Vertical, longitudinal and seasonal variation in the benthic fauna at the Fernow Experimental Forest, Parsons, West Virginia.

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Robert William Hood

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as meeting the research requirement for the Master's Degree.

Leonard J. Deutsch
Dean of the Graduate School

Advisor: Donald Tarter
Department of Biological Sciences

T. K. Pauley
Department of Biological Sciences

Dan K. Evans
Department of Biological Sciences

Ted
United States Forest Service
Northeast Forest Experiment Station

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ABSTRACT

Multi-level basket samplers were placed within the shallow hyporheic zone (0 - 30 cm) of first through fourth-order streams in the Elklick Run drainage at the Fernow Experimental Forest, Parsons, West Virginia. Samplers were colonized by macroinvertebrates over three month intervals and collected during three different seasons. Seasonal, longitudinal, and vertical variation in the macroinvertebrate assemblage were examined to better understand the structure and function of the interstitial macroinvertebrate assemblage and important underlying factors. Surber samples were collected for comparison between surface and hyporheic macroinvertebrate assemblages. Temperature, dissolved oxygen, water chemistry, and interstitial water movement were measured at sampler locations. Analysis indicated that most macroinvertebrates decrease in numbers with depth (vertically), especially at the first-order site. The structure of the macroinvertebrate community at the first order site was unique among sites. The family Chironomidae increased in relative abundance with depth at all sites. The effect of depth on macroinvertebrate abundance and taxonomic composition varied among sites in each season. During the study, a drought and flood event occurred, resulting in low densities of fauna in top basket levels and greater abundances with depth. The drought effect was a result of low water levels in top baskets. Flooding caused scouring of top basket contents. There were stronger correlations between velocity and density during the fall when dissolved oxygen was lowest.

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CHAPTER I

INTRODUCTION

Quantification of stream macrobenthos is difficult despite several attempts to improve techniques (Poole and Stewart 1976). Surber samplers are probably the most often used samplers for measuring benthos on the stream bottom (Poole and Stewart 1976). However, the Surber sampler has limitations because many studies have shown the majority of macrobenthos occur below the surface of the streambed (Coleman and Hynes 1970, Hynes 1974, Williams and Hynes 1974, Godbout and Hynes 1982). By only sampling the top few centimeters, Surber samples do not include all of the benthos.

The hyporheic zone is the subsurface area of streams that exchanges water with surface waters (Valett et al. 1993). This zone differs from true groundwater because it is more chemically variable due to interactions with surface water (Williams 1984). The hyporheic environment can vary in size depending on flow, geology, and porosity of the substrate of streams. The hyporheic zone is quite different from the stream bottom because current, light, and temperature decline rapidly with depth into the substrate. The hyporheic zone is an important habitat to aquatic insects and typically extends 30 cm or more into the substrate (Coleman and Hynes 1970).

Factors that may influence macroinvertebrate assemblages within the hyporheic zone include stream flow, interstitial flow, sediment characteristics, water chemistry, and organic matter (Godbout and Hynes 1982, Pennak and Ward 1986, Williams 1989, Palmer 1990, Boulton et al. 1992, Dole-Olivier and Marmonier 1992, Sterba et al. 1992). Stream flow increases downstream, which fluctuates on a seasonal basis and during droughts, and flood events. Stream velocity depends on gradient, habitat (riffle/pool), and catchment. Interstitial flow also depends on gradient, habitat, and catchment but also important is substrate type. Sediment characteristics affect the amount of interstitial spaces available within the hyporheic environment. Dissolved oxygen is an important chemical property of water that can limit the number of organisms deep in the substrate. Heavy detritus inputs from deciduous forests provide an essential source of energy for macroinvertebrates in headwater streams. Distribution and size of organic matter within the hyporheic zone can affect assemblages of benthic fauna. Vertical, longitudinal and seasonal variations in these factors are likely to underly patterns of variation in macroinvertebrate communities.

Extensive research has been conducted on longitudinal patterns of biotic and abiotic variables (Vannote et al. 1980, Minshall 1984, Ward 1989). The river continuum concept links downstream processes to upstream reaches (Vannote et al. 1980, Naiman et al. 1987, Allan 1995). Flow has a large influence downstream with increasing catchment size. Higher velocities downstream penetrate deeper into the substrate, resulting in increased streamwater mixing. This may play a large role in longitudinal variation in hyporheic organic matter, fine sediment, temperature, and dissolved oxygen.

Seasonal variation of stream flow strongly affects benthic fauna. Seasonal droughts and flooding in Appalachian headwater streams can have a significant effect on shaping community assemblages (Griffith and Perry 1993, Boulton and Stanely 1995, Angradi in press). Angradi (in press) reported 70-95% decreases in abundance of surface taxa immediately following a winter flood event. Griffith and Perry (1993) reported that benthic fauna use the hyporheic zone as a refuge during a seasonal drought. The hyporheic zone may serve as an important refuge for invertebrates from predation, spates and extreme temperatures (Schwoerbel 1967, Thorp and Covich 1991, Ward 1992). Fauna in the hyporheic zone offer a reserve for surface benthos to recolonize after catastrophic events (Ward 1992, Griffith and Perry 1993, Angradi in press).

Few studies have examined sources of variation in the hyporheic zone of high gradient Appalachian streams, an otherwise well-studied fauna (Huryn and Wallace 1987, Angradi 1996). An improved understanding of hyporheic structure and function is important because studies which ignore hyporheic fauna and processes may result in misleading conclusions regarding effects of natural and anthropogenic disturbance on headwater ecosystems.

The study objectives were to 1) examine vertical, longitudinal, and seasonal variation in the abundance, diversity, and taxonomic composition of hyporheic macroinvertebrate assemblages on streams at the Fernow Experimental Forest, Parsons, West Virginia, and 2) relate this variation to underlying factors including interstitial velocity, particulate organic matter (very coarse particulate organic matter (VCPOM), coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), and total particulate organic matter (TPOM), sediment (coarse particulate inorganic sediment (Cpash), fine particulate inorganic sediment (Fpash), temperature, dissolved oxygen and water chemistry.

CHAPTER II

REVIEW OF LITERATURE

At the turn of the century, scientists discovered the importance of the bed sediments of lotic systems as a habitat for aquatic invertebrates. Over the last several decades many studies have been conducted on macroinvertebrates within this habitat termed the "hyporheic zone". Extensive research has taken place in France, Austria, Canada, in desert streams, and in alluvial rivers of the western U.S. Many of these well-studied systems have relatively strong surfacewater/groundwater interactions in the hyporheic zone, often supporting unique fauna within the hyporheos. For example, research on the alluvial Flathead River in Montana has revealed riverine invertebrates from shallow wells up to 2 km from the main channel (Ward 1989). Unlike the western U.S., few studies have been conducted in southeastern U.S. streams (Strommer and Smock 1989, Palmer et al 1992, Griffith and Perry 1993) . Griffith and Perry (1993) conducted the only previous hyporheic study on the Fernow Experimental Forest. This study extends the work of Griffith and Perry (1993) to more sites and incorporates a technique for measuring interstitial flow, and extensive physical measurements for a better understanding of environmental factors underlying hyporheic assemblages on the Fernow.

The purpose of this review of the literature is to focus on hyporheic macroinvertebrate studies worldwide over the last few decades. Table 1. is a summary of the different sampling techniques, locations, maximum depth sampled, and parameters measured that are found in the literature.

Table 1. Summary of selected hyporheic studies. Studies are in chronological order. Mesh size refers to filtering size during processing of samples. Depth refers to the extent at which samplers measure fauna distribution. L, V, S, Sp refer to measured parameters in the study; L=Longitudinal variations (upstream/downstream), V=Vertical variations, S=Seasonal variations, Sp=Spatial variations..

Reference	Location	Sampler	Mesh (*u*m)	Max. depth (cm)	Measured Parameters
Coleman and Hynes 1970	Speed R., Ontario	Substrate colinization	170	30	V,S
Mundie 1971	Small Ck. B.C spawning channel, B.C.	Modified Hess type sampler	50	15-30	V,S
Radford and Hartland-Rowe 1971	Kananaskis R., Lusk Creek, Alberta	Surbers Juice cans	1000 250	4 18	V,S
Bishop 1973	Sungai Gonbak, Malaysia	Artificial substrate samplers	90	40	V,S
Williams and Hynes 1974	Speed R., Ontario	Substrate colonization. Williams corer and kick sampler	100	75	V,S
Hynes 1974	Speed R., Ontario	Substrate colonization	170	40	V,S
Danielopol 1976	Danube R., Piesting River, Austria	Pumping groundwater from standpipe	50,80	65	V,S
Williams and Hynes 1976	Kirkland Ck., Ontario	Williams corer and kick sampler	130	65	V,S
Hynes et al. 1976	Afon Hirnant, Wales	Williams corer and kick sampler	130	25	V,S
Gilpin and Brusven 1976	Spawning channel, Idaho	Substrate colonization	?	30	V
Poole and Stewart 1976	Brazos R., Texas	Substrate colonization	500	40	V,S
Morris and Brooker 1979	Wye R., Wales	Substrate colonization	440	33	V,S
Bretschko 1981	Oberer Seebach, Austria	Steel corer, plastic tubes	?	60	V,S
Godbout and Hynes 1982	Salem Ck., Ontario	Williams corer Surber sampler	110 235	65	V,S
Klemens 1982*	Oberer Seebach, Austria	Nitrogen freezing corer	100	70	V,S

Reference	Location	Sampler	Mesh (*u*m)	Max. depth (cm)	Measured Parameters
Pugsley and Hynes 1983	Speed R., Ontario	Nitrogen freezing corer	160	50	V,S
Bretschko 1983*	Kleine Ysper, Austria	Nitrogen freezing corer	100	30	V,S
Klemens 1983*	Oberer Seebach, Austria	Nitrogen freezing corer	100	70	V,S
Bretschko and Klemens1986	Donau, Austria	Surbers, Nitrogen freezing corer	100	60	V,S
Jeffrey et al. 1986	Dam Ck., Ontario	Standpipe corer	?	10-70	V,S
Pehofer 1986*	Alpbacher Ache, Austria	Nitrogen freezing corer	100	60	V,S
Pennak and Ward 1986	South Fork of Platte R., Colorado	Standpipe corer	48	50	V,S,L
Pugsley and Hynes 1986	Speed R., Ontario	Artificial substrate chanbers	160	50	V,S
Bretschko 1987*	Donau, Austria	Nitrogen freezing corer with electric field	100	60	V,S
Klemens 1987*	Walchenbach, Austria	Nitrogen freezing corer with electric field	100	65	V,S
Bretschko and Moog 1987*	Bregenzer Ache, Austria	Nitrogen freezing corer with electric field	100	60	V,S
Giberson and Hall 1988	Harp Lake outflow, Ontatrio	Artifical substrate Williams corer	600	65	V,S
Marchant 1988	Thomson R., Victoria	Surber, Nitrogen freezing corer	150	30	V,S
Strommer and Smock 1989	Buzzards Branch, Virginia	Standpipe corer	53	40	V,S
Williams 1989	Duffin Ck., Ontario	Standpipe corer	53	30	V,S
Tabacchi 1990	Adour R., SW France	PVC pipes	200	80	V,S
Boulton et al 1991	Sycamore Ck., AZ	Buried PVC traps	63	30	V,S
McElravey and Resh 1991	Big Canyon Ck., CA	Surber, Hyporheic pot samplers	63	35	V,S
Marmonier, Creuze des Chatelliers 1991	Upper Rhone R., Lyon, France	Hand pump corer	160	50	V,S,Sp

Reference	Location	Sampler	Mesh (*u*m)	Max. depth (cm)	Measured Parameters
Bass and Walker 1992	North Canadian R., OK	Ponar grab, core samples	250	30	V
Boulton et al 1992	Sycamore Ck., AZ Big Sandy R., AZ Hassayampa R., AZ Santa Maria R., AZ Bridle Ck., AZ	Pumped from plastic PVC wells	50	200	V,S,Sp
Maridet et al. 1992	Loire R., France Galaure R., France Drac R., France	Nitrogen freezing corer	50	60	V,S
Dole-Olivier and Marmonier 1992	Miribel Canal, part of upper Rhone R., France	Pump, permanent standpipes	300	2	V,S,Sp
Palmer et al. 1992	Goose Ck., VA	Standpipe, box cores, flume channel	44	50	V,S
Griffith and Perry 1993	Watershed 3,4 Fernow Experimental Forest, Parsons, WV	Artificial substrate samplers	250	30	V,S,Sp
Nelson et al. 1993	Arkansas R., CO	Hyporheic pot samplers, Surbers	728	30	L,V,S
Boulton and Stanley 1995	Sycamore Ck., AZ	Bilge pump from wells	63	100	V,S
Clinton et al. 1996	Rock Ck. of Sycamore Ck., AZ	PVC tube wells	63	100	V,S
This study	Elklick Run drainage,Fernow Experimental Forest, Parsons, WV	Surbers artificial substrate samplers	250	10 30	L,V,S

*cited by Klemens 1991

CHAPTER III

STUDY SITES

This study was conducted on the Fernow Experimental Forest within the Monongahela National Forest near Parsons, Tucker County, West Virginia, U.S.A. The Fernow is located in the Allegheny Mountain section of the unglaciated Allegheny Plateau. The area is rugged with narrow valleys and slopes of 20 to 30 percent are common. The Fernow receives about 150 cm of annual precipitation (Yokum et al. 1996). Vegetation consists of mature 2nd-growth stands of Central Appalachian hardwoods (Angradi 1996). Watersheds in this study are primarily underlain by sedimentary rock of the Hampshire formation. Stream sediments are of colluvial origin, coarse, and a mixture of gravel, cobble and boulder-sized slabs of sandstone and siltstone with some sand (Griffith 1992). Stream flow on the Fernow is dominated by groundwater inputs, seasonal variation in which is linked to the evapotranspirational demand of forest vegetation (Adams et al. 1994).

Four 100 m study reaches were established on first through fourth order connected tributaries of Elklick Run, the main drainage of the Fernow (Figs. 1,2). Physical, chemical, and sedimentological characteristics of the study sites are summarized in Appendix II, Table I.

Measurements of the depth of bedrock below the stream bed bottom at Elklick (fourth order) and Camp Hollow (third order) sites ranged from 75 to 110 cm. At Watershed 5 (second order) there are numerous bedrock outcrops. At Subwatershed 5 (1st order), there is a layer of clay at 25-40 cm deep which served as a barrier below the stream bed.

