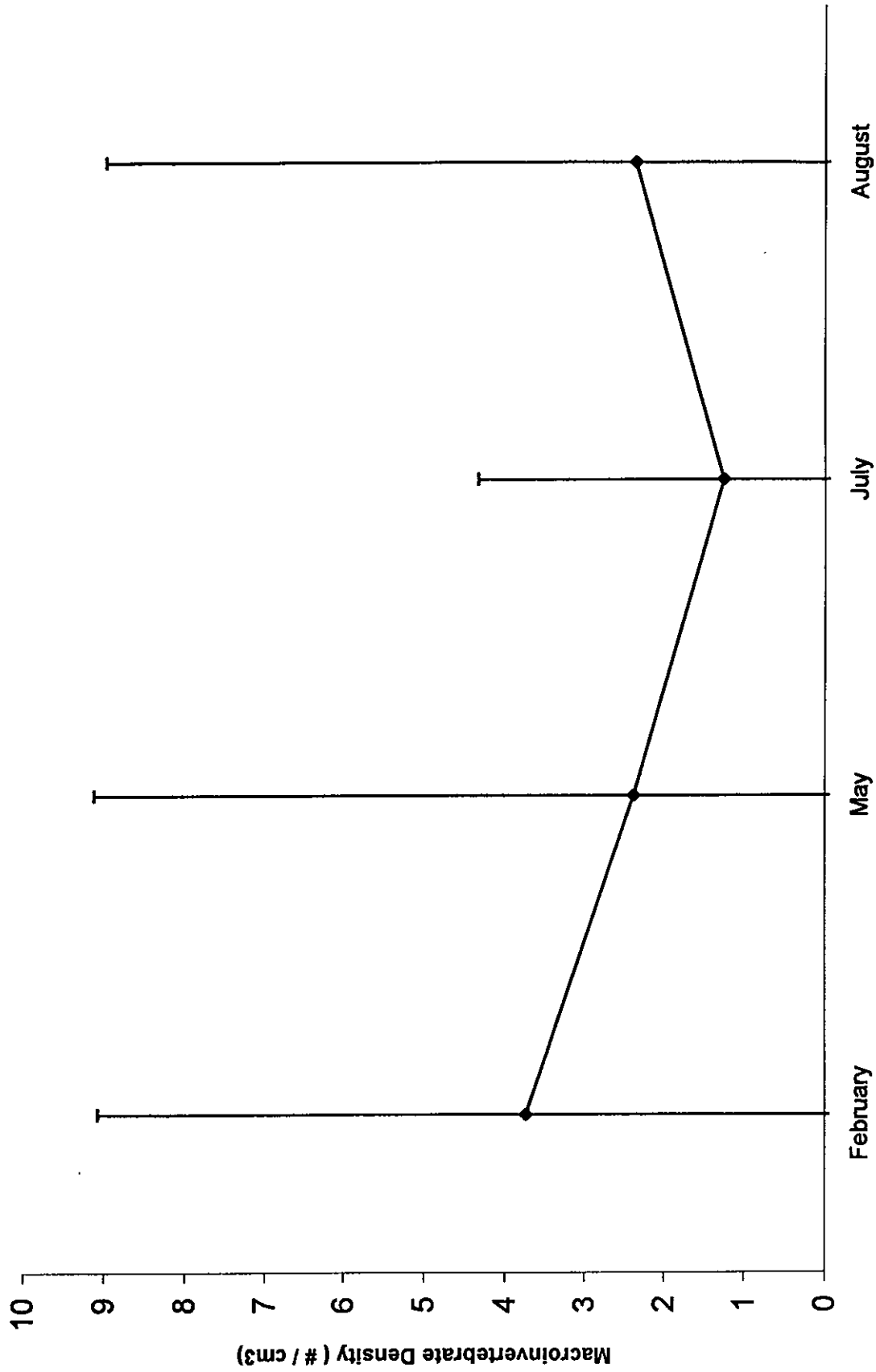


Figure 11. Mean macroinvertebrate density (\pm SE) compared across all experiments. Pooled from all cores for each experiment.