Subwatershed 5 contained large amounts of woody debris and detritus. The stream

Figure 1. Study sites.

a. Subwatershed 5

b. Watershed 5

c. Camp Hollow

d. Elklick Run

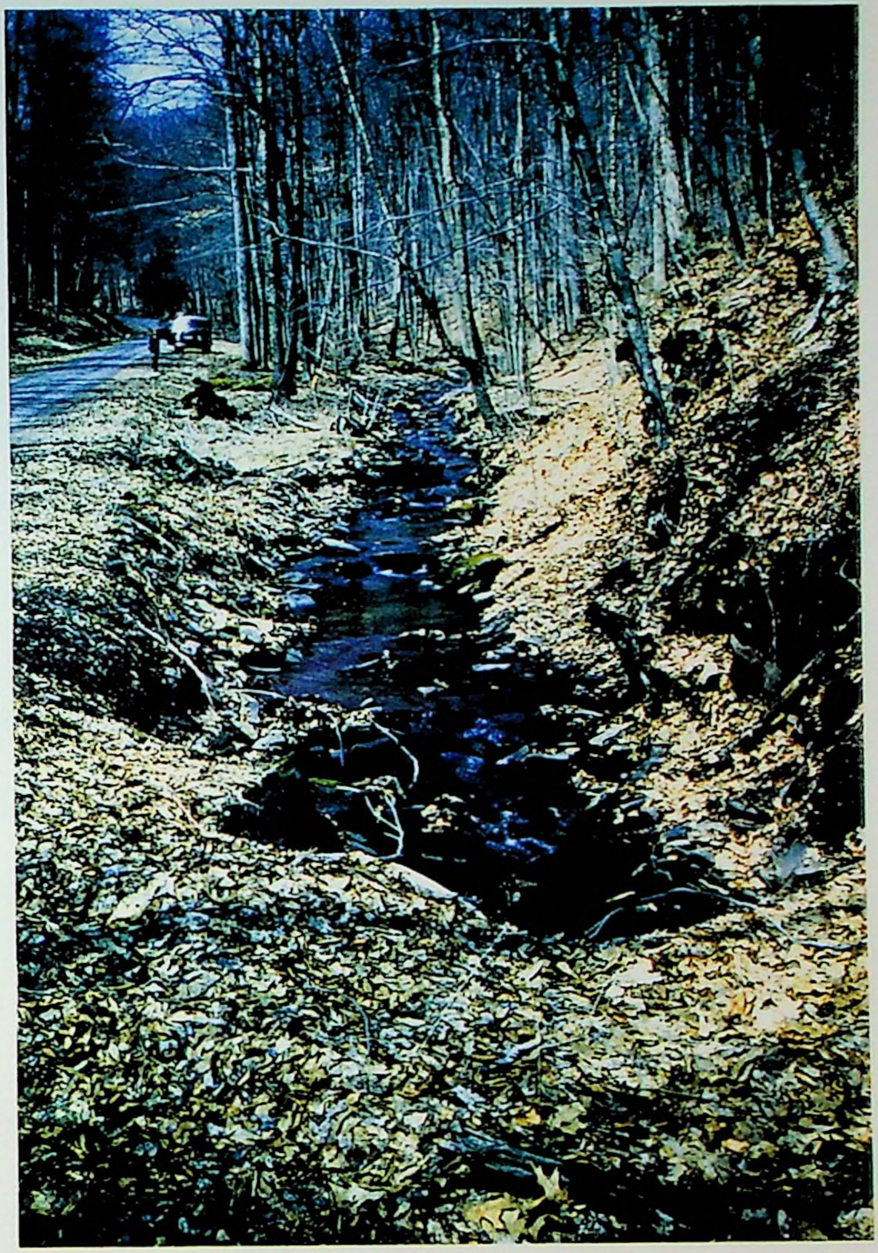

Figure 2. Map of the Fernow Experimental Forest with study streams indicated.

FERNOW EXPERIMENTAL FOREST

WATERSHED LOCATION MAP

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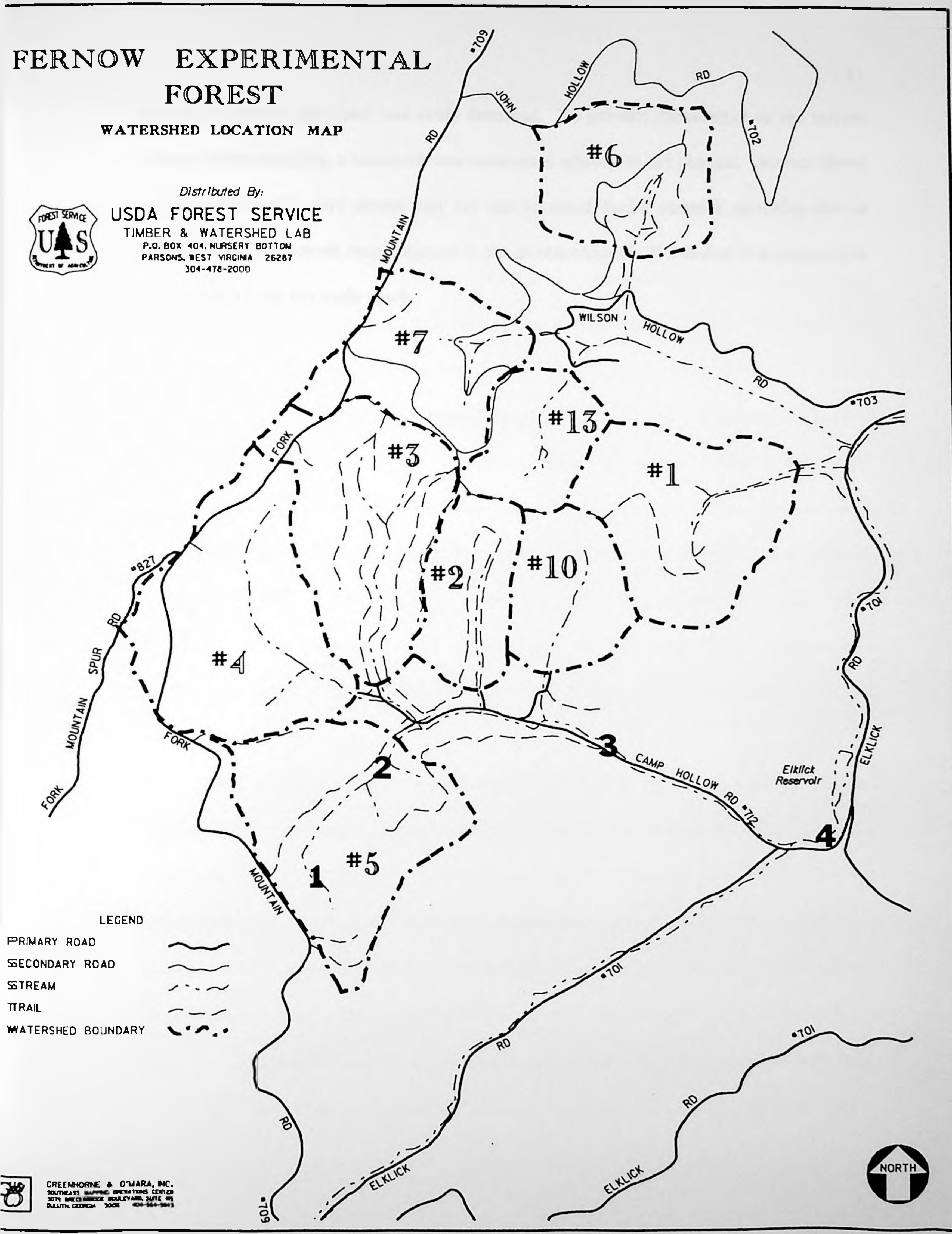
PARSONS, WEST VIRGINIA 26287
304-478-2000



bottom is heavily silted and was easily disturbed. To prevent disturbance to the stream channel during sampling, a boardwalk was constructed adjacent to the channel. Surface flows at Subwatershed 5 were always very low but persisted during summer, probably due to groundwater influence via seeps adjacent to the stream channel. Watershed 5 is gauged just downstream from the study reach.

CHAPTER IV

METHODS AND MATERIALS

Sampler Design

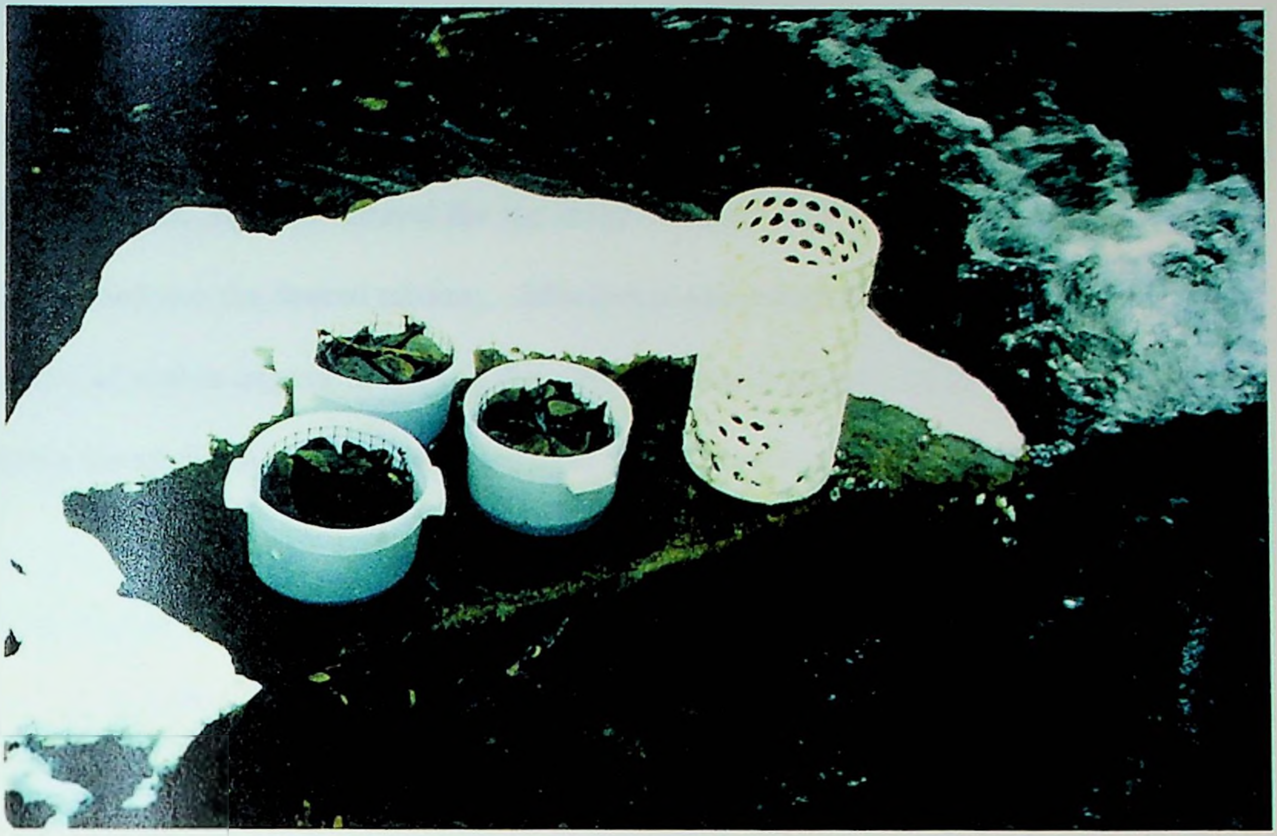
Two different methods were used to sample macroinvertebrates: a Surber sampler and artificial substrate samplers. Artificial substrate samplers were constructed of PVC pipe (15-cm internal diameter, 30-cm lengths) drilled with 2 cm holes removing >40% of the surface area to allow colonization by macroinvertebrates (Fig. 3). Within the PVC sampler, baskets (approximately 14.5-cm diameter and 10-cm high) were placed. The baskets were constructed of 11 mm mesh galvanized hardware cloth fastened to 14.5 cm diameter bases of a 9 mm thick plywood ring (inner dia. 11-cm). The coarse mesh was used to prevent restriction of larger taxa (e.g.,crayfish, salamanders, *Pteronarcys*) from the baskets. Nitex cloth (0.25-mm mesh) was glued to the bottom of each plywood base. Similar samplers have been used in other studies (Griffith and Perry 1993, Gilpin and Brusven 1976, Poole and Stewart 1976).

PVC samplers were buried at random locations in riffle/run areas so that the top was flush with the stream bottom. Three baskets with a known standardized gravel mixture were placed within each PVC sampler. Attempts were made to match the size distribution of the standardized gravel mixture used within the baskets to mean ambient conditions of all study reaches. The desired gravel mixture was determined as the mean substrate size of the four sites combined. This mixture was determined by collecting six gravel samples at each site with a shovel, drying the samples, and shaking the gravel through a sieve series (Grost et al., 1991). Four sizes of gravel were used; 8-12 mm, 12-16 mm, 16-32 mm, and 32-64 mm

Figure 3. Hyporheic samplers used in study.

a. Sampler and baskets

b. Sampler within substrate.



(Appendix II, fig. 1). Gravel for the study was collected in at Elklick Run, dried, and recombined into the desired mixture. After gravel was sorted through the sieve series, it was picked of visible organic matter so that accumulation of organic matter could be measured during the study. Accumulation of sediment (inorganic material <8mm) was also measured.

Field studies

Ten PVC samplers were buried at each of the four study sites during three seasons, totaling 40 samplers per season (Table 1). Each 10-cm high basket was placed within the PVC sampler so that the top basket represented the first 0-10 cm, the middle basket represented 10-20 cm and the bottom basket represented 20-30 cm. All baskets contained the same mean gravel mixture totaling 120 baskets per season. The substrate samplers were then allowed to colonize for at least 12 weeks.

Table 2. Number of samples collected at each study site, including missing samples from winter flooding and lost during processing. Number in parentheises is actual number collected. + = sample lost during processing. * missing samples because of winter flooding.