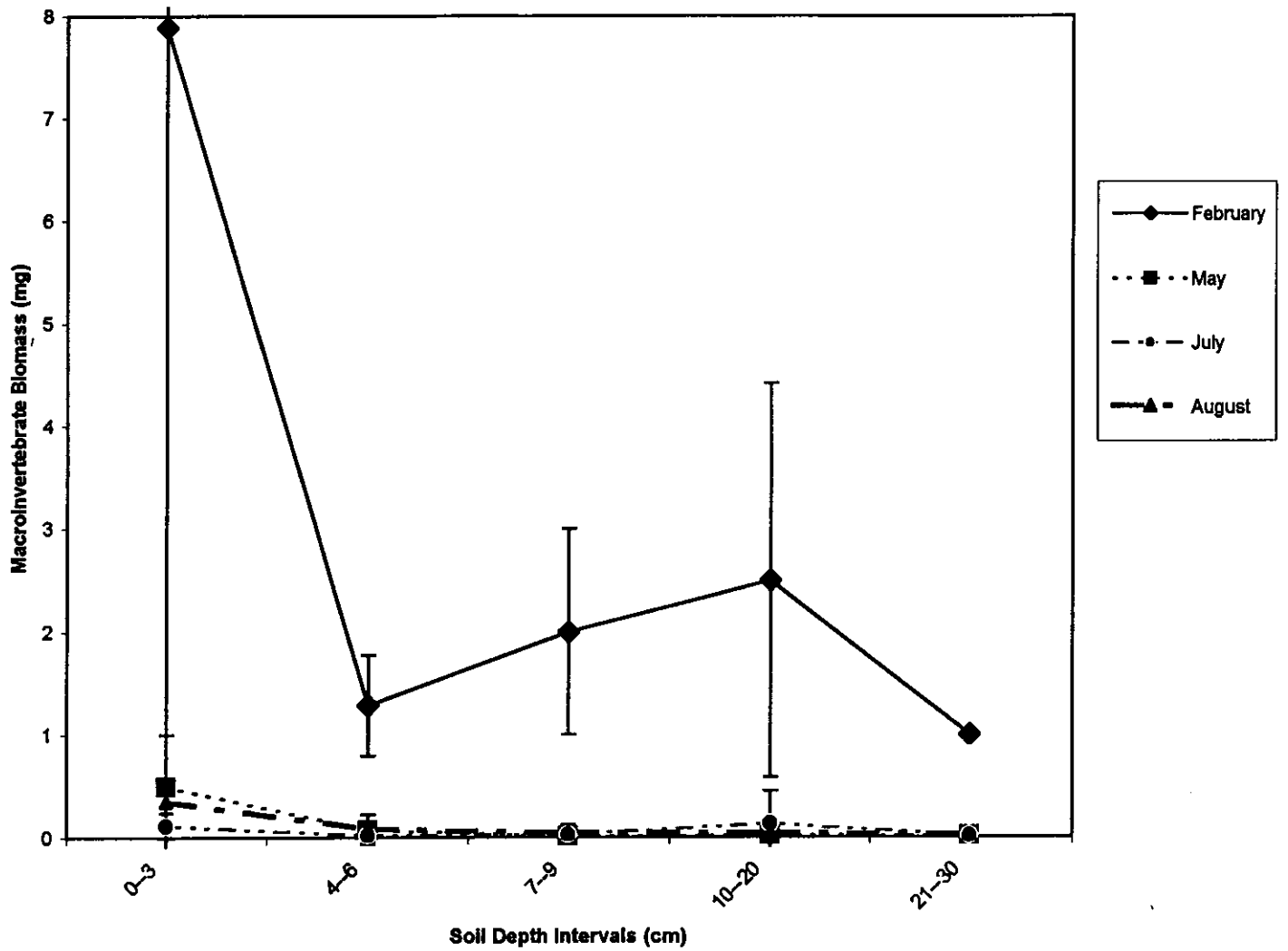
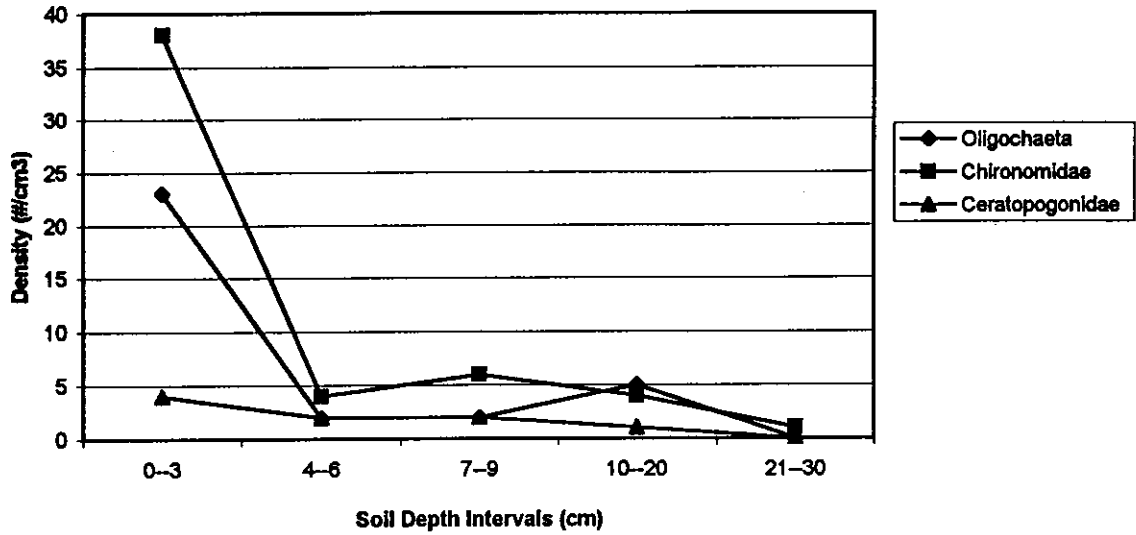