	Spring				Fall				Winter			
Level	SWS5	WS5	CH	EL	SWS5	WS5	CH	EL	SWS5	WS5	CH	EL
Surber	10	10	10	10	10	10	10	10	10	10	10	10
T(0-10)	10	10	10	10	10	10	10	10	10	10	10(6)*	10(5)*
M(10-20)	10	10	10	10	10	10	10	10(9)+	10	10	10(6)*	10(5)*
B(20-30)	10	10	10	10	10	10	10	10	10	10	10(6)*	10(5)*

At the time of sample collection in spring (June), fall (September-October) and winter (January), top baskets were removed from the PVC samplers using needle nose pliers.

Middle and bottom baskets were removed with the aid of wire bails preattached to the baskets. The baskets were then placed in individual plastic containers and returned to the laboratory for processing. Basket contents were washed through nested 8 mm and 0.25 mm sieves. Organic matter and animals larger than 8 mm were added to the contents of the 0.25 mm sieve. Gravel larger than 8 mm was discarded so that accumulation of gravel smaller than 8 mm could be determined. Contents of the 0.25 mm sieve were then placed in jars, preserved in 100% ethanol, and labeled. When baskets were retrieved after the three month periods, samplers were again randomly buried at each site so as not to sample the same location twice.

Ten random Surber samples were collected in riffle/run areas at each study site within a few days after baskets had been removed. An effort was made to disturb the upper 10 cm of substrate when taking the Surber samples for comparison with the top level of the artificial samplers. Contents of Surber samples were preserved in 100% ethanol in the field and stored for later processing. Sediment (inorganic material) collected in surber samples were discarded.

Laboratory

Samples were processed by washing the sample through a nested series of 8 mm, 1 mm and 0.25 mm sieves. Contents of 8 mm sieve contained very coarse particulate organic matter (VCPOM). Animals in the 8mm sieve were placed with contents of the 1 mm sieve. Animals, coarse particulate organic matter (CPOM), and coarse particulate inorganic matter (CPash), were placed in plastic trays and the animals were removed, sorted, and placed in vials of 100% ethanol for later identification. Contents of the 0.25 mm sieve, fine particulate organic matter (FPOM), and fine particulate inorganic matter (FPash) were subsampled. FPOM was placed in a partitioned vessel, agitated, and the contents of 1 unit pipetted out and, if necessary, resubsampled. Subsamples of FPOM ranged from 1/2 to 1/16, depending on the number of animals and/or amount of sediment in FPOM. After the animals were removed, CPOM and FPOM samples were dried (60 C) to a constant mass, and ashed (2-3 h, 550 C). CPash and FPash (=sediment + ashed organic matter) from basket samples were also weighed to determine the amount of sediment accumulation during the colonization period. Sorted organisms were identified, usually to genus or family (except Chironomidae which was generally identified to subfamily and/or tribe) and counted.

Habitat Parameters

During the recolonization period, weekly routines measured depth and dissolved oxygen. Water depth was measured to the nearest 1 cm at the top of each sampler. If water depth was below the top of the sampler, it was recorded as zero. Stream velocity was measured to the nearest 0.1 m/sec with a digital turbo-prop velocity meter (Global Water, Fair Oaks, CA) at the top of each sampler. When flow was too low to be measured with the velocity meter during the summer months, velocity was recorded as zero. Two electronic thermographs were buried within the substrate at the mid-reach of each study site at -5 and -25 cm. Three sets of access tubes were placed at the upstream end, midway, and near the downstream end of each study reach for collection of water for chemical analyses. Access tubes were constructed of 2.6 cm diameter PVC pipe (approx. 70 cm in length), closed on the bottom and with 2 mm holes drilled at different depths for each pipe in the sets. For sampling, standing water was removed from pipes with a peristaltic pump. Dissolved oxygen and temperature measurements were made by inserting a probe into each access pipe after initial pumping (YSI Inc. Model 57, Yellow Springs, OH). Dissolved oxygen and temperature were then measured in each access tube to determine ambient conditions at 0-10 cm, 10-20 cm, and 20-30 cm within the substrate. Monthly water samples were collected to characterize water chemistry at each study site. Water samples were analyzed by the USDA Forest Service Timber and Watershed Laboratory, Parsons, West Virginia. Samples were analyzed for pH, conductivity, alkalinity, Ca, Na, K, Mg, Cl, NO_3-N, and SO_4. All physical parameters were measured from March 1995 through January 1996. These routines continued through the recolonization period.

Interstitial velocity

A novel method was used to characterize interstitial flow within the shallow hyporheic zone at each sampler before and after each colonization period (Appendix II). Before the baskets were placed in PVC samplers for the macroinvertebrate colonization period, preweighed plaster clods were placed in the center of each basket surrounded by gravel mix. Baskets with clods were then placed in samplers for a three-day period. Three days allowed an adequate dissolution period (determined in preliminary tests). After three days, clods were removed and allowed to dry at room temperature for at least a week before reweighing. Interstitial water velocity was determined from calibration models which allowed determination of velocity (cm/s) from mass loss of clods. Details of the method are given in Appendix II.

CHAPTER V

RESULTS

Macroinvertebrate density

Macroinvertebrate densities in baskets varied significantly among levels (depth), sites, and seasons (Table 3). Across seasons and sites, densities were greatest in the top baskets (0-10cm) (Fig. 4a). Macroinvertebrate densities were highest at Subwatershed 5 and decreased slightly downstream (Fig. 4b). Across sites and levels macroinvertebrate density was lowest in fall (Fig. 4c).

There were significant interactions between level and season and between level and site for density (Table 3). The difference among levels was greater in spring than in other seasons (Figs. 5b,6). There was a decrease in density with level at all sites and seasons with the exception of Camp Hollow and Elklick in winter (Figs. 6c,d) Across seasons there was a greater effect of level upstream than downstream (Fig. 5c).

Density of macroinvertebrates at the substrate surface as determined by Surber samples varied among sites and seasons (Table 4). Compared to hyporheic baskets, Surber samples had lower densities at all sites in all seasons, but cannot be directly compared with baskets because of differences in sampling technique and actual depth sampled. (Figs. 5b,c). There was a downstream decrease in density from Subwatershed 5 to Elklick, and a general decrease in Surber density from spring to winter (Figs. 5b,c,7a).

Macroinvertebrate taxa richness

Macroinvertebrate taxa richness in the baskets varied significantly among levels,

Table 3. Repeated measures ANOVA tests for between-subjects (season, site) effects and MANOVA tests for level effects of baskets.

Dependent variable	Effect	df	F	P
Density (#/m^2)	Site	3,94	16.2	0.05
	Season	2,94	16.2	<0.05
	Site*Season	6,94	0.3	2.95
	Level	2,93	31.4	<0.05
	Level*Season	4,186	6.7	<0.05
	Level*Site	6,186	7.9	<0.05
Taxa richness (#/sample)	Site	3,94	2.5	0.06
	Season	2,94	10.1	<0.05
	Site*Season	6,94	1.3	0.25
	Level	2,93	125.4	<0.05
	Level*Season	4,186	9.5	<0.05
	Level*Site	6,186	5.9	<0.05
VCPOM (gAFDW/m^2)	Site	3,96	9.9	<0.05
	Season	2,96	4.0	<0.05
	Site*Season	6,96	3.3	<0.05
	Level	2,95	29.0	<0.05
	Level*Season	4,190	2.8	<0.05
	Level*Site	6,190	4.4	<0.05
CPOM (gAFDW/m^2)	Site	3,95	10.4	<0.05
	Season	2,95	3.6	<0.05
	Site*Season	6,95	4.6	<0.05
	Level	2,94	39.8	<0.05
	Level*Season	4,188	2.4	0.05
	Level*Site	6,188	5.8	<0.05

Table 3. Continued.

Dependent variable	Effect	df	F	P
CPash (gAFDW/m^2)	Site	3,92	13.2	<0.05
	Season	2,92	36.2	<0.05
	Site*Season	6,92	4.9	<0.05
	Level	2,91	48.6	<0.05
	Level*Season	4,182	9.2	<0.05
	Level*Site	6,182	4.9	<0.05
FPOM (gAFDW/m^2)	Site	3,93	13.2	<0.05
	Season	2,93	2.1	0.12
	Site*Season	6,93	4.9	<0.05
	Level	2,91	24.2	<0.05
	Level*Season	4,182	1.8	0.14
	Level*Site	6,182	4.8	<0.05
FPash (gAFDW/m^2)	Site	3,87	4.1	<0.05
	Season	2,87	40.7	<0.05
	Site*Season	6,87	7.8	<0.05
	Level	2,86	31.7	<0.05
	Level*Season	4,172	0.3	0.87
	Level*Site	6,172	3.2	<0.05
TPOM (gAFDW/m^2)	Site	3,91	20.0	<0.05
	Season	2,91	4.4	<0.05
	Site*Season	6,91	7.4	<0.05
	Level	2,90	64	<0.05
	Level*Season	4,180	2.2	0.07
	Level*Site	6,180	8.1	<0.05

Figure 4.

a. Mean (± 1 SE) density (1000/m^2) of benthic fauna in both Surber samples and hyporheic baskets.

b. Mean (± 1 SE) density (1000/m^2) of benthic fauna at each site in both Surbers and baskets. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

c. Mean (± 1 SE) density (1000/m^2) of benthic fauna in each season in Surbers and baskets.

*Error bars may be hidden by symbols.

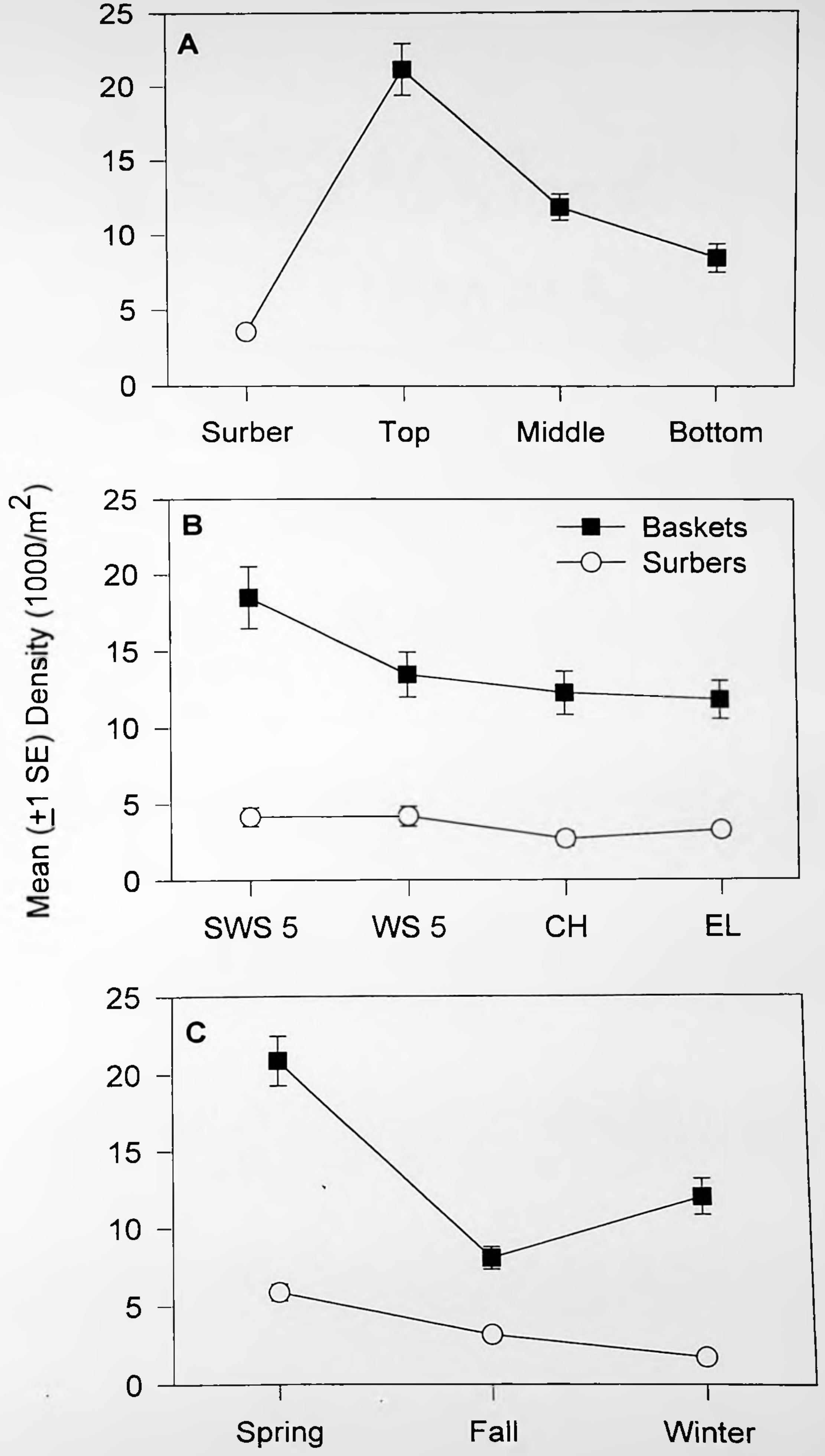

Mean (±1 SE) Density (1000/m^2)
25
20
15
10
5
0
A
Surber
Top
Middle
Bottom
B
Baskets
Surbers
SWS 5
WS 5
CH
EL
C
Spring
Fall
Winter

Figure 5. a. Mean (± 1 SE) density (1000/m^2) of benthic fauna in each season at each site.

b. Mean (± 1 SE) density (1000/m^2) of benthic fauna in each season at each level.

c. Mean (± 1 SE) density (1000/m^2) of benthic fauna at each site at each level in Surbers and baskets. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

*Error bars may be hidden by symbols.