Figure 12. Mean macroinvertebrate biomass (+SE) pooled at each depth interval for each experiment.

Dominant Taxa: February



Dominant Taxa: May

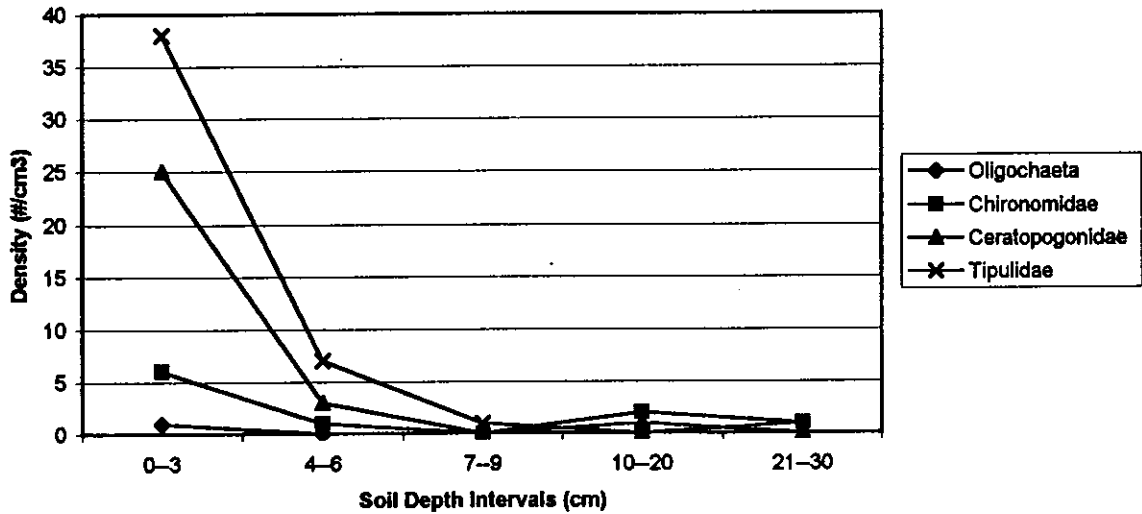
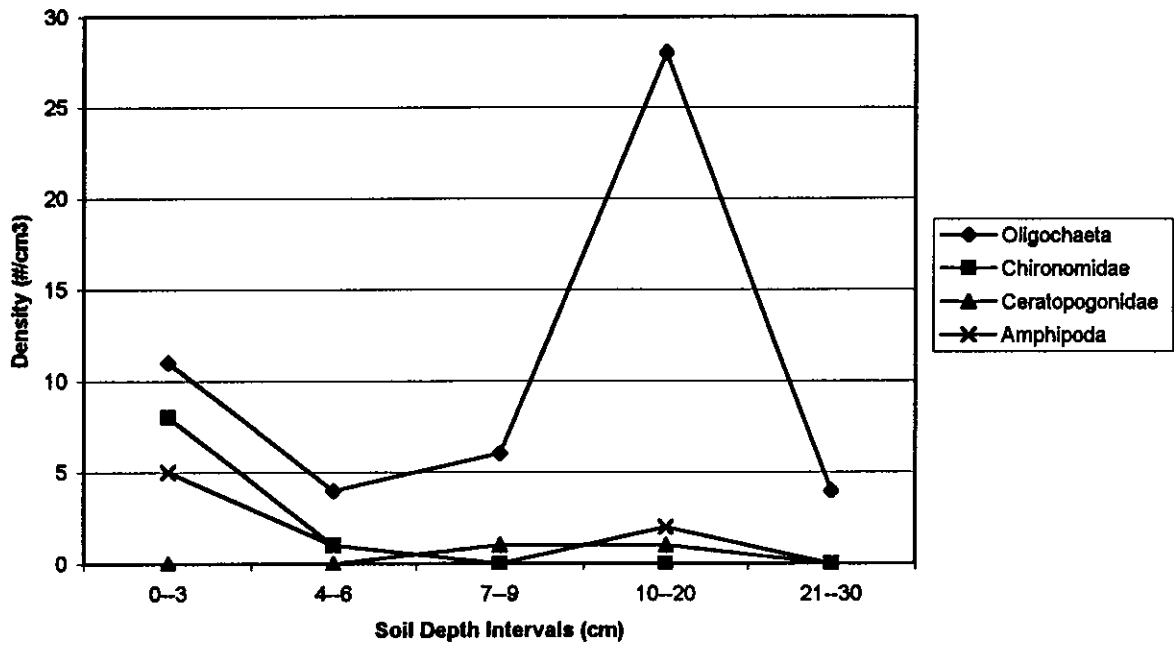