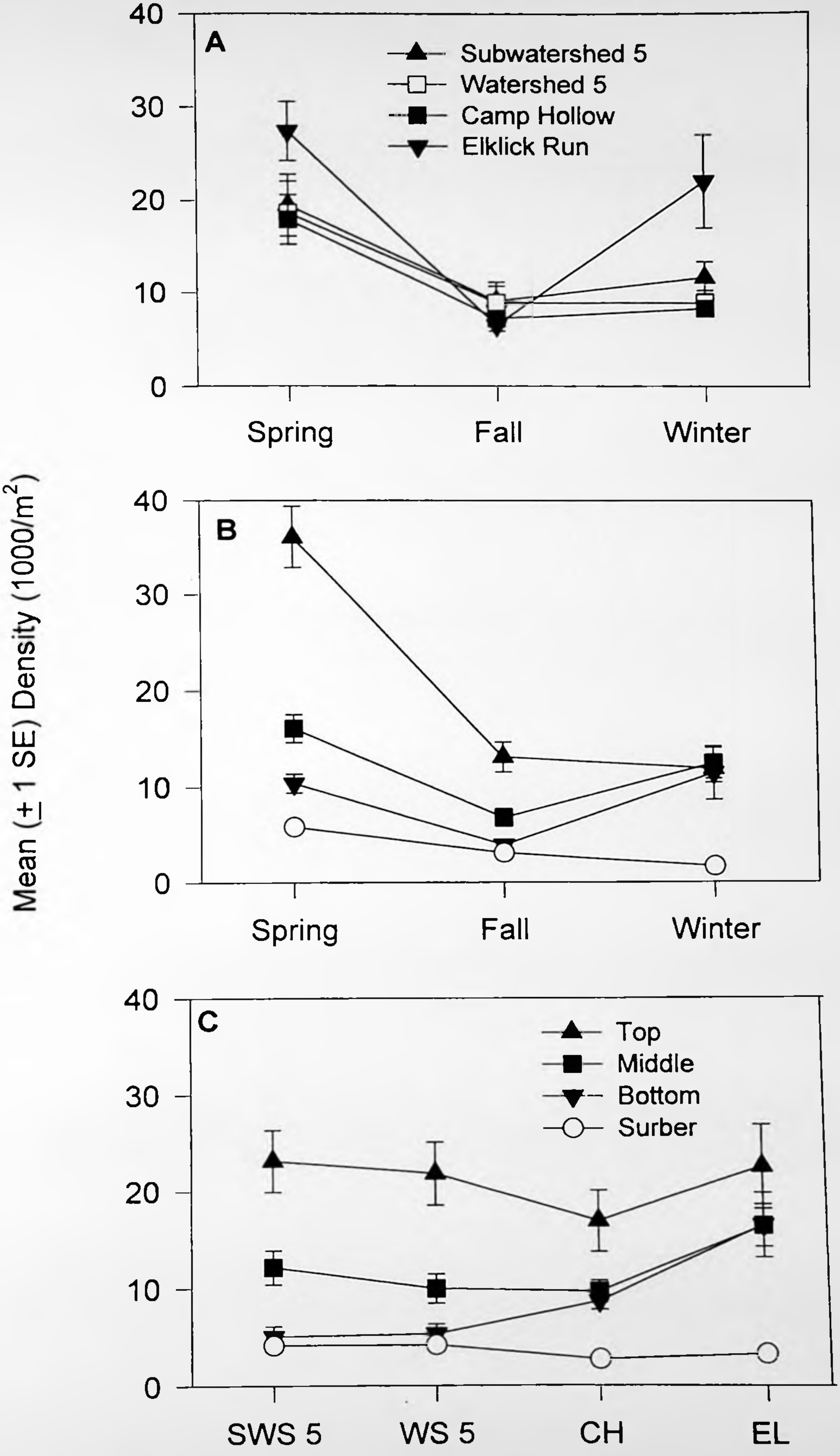

Mean (± 1 SE) Density (1000/m^2)
A
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
0
10
20
30
40
Spring
Fall
Winter
B
0
10
20
30
40
Spring
Fall
Winter
C
Top
Middle
Bottom
Surber
0
10
20
30
40
SWS 5
WS 5
CH
EL

Figure 6. Mean (± 1 SE) density (1000/m^2) of benthic fauna in each season at each depth.

*Error bars may be hidden by symbols.

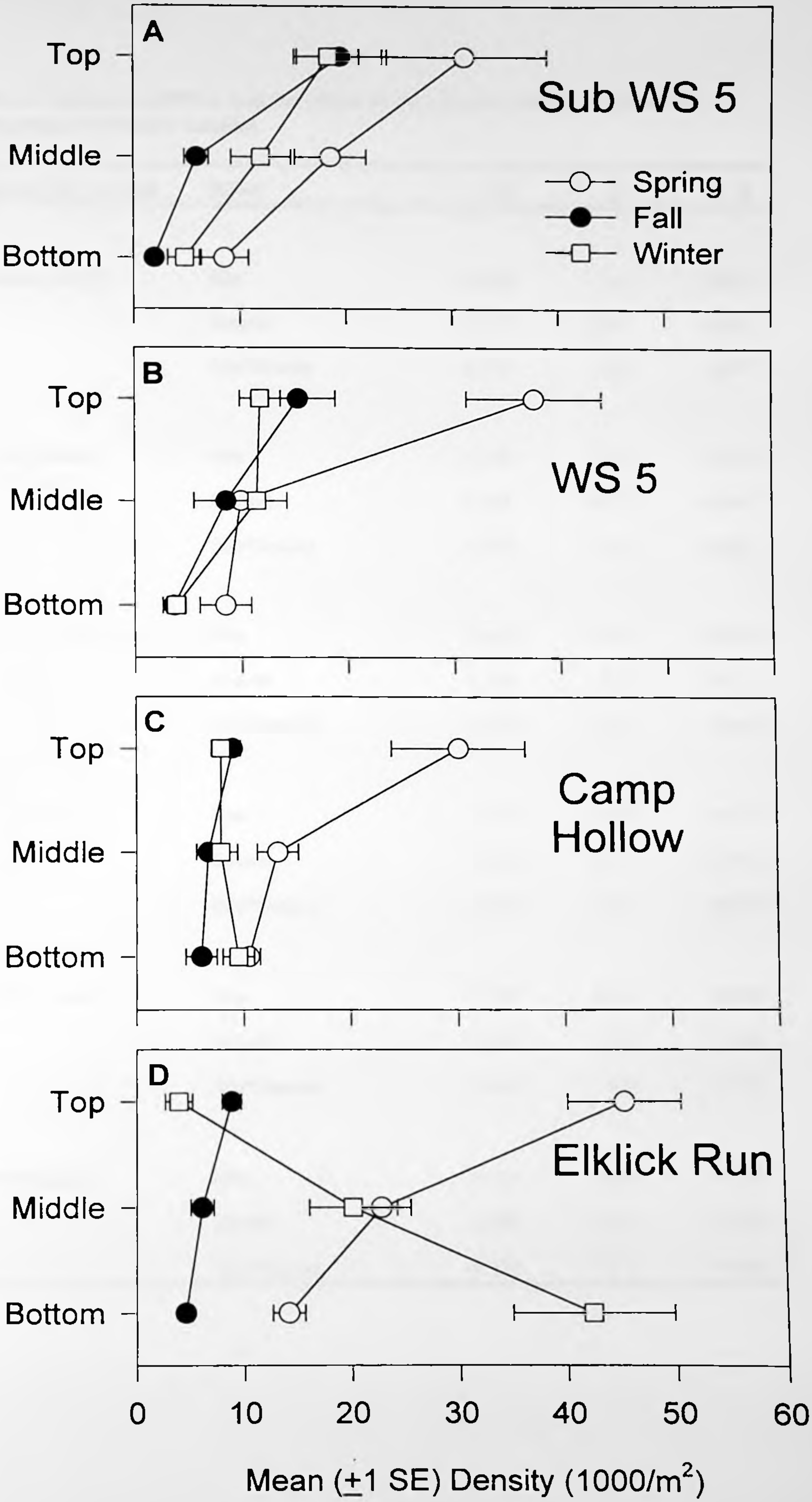
A
Sub WS 5
Spring
Fall
Winter
B
WS 5
C
Camp Hollow
D
Elklick Run
Top
Middle
Bottom
0
10
20
30
40
50
60
Mean (±1 SE) Density (1000/m²)

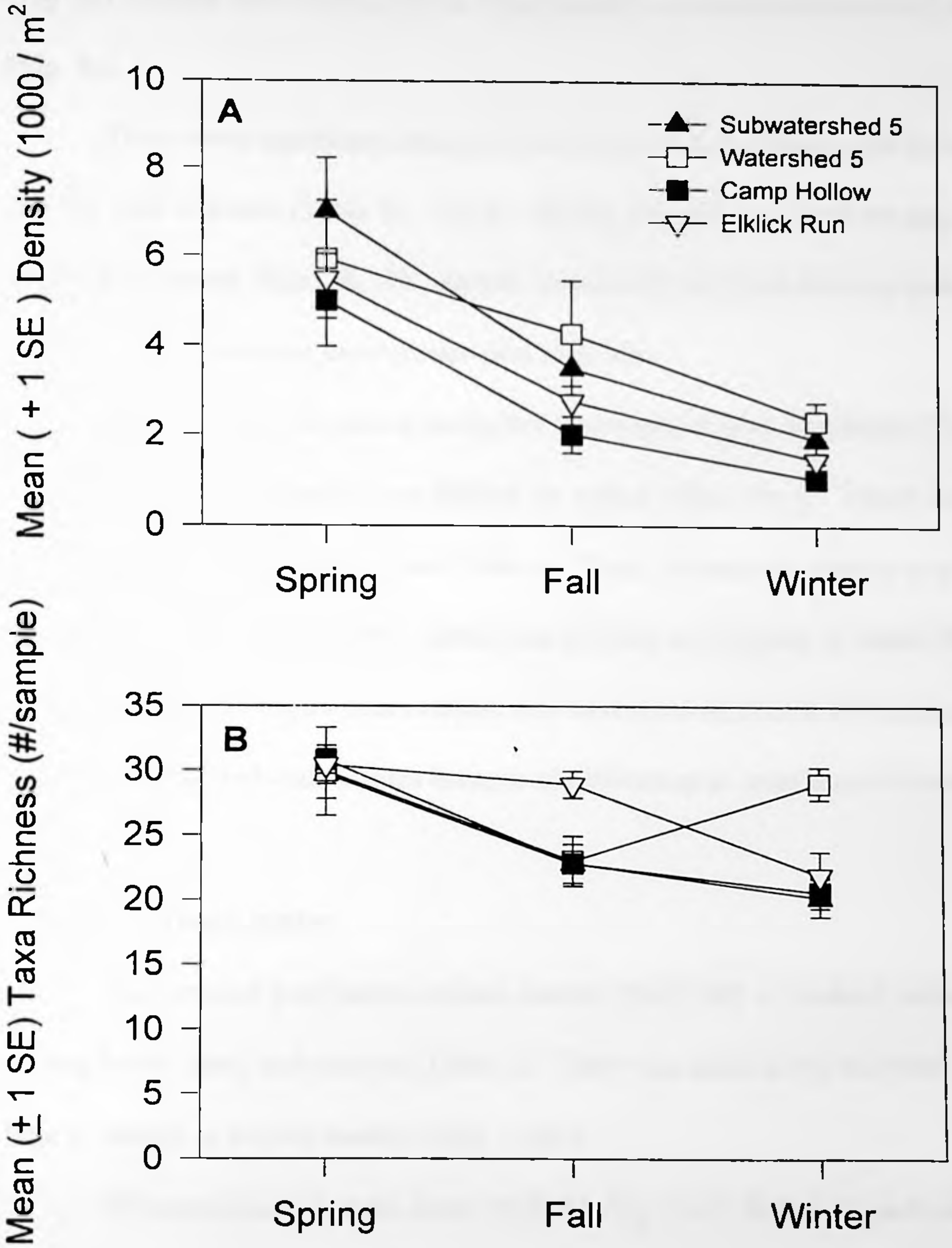
Table 4. Two-way ANOVA tests for effects of site, season, and site and season interactions for Surber samples.

Dependent variable	Effect	df	F	P
Density (# /m^2)	Site	3,108	2.8	<0.05
	Season	2,108	32.8	<0.05
	Site*Season	6,108	0.8	0.57
Taxa richness (#/sample)	Site	3,108	2.6	0.06
	Season	2,108	20.7	<0.05
	Site*Season	6,108	3.3	<0.05
VCPOM (g/m^2)	Site	3,108	15.9	<0.05
	Season	2,108	6.5	<0.05
	Site*Season	6,108	5.3	<0.05
CPOM (g/m^2)	Site	3,108	46.9	<0.05
	Season	2,108	17.2	<0.05
	Site*Season	6,108	9.7	<0.05
FPOM (g/m^2)	Site	3,108	28.8	<0.05
	Season	2,108	2.9	0.06
	Site*Season	6,108	6.7	<0.05
TPOM (g/m^2)	Site	3,108	38.3	<0.05
	Season	2,108	11.7	<0.05
	Site*Season	6,108	7.3	<0.05

Figure 7. a. Mean (± 1 SE) density (1000/m^2) of benthic fauna in Surber samples.

b. Mean (± 1 SE) taxa richness (#/sample) of benthic fauna in Surber samples.

*Error bars may be hidden by symbols.

A
Mean (+ 1 SE) Density (1000 / m2)
10
8
6
4
2
0
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
Spring
Fall
Winter
B
Mean (± 1 SE) Taxa Richness (#/sample)
35
30
25
20
15
10
5
0
Spring
Fall
Winter

sites, and seasons (Table 3). Taxa richness was highest in top baskets at all sites and in all seasons (Figs. 8a,9). Across seasons and levels, taxa richness increased slightly downstream (Fig. 8b). Highest taxa richness was in spring samples and decreased through fall and winter (Fig. 8c).

There were significant interactions between level and season and between level and site for taxa richness (Table 3). As for density, the effect of level on taxa richness was greatest in spring (Figs. 9b,10). Across seasons the effect of level on taxa richness was greater at upstream than downstream sites (Fig. 9c).

Effects of site and season on Surber taxa richness were significant (Table 4). Taxa richness in Surber samples was highest in spring (Figs. 8b,c). There were significant interactions between season and site (Table 4). Taxa richness was highest in spring and least in winter except at Watershed 5 where taxa richness was highest in winter (Figs. 7,9b,c,). Surber samples had higher taxa richness than baskets at all sites in all seasons (Fig. 8a), but cannot be compared with baskets because of differences in sampling technique and level.

Particulate organic matter

Very coarse particulate organic matter (VCPOM) in baskets varied significantly among levels, sites, and seasons (Table 3). There was much more VCPOM in top baskets than in middle or bottom baskets (Figs. 11b,c).

Subwatershed 5 had the most VCPOM (Fig. 11a). Effect of level on VCPOM was greatest in spring (Fig. 11b). Effect of level on VCPOM was greatest at Subwatershed 5 and decreased downstream (Fig. 11c).

VCPOM in Surber samples varied significantly among season and site, and there was

Figure 8. a. Mean (± 1 SE) taxa richness (#/sample) of benthic fauna in Surber samples and hyporheic baskets.

b. Mean (± 1 SE) taxa richness (#/sample) of benthic fauna at each site in both Surbers and baskets. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

c. Mean (± 1 SE) taxa richness (#/sample) of benthic fauna during in each season in Surbers and baskets.

*Error bars may be hidden by symbols.

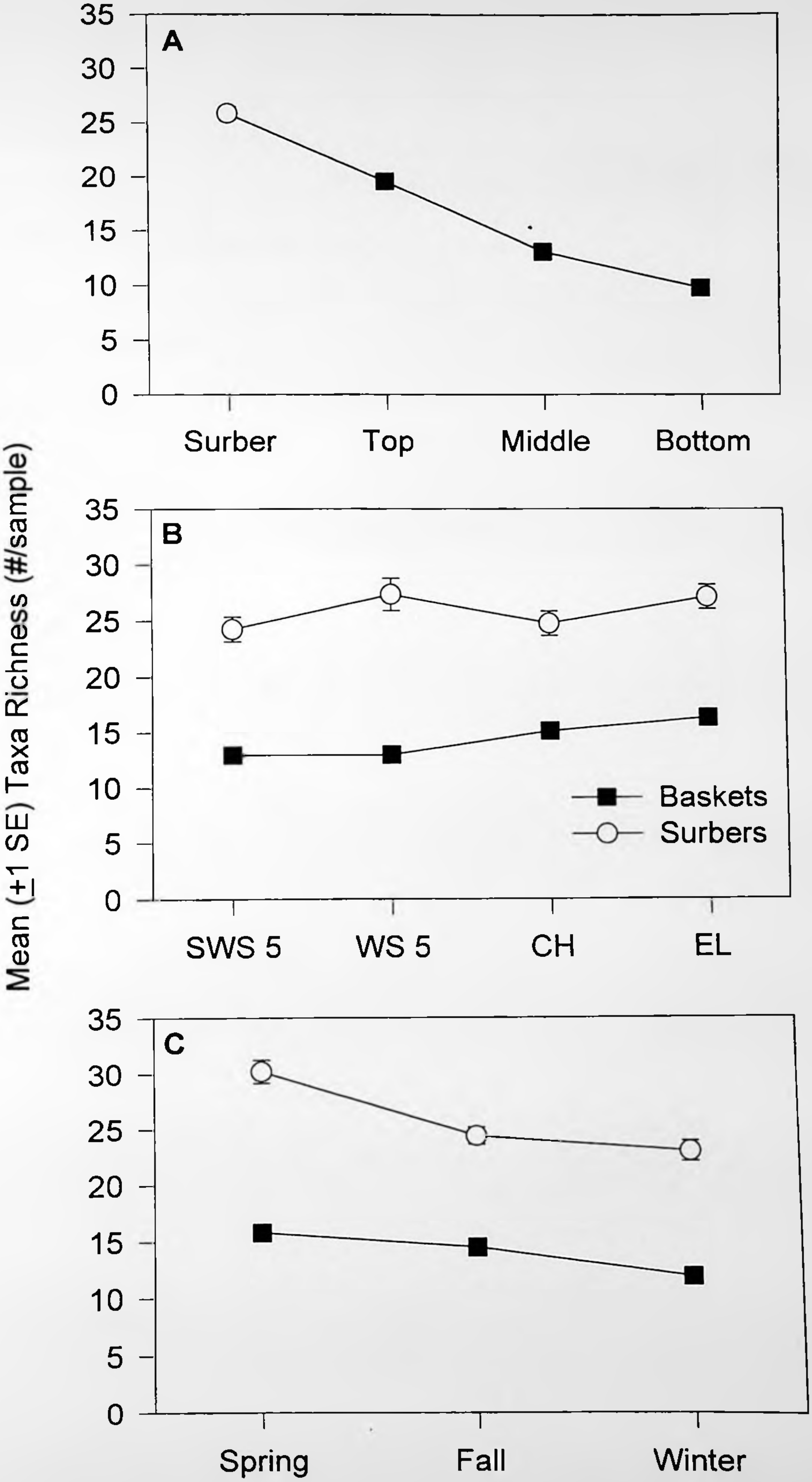

Mean (±1 SE) Taxa Richness (#/sample)
A
35
30
25
20
15
10
5
0
Surber
Top
Middle
Bottom
B
35
30
25
20
15
10
5
0
Baskets
Surbers
SWS 5
WS 5
CH
EL
C
35
30
25
20
15
10
5
0
Spring
Fall
Winter

Figure 9. a. Mean (± 1 SE) taxa richness (#/sample) of benthic fauna in each season at each site.

b. Mean (± 1 SE) taxa richness (#/sample) of benthic fauna in each season at each level.

c. Mean (± 1 SE) taxa richness (#/sample) of benthic fauna at each site at each level. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

*Error bars may be hidden by symbols.

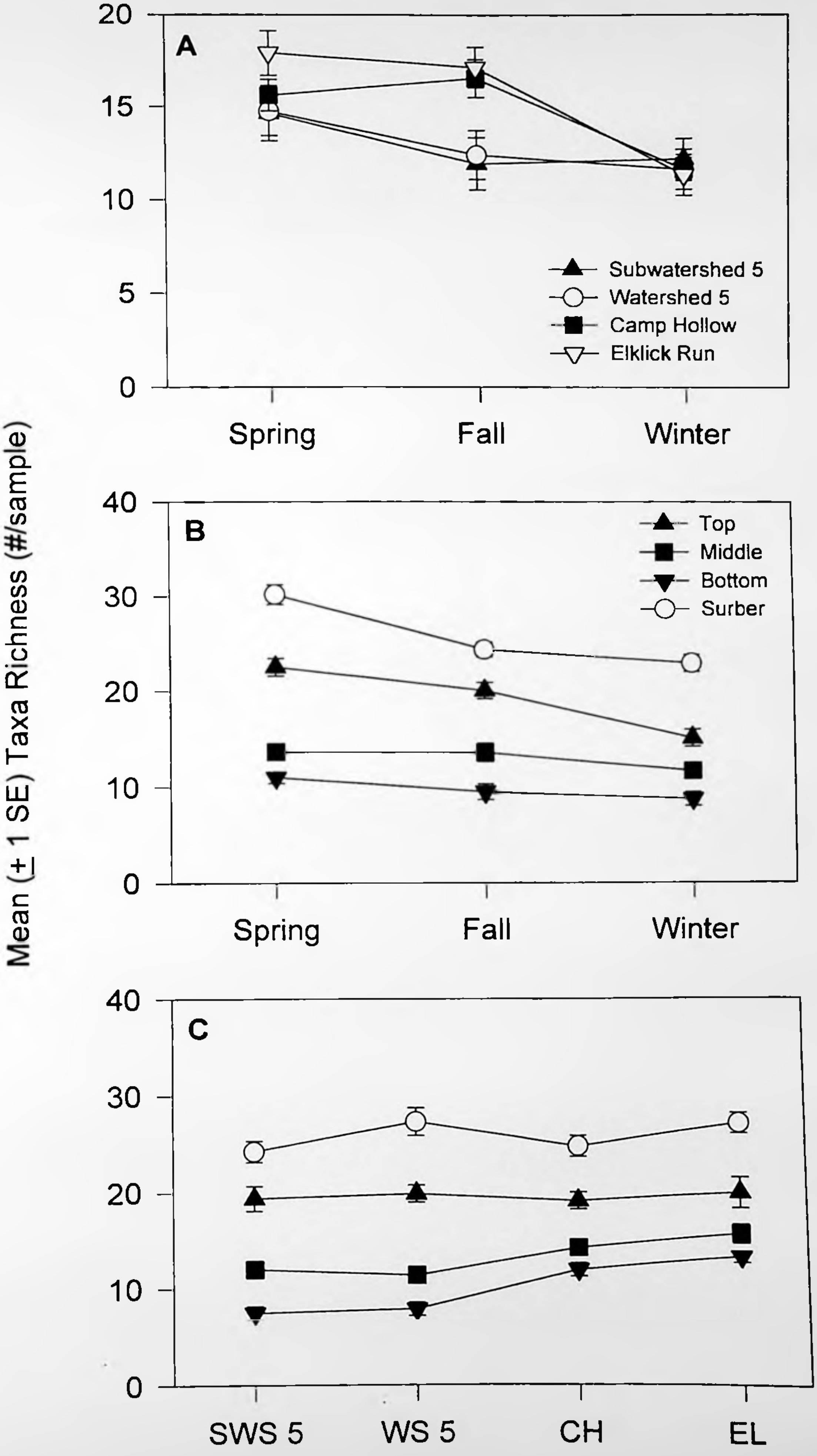

Mean (± 1 SE) Taxa Richness (#/sample)
A
20
15
10
5
0
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
Spring
Fall
Winter
B
40
30
20
10
0
Top
Middle
Bottom
Surber
Spring
Fall
Winter
C
40
30
20
10
0
SWS 5
WS 5
CH
EL

Figure 10. Mean (± 1 SE) taxa richness (#/sample) of benthic fauna in each season at each depth.

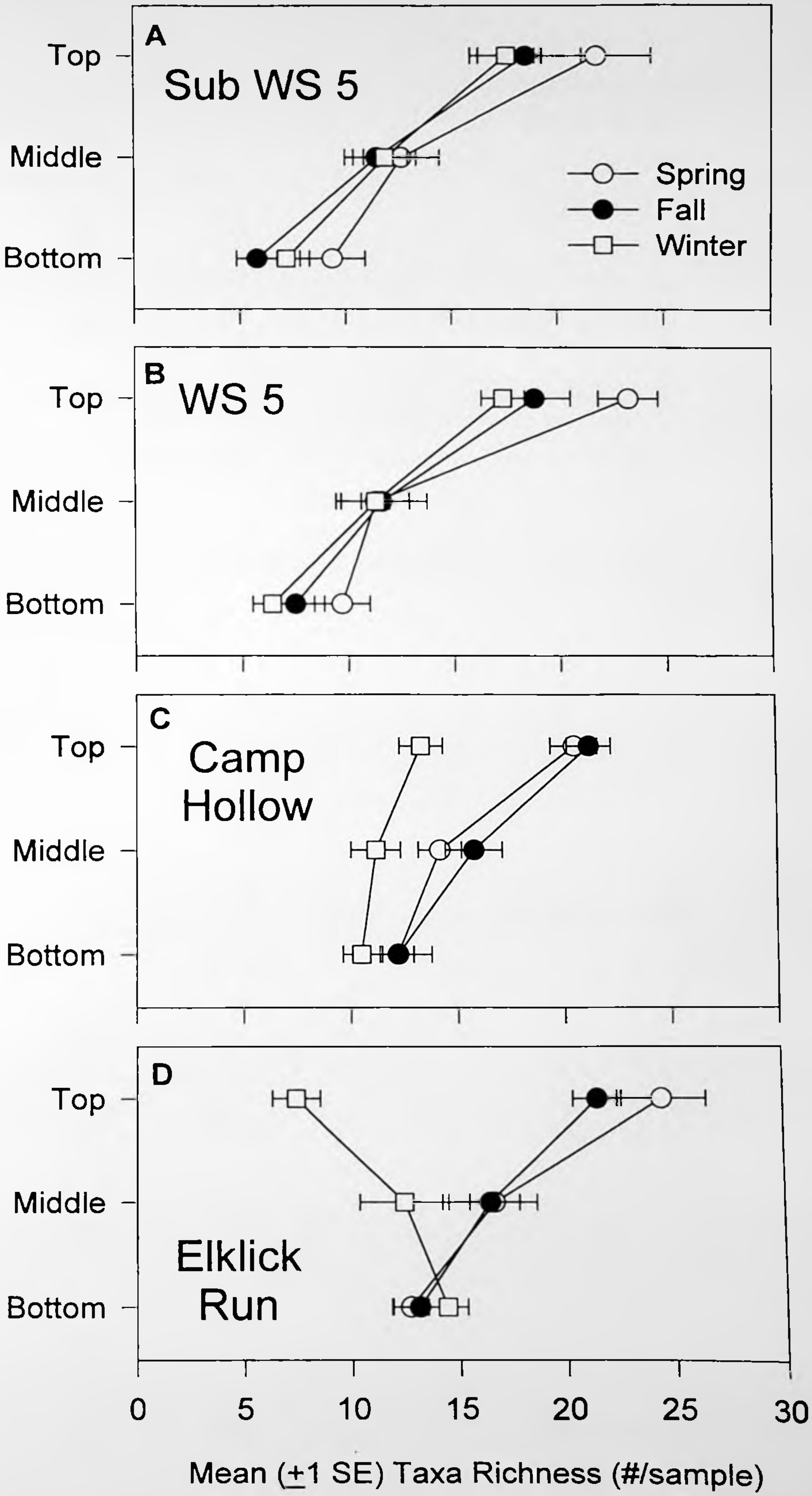
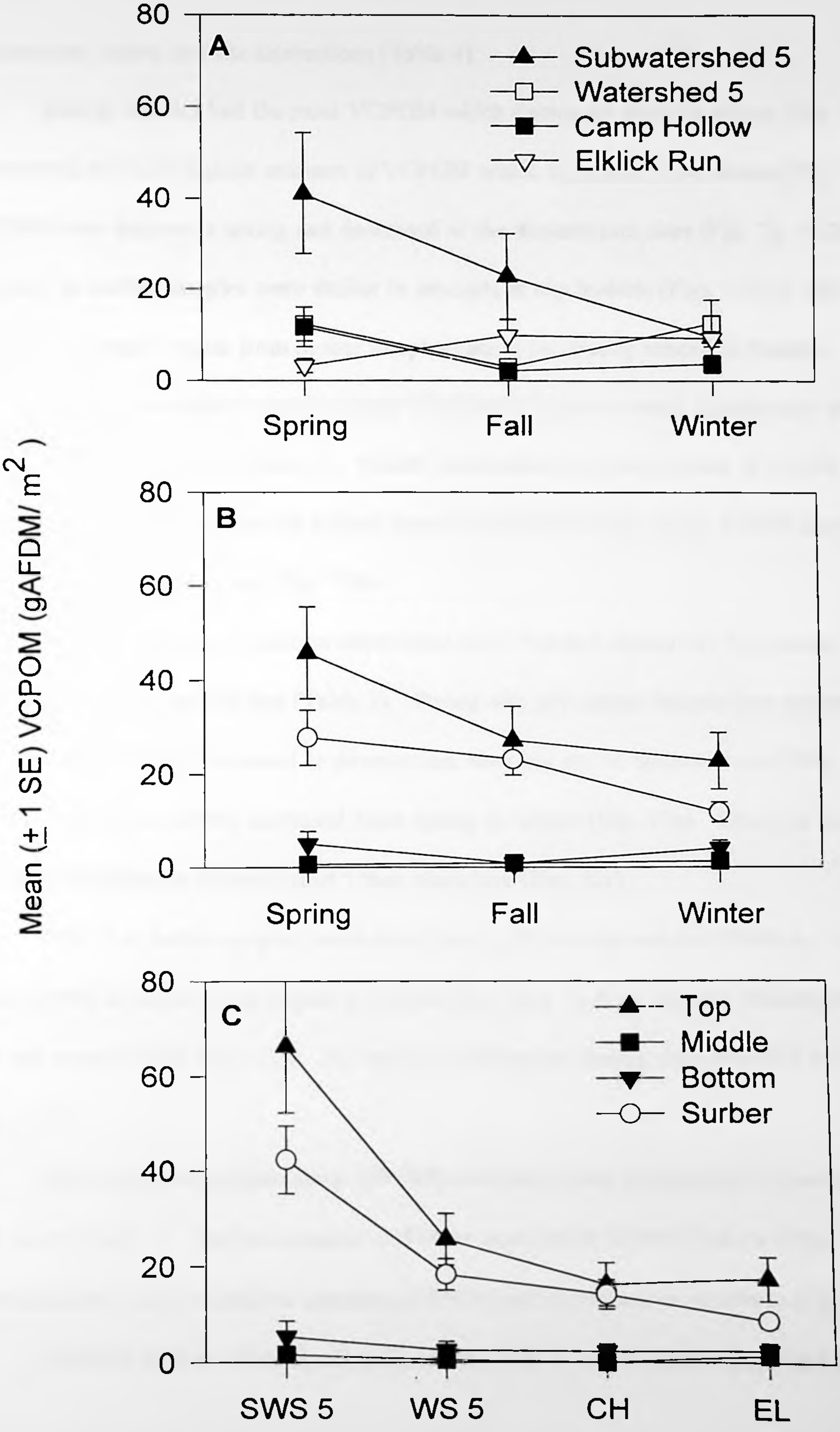