Figure 13. Dominant taxa at each soil depth increment for February and May.

Dominant Taxa: July



Dominant Taxa: August

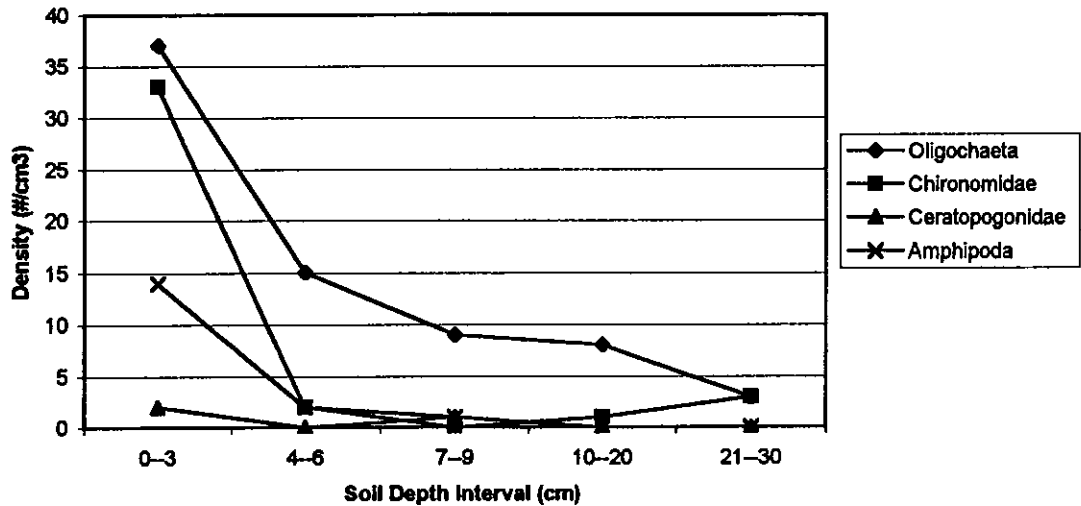


Figure 14. Dominant taxa at each soil depth increment for July and August.