A
Sub WS 5
B
WS 5
C
Camp Hollow
D
Elklick Run
Top
Middle
Bottom
Spring
Fall
Winter
0
5
10
15
20
25
30
Mean (±1 SE) Taxa Richness (#/sample)

Figure 11. a. Mean (± 1 SE) VCPOM (gAFDW/m^2) in each season at each site.

b. Mean (± 1 SE) VCPOM (gAFDW/m^2) in each season at each level.

c. Mean (± 1 SE) VCPOM (gAFDW/m^2) at each site at each level. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

*Error bars may be hidden by symbols.


Mean (± 1 SE) VCPOM (gAFDM/ m^2)
A
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
80
60
40
20
0
Spring
Fall
Winter
B
80
60
40
20
0
Spring
Fall
Winter
C
Top
Middle
Bottom
Surber
80
60
40
20
0
SWS 5
WS 5
CH
EL

a significant season and site interactions (Table 4).

Spring Surbers had the most VCPOM which decreased through winter (Fig. 11b). Subwatershed 5 had highest amounts of VCPOM which decreased downstream (Fig. 11c). VCPOM was highest in spring and decreased at the downstream sites (Fig. 7). VCPOM amounts in Surber samples were similar to amounts in top baskets (Figs. 11b,c), although particulate organic matter from Surber samples cannot be directly related to baskets.

Coarse particulate organic matter (CPOM) in baskets varied significantly among levels, sites, and seasons (Table 3). Middle baskets had the least amount of CPOM (Fig. 12b,c). Subwatershed 5 had the highest amounts of CPOM (Fig. 12,c). CPOM increased slightly from spring to winter (Fig. 12b).

CPOM in baskets, significant interactions were detected among site and season, level and season, and level and site (Table 3). Strong site and season interactions occurred in winter, when CPOM increased at downstream sites but not at upstream sites (Fig. 12a). Effect of level on CPOM increased from spring to winter (Fig. 12b). Effect of level on CPOM was higher at Subwatershed 5 than elsewhere (Fig. 12c).

CPOM in Surber samples varied significantly with season and site (Table 4). Across sites, CPOM in Surbers was highest in the fall (Fig. 12b). Across seasons, Subwatershed 5 had the most CPOM (Fig. 12c). The greatest differences among sites occurred in the fall (Fig. 13b).

Fine particulate organic matter (FPOM) in baskets varied significantly between levels and sites (Table 4). Highest amounts of FPOM occurred in bottom baskets (Figs. 14b,c) Subwatershed 5 had the highest amounts of FPOM and decreased downstream (Fig. 14,c).

FPOM in baskets varied significantly among level & season interactions, and site and

Figure 12. a. Mean (± 1 SE) CPOM (gAFDW/m^2) in each season at each site.

b. Mean (± 1 SE) CPOM (gAFDW/m^2) in each season at each level.

c. Mean (± 1 SE) CPOM (gAFDW/m^2) at each site at each level. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

*Error bars may be hidden by symbols.

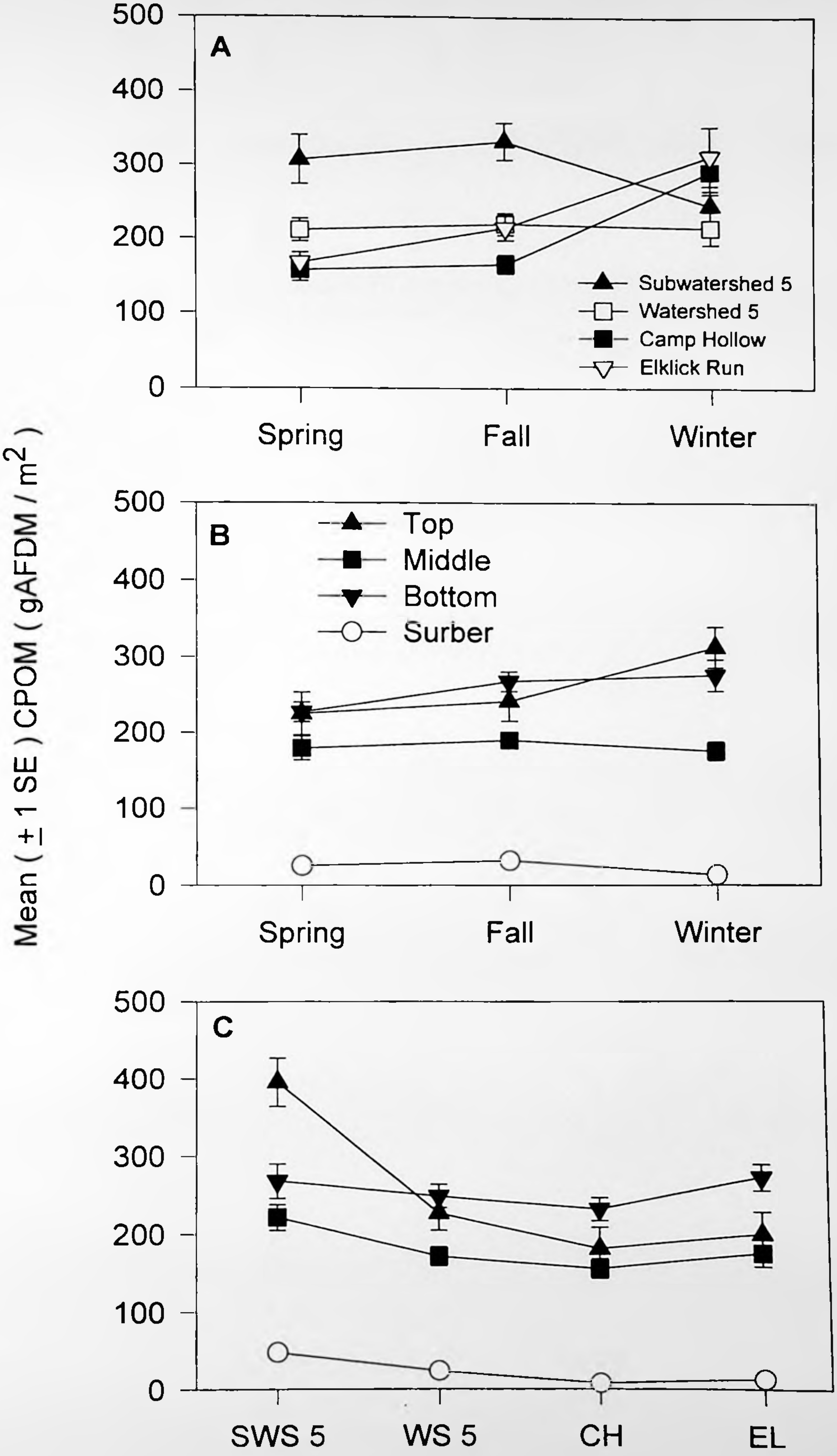

Mean (± 1 SE) CPOM (gAFDM / m^2)
A
500
400
300
200
100
0
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
Spring
Fall
Winter
B
Top
Middle
Bottom
Surber
500
400
300
200
100
0
Spring
Fall
Winter
C
500
400
300
200
100
0
SWS 5
WS 5
CH
EL

Figure 13. Mean (± 1 SE) particulate organic matter in Surber samples in each season at each site.

*Error bars may be hidden by symbols.

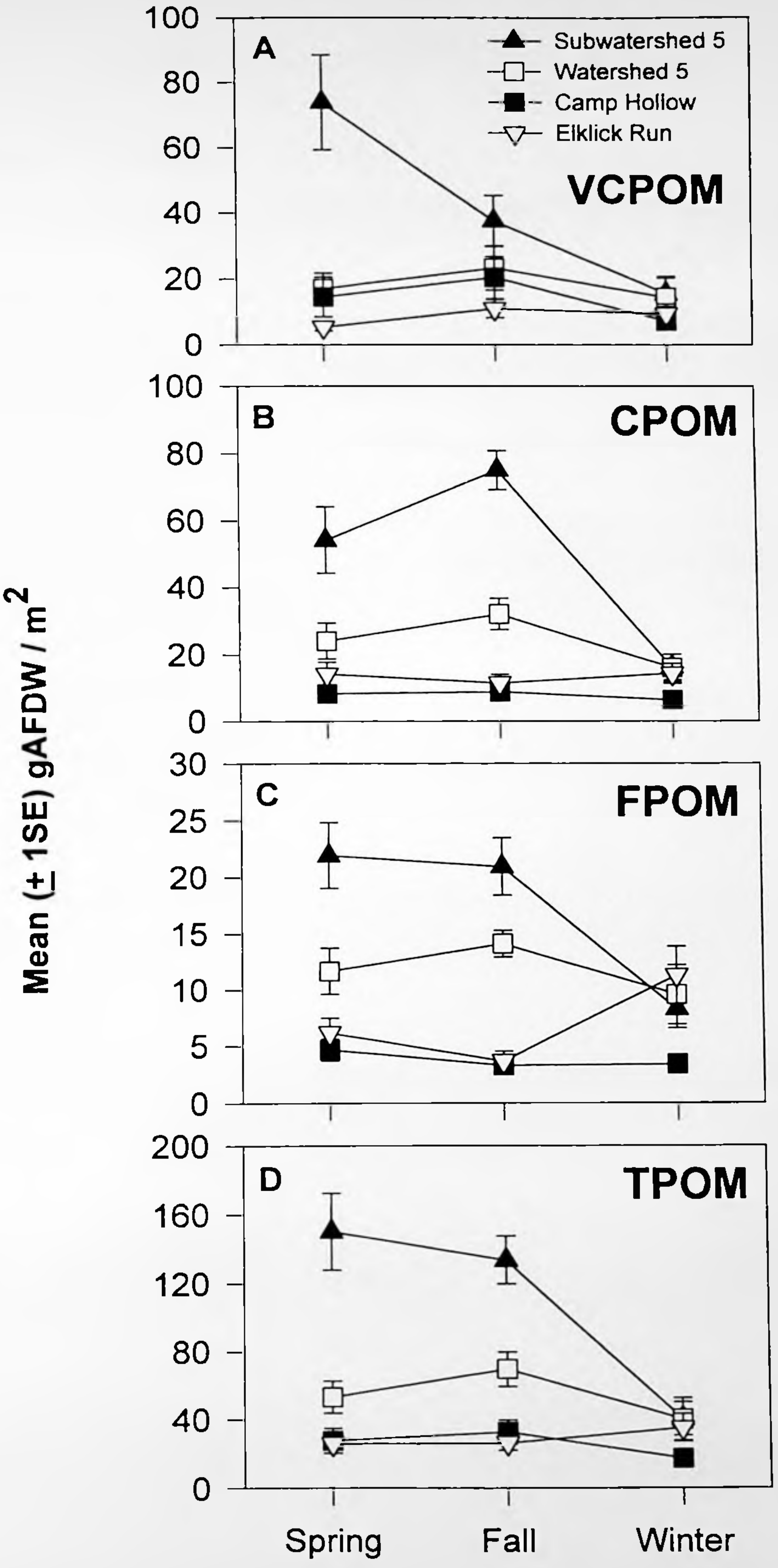
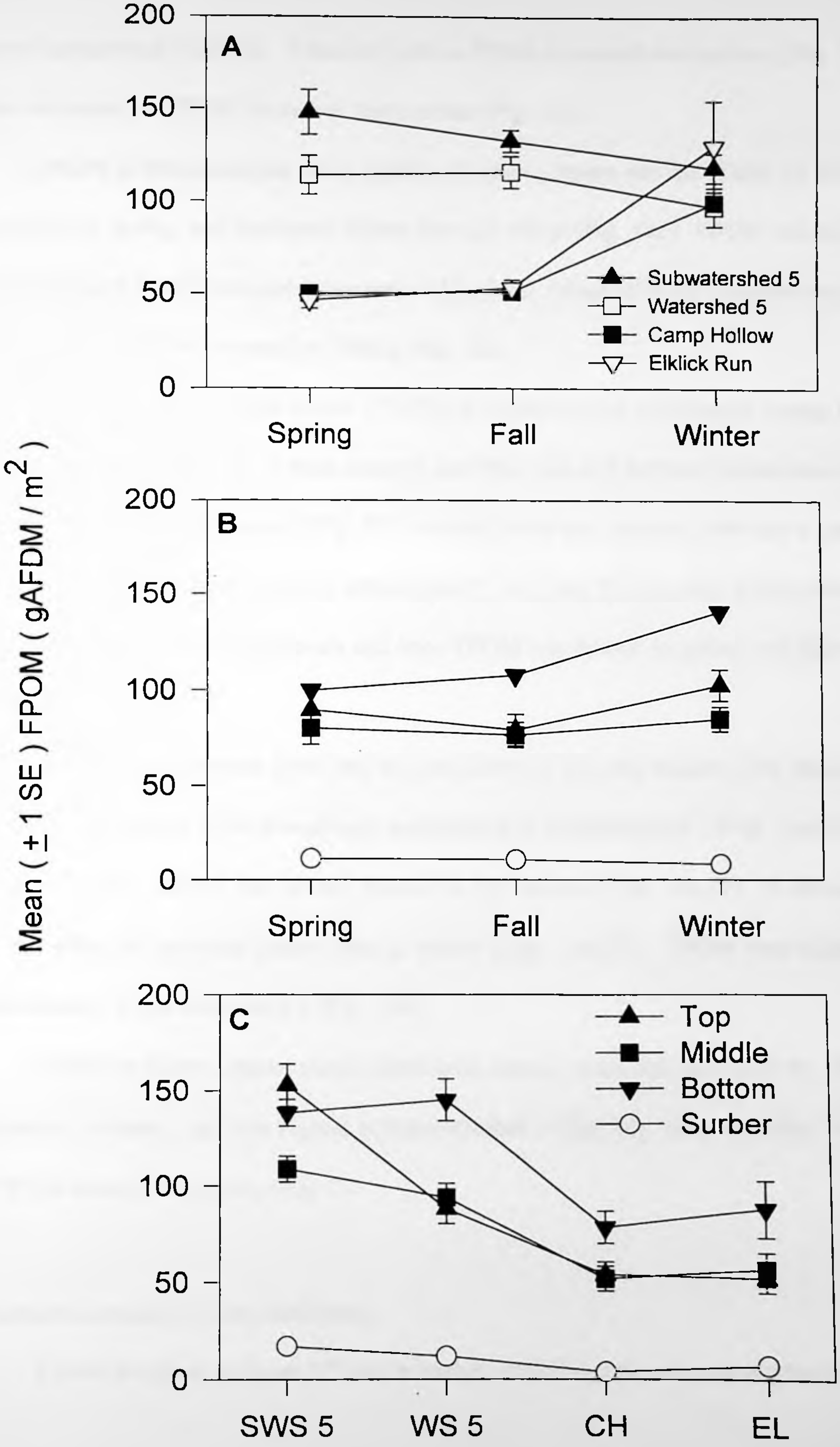

Mean (± 1SE) gAFDW / m^2
A
VCPOM
B
CPOM
C
FPOM
D
TPOM
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
0
20
40
60
80
100
0
5
10
15
20
25
30
0
40
80
120
160
200
Spring
Fall
Winter

Figure 14. a. Mean (± 1 SE) FPOM ($gAFDW/m^2$) in each season at each site.

b. Mean (± 1 SE) FPOM ($gAFDW/m^2$) in each season at each level.

c. Mean (± 1 SE) FPOM ($gAFDW/m^2$) at each site at each level. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

*Error bars may be hidden by symbols.


Mean (± 1 SE) FPOM (gAFDM / m^2)
A
200
150
100
50
0
Spring
Fall
Winter
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
B
200
150
100
50
0
Spring
Fall
Winter
C
200
150
100
50
0
Top
Middle
Bottom
Surber
SWS 5
WS 5
CH
EL

season interactions (Table 4). Effect of level on FPOM increased downstream (Fig. 14b). Effect of season on FPOM decreased downstream (Fig. 13c).

FPOM in Surber samples varied significantly among season and site (Table 4). FPOM was highest in spring, and decreased slightly through winter (Fig. 13c). FPOM was highest at Subwatershed 5 and decreased downstream (Fig. 14c). Greatest effect of season occured in winter when FPOM increased at Elklick (Fig. 14a).

Total particulate organic matter (TPOM) in baskets varied significantly among level, season, and site (Table 3). Across seasons and sites, top and bottom baskets had more TPOM than the middle baskets (Fig. 15). Across levels and seasons there was a general decrease in TPOM downstream from Subwatershed 5 to Camp Hollow then a slight increase at Elklick (Fig. 15b). Across levels and sites TPOM was lowest in spring and highest in winter (Fig. 15c).

Interactions between level and site and between site and season were significant (Table 3). The effect of level was most pronounced at Subwatershed 5 (Fig. 16c) where, unlike other sites, TPOM was always greatest in top baskets (Figs. 16c,17). In spring and fall, the effect of site was greater than in winter (Figs. 16a,13). TPOM was highest at Subwatershed 5 and Watershed 5 (Fig. 16b).

TPOM in Surber samples varied significantly among season and site (Table 4). TPOM was lowest in winter, and was highest at Subwatershed 5 (Fig. 16). Greatest effect of level on TPOM occurred in spring (Fig. 7).

Particulate Inorganic Matter (sediment)

Coarse inorganic sediment (CPash) in baskets varied significantly among levels, sites,

Figure 15. a. Mean (± 1 SE) TPOM (gAFDW/m^2) in Surber samples and hyporheic baskets.

b. Mean (± 1 SE) TPOM (gAFDW/m^2) at each site in Surbers and baskets. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

c. Mean (± 1 SE) TPOM (gAFDW/m^2) in each season in Surbers and baskets.

*Error bars may be hidden by symbols.

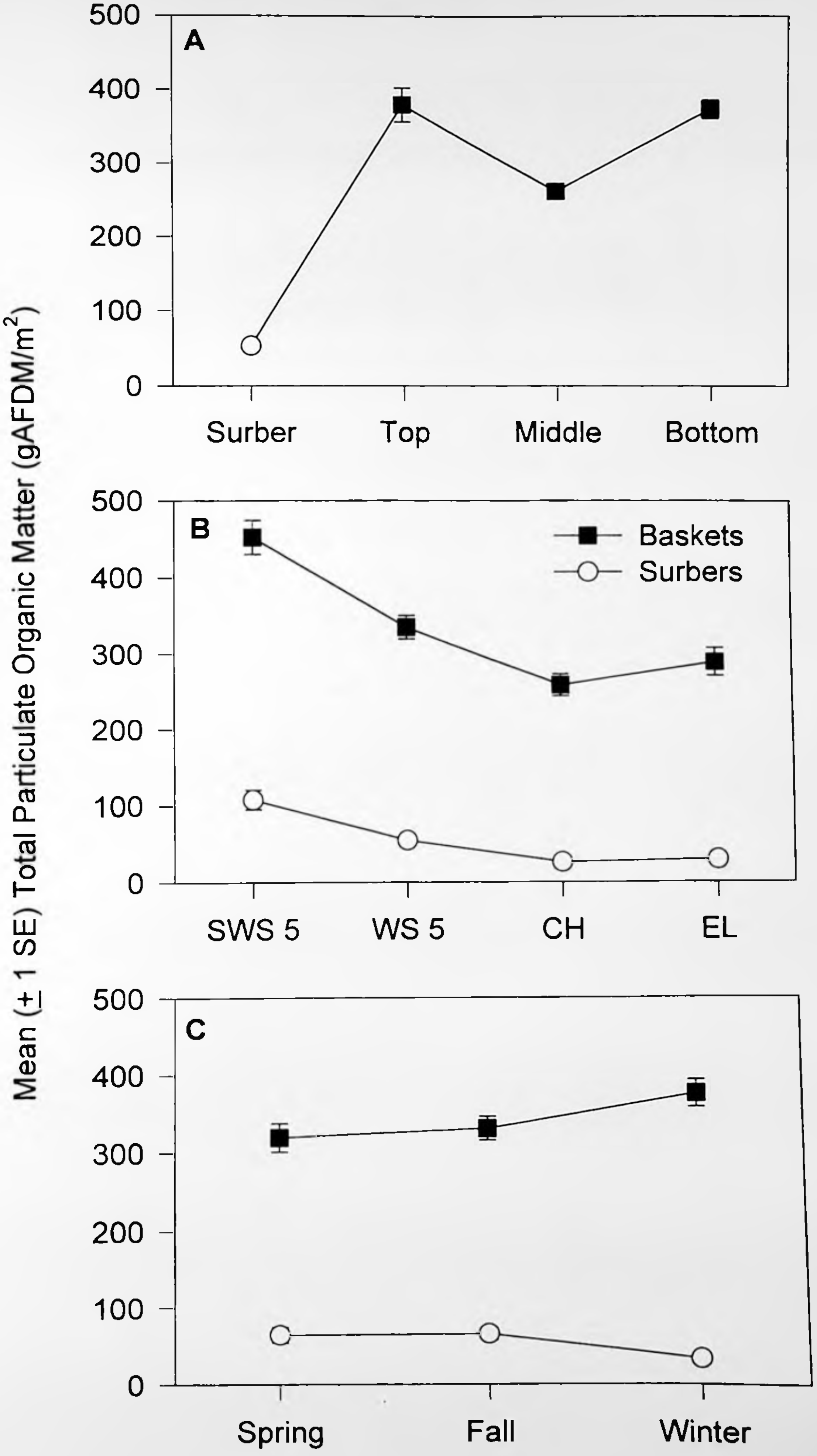

Mean (+ 1 SE) Total Particulate Organic Matter (gAFDM/m^2)
A
500
400
300
200
100
0
Surber
Top
Middle
Bottom
B
Baskets
Surbers
500
400
300
200
100
0
SWS 5
WS 5
CH
EL
C
500
400
300
200
100
0
Spring
Fall
Winter

Figure 16. a. Mean (± 1 SE) TPOM (gAFDW/m^2) in each season at each site.

b. Mean (± 1 SE) TPOM (gAFDW/m^2) in each season at each level.

c. Mean (± 1 SE) TPOM (gAFDW/m^2) at each site at each level. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

*Error bars may be hidden by symbols.

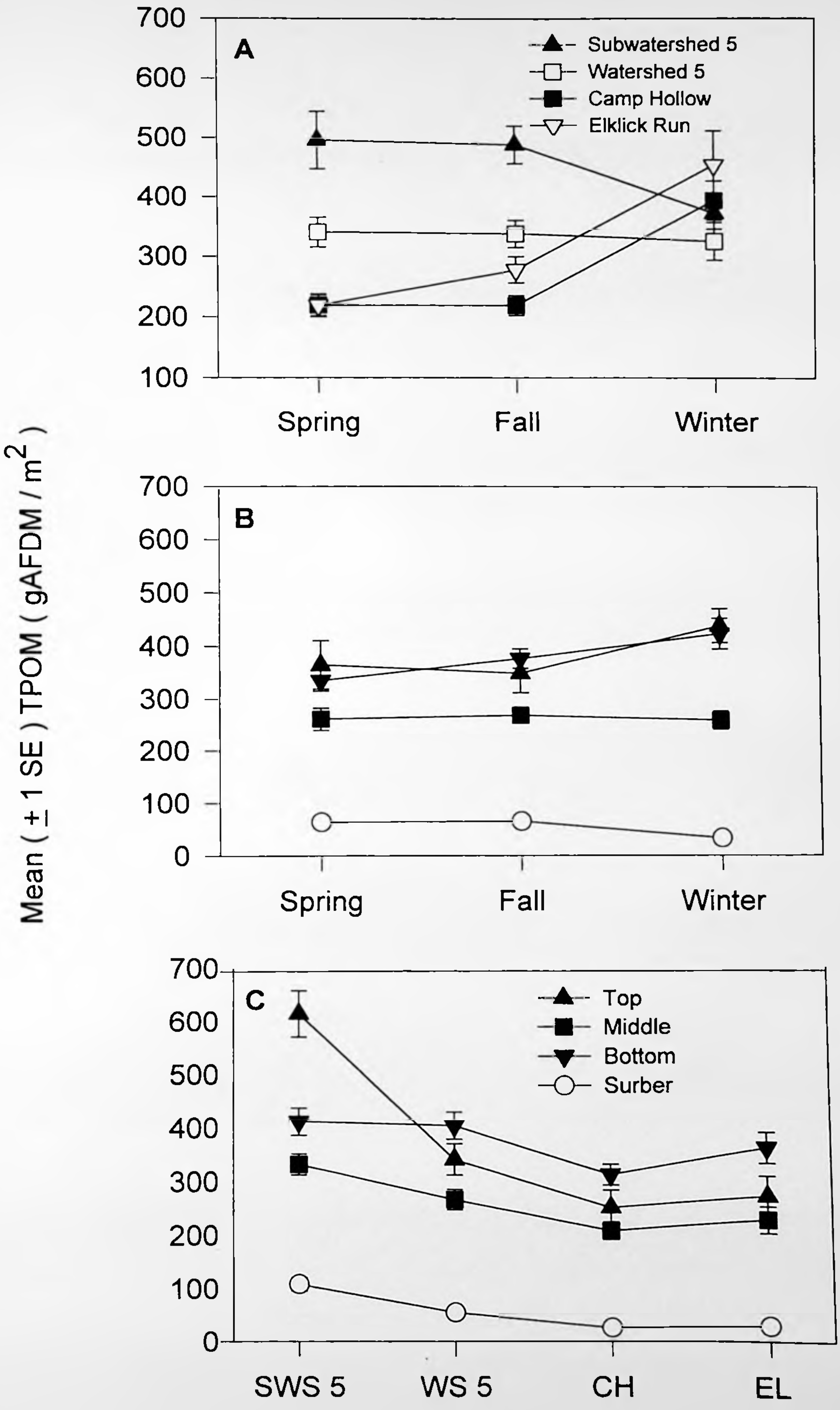
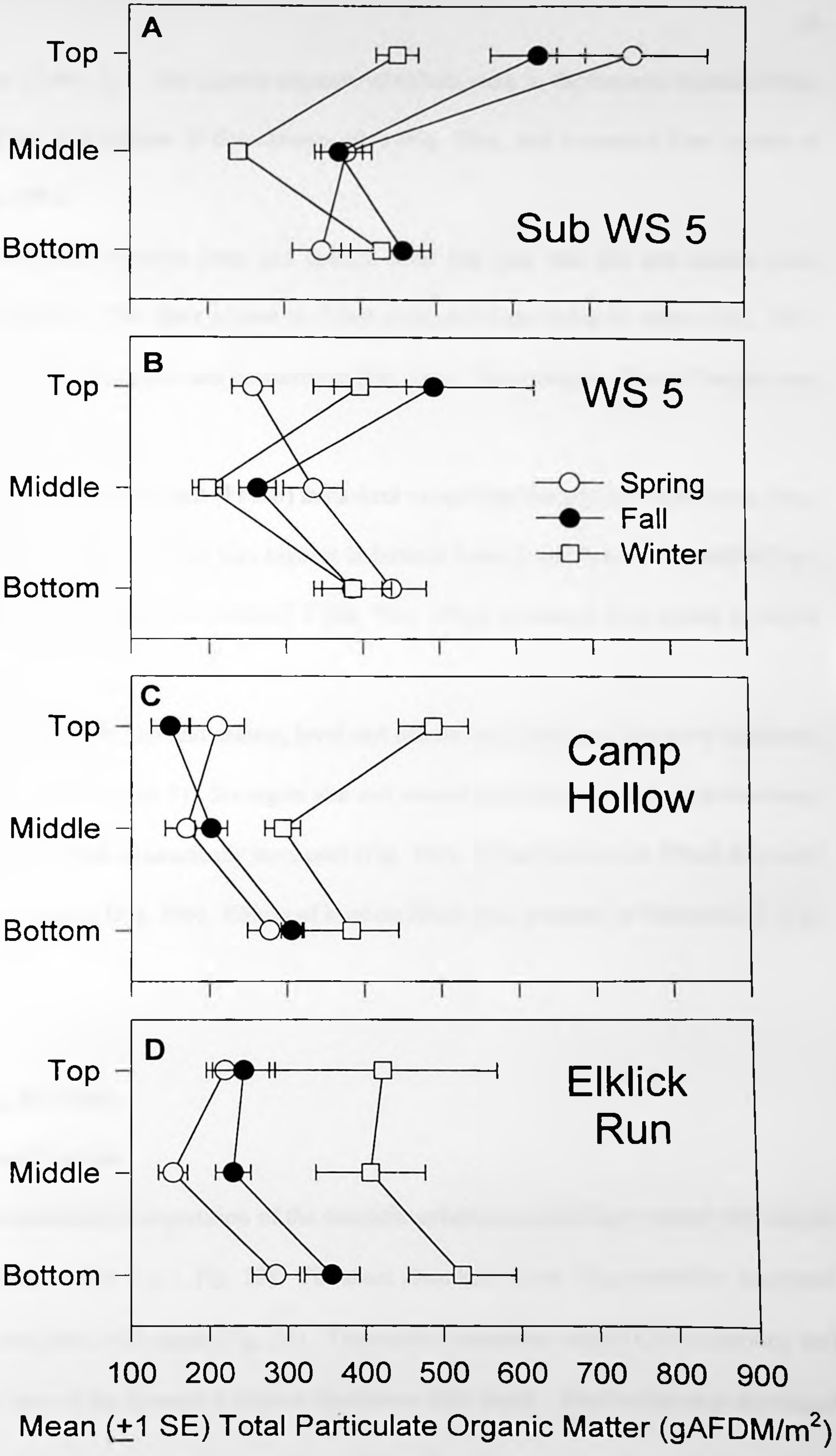