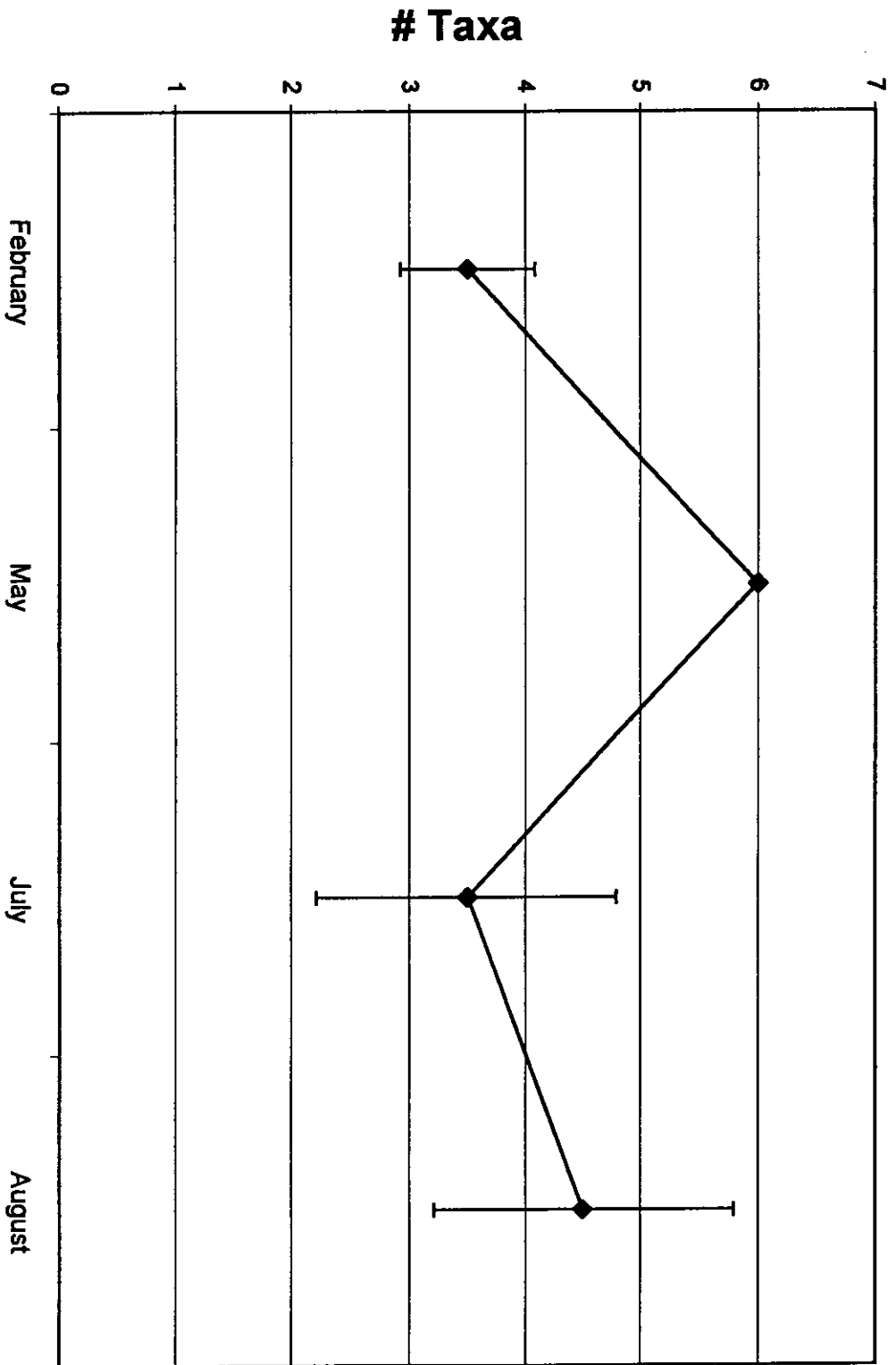


Figure 15. Mean total species richness for individual experiments.