Mean (± 1 SE) TPOM (gAFDM / m^2)
A
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
700
600
500
400
300
200
100
Spring
Fall
Winter
B
700
600
500
400
300
200
100
0
Spring
Fall
Winter
C
Top
Middle
Bottom
Surber
700
600
500
400
300
200
100
0
SWS 5
WS 5
CH
EL

Figure 17. Mean (± 1 SE) TPOM (gAFDW/m^2) in each season at each depth.

*Error bars may be hidden by symbols.


A
Top
Middle
Bottom
Sub WS 5
B
WS 5
Spring
Fall
Winter
C
Camp Hollow
D
Elklick Run
100
200
300
400
500
600
700
800
900
Mean (±1 SE) Total Particulate Organic Matter (gAFDM/m²)

and seasons (Table 3). The highest amounts of CPash were in the bottom baskets (Figs. 18b,c). CPash was highest at downstream sites (Fig. 18c), and increased from spring to winter (Fig. 18b).

Interactions between level and season, level and site, and site and season were significant (Table 3). The effect of level on CPash increased from spring to winter (Fig. 18b). Effect of level on CPash increased downstream (Fig. 18c). The strongest effect of season was in winter (Figs. 18a,b).

Fine inorganic sediment (FPash) in baskets varied significantly between levels, sites, and seasons (Table 3). FPash was highest in bottom baskets and lowest in middle (Figs. 19b,c). FPash was greatest at Watershed 5 (Fig. 19c). FPash increased from spring to winter (Fig. 19b).

Interactions of site and season, level and season, and level and site were significant for Fpash in baskets (Table 3). Strongest site and season interactions occurred downstream in winter where FPash dramatically increased (Fig. 19a). Effect of level on FPash increased from spring to winter (Fig. 19b). Effects of level on FPash were greatest at Watershed 5 (Fig. 19c).

Community Structure

Vertical distribution

The taxonomic composition of the macroinvertebrate assemblage varied with depth, site and season (Table 5,6,7, Fig. 20). The most abundant taxon, Chironomidae, increased in relative abundance with depth (Fig. 20). Tanytarsini dominated within Chironomidae, and constituted most of the increase in relative abundance with depth. Most other taxa decreased

Figure 18. a. Mean (± 1 SE) CPash (gAFDW/m^2) in each season at each site.

b. Mean (± 1 SE) CPash (gAFDW/m^2) in each season at each level.

c. Mean (± 1 SE) CPash (gAFDW/m^2) at each site at each level. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

*Error bars may be hidden by symbols.

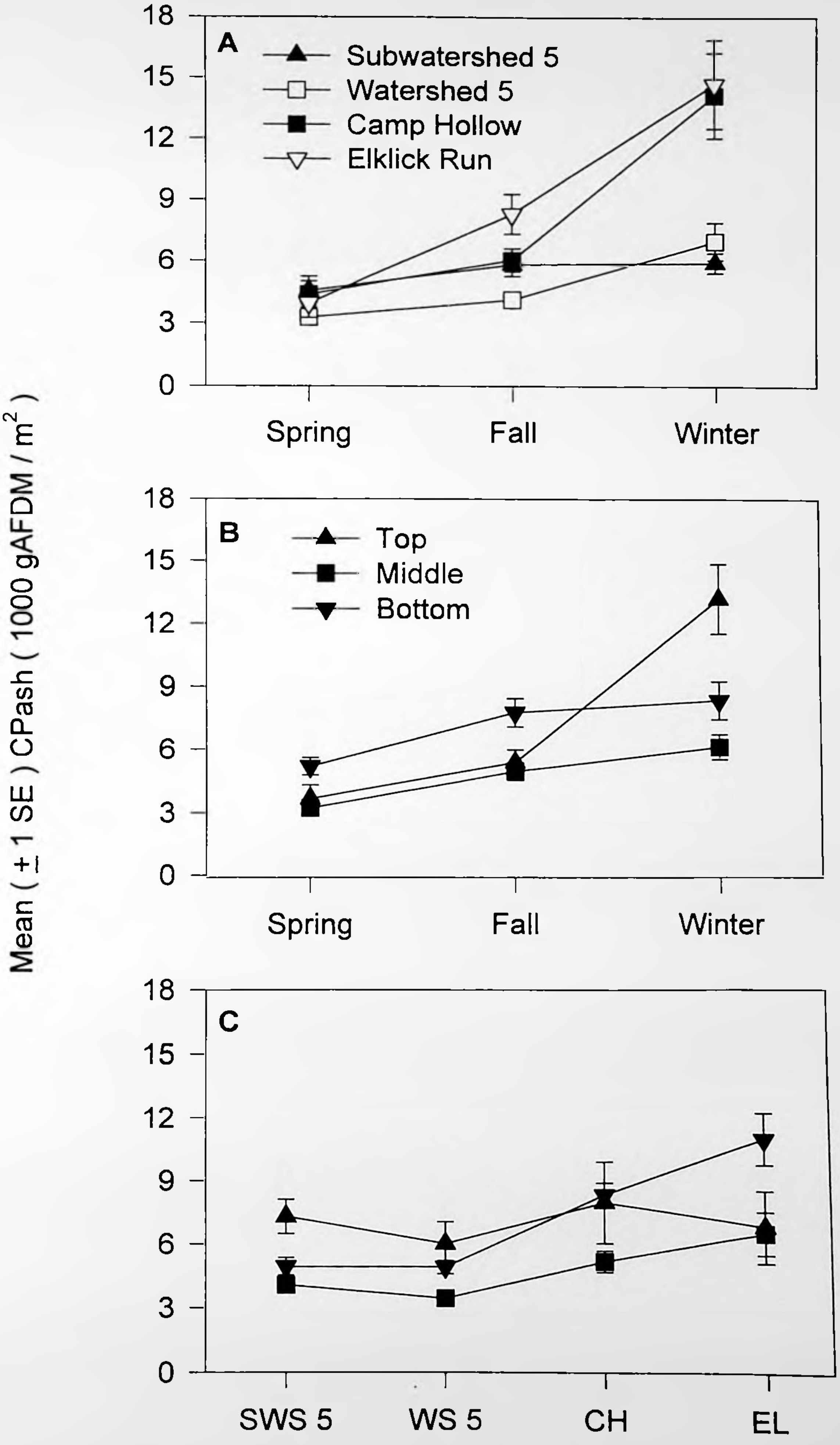

Mean (+ 1 SE) CPash (1000 gAFDM / m2)
A
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
0
3
6
9
12
15
18
Spring
Fall
Winter
B
Top
Middle
Bottom
0
3
6
9
12
15
18
Spring
Fall
Winter
C
0
3
6
9
12
15
18
SWS 5
WS 5
CH
EL

Figure 19. a. Mean (± 1 SE) FPash ($gAFDW/m^2$) in each season at each site.

b. Mean (± 1 SE) FPash ($gAFDW/m^2$) in each season at each level.

c. Mean (± 1 SE) FPash ($gAFDW/m^2$) at each site at each level. Site abbreviations are SWS 5=Subwatershed 5, WS 5=Watershed 5, CH=Camp Hollow, EL=Elklick Run.

*Error bars may be hidden by symbols.

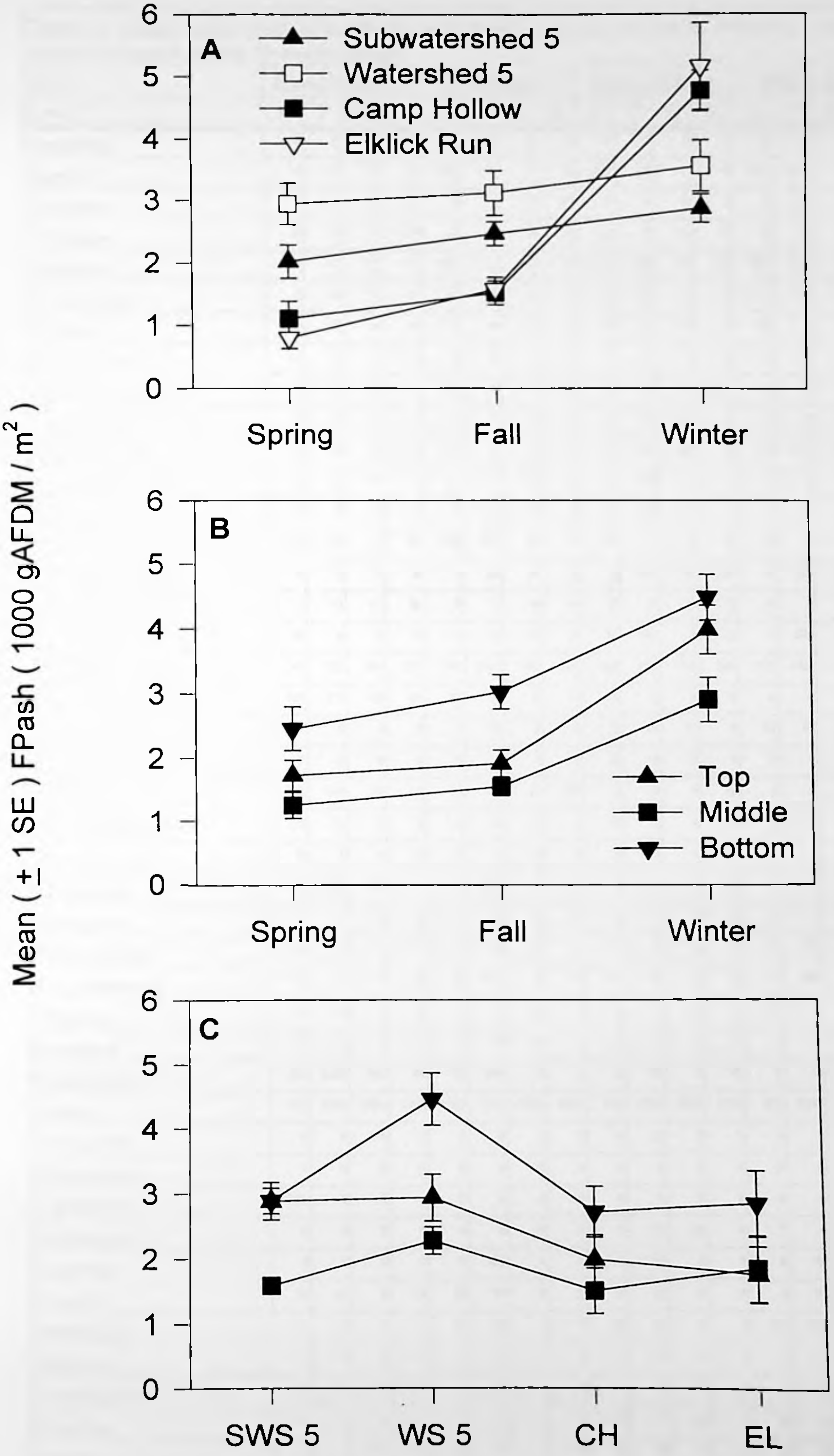

Mean (+ 1 SE) FPash (1000 gAFDM / m^2)
A
Subwatershed 5
Watershed 5
Camp Hollow
Elklick Run
0
1
2
3
4
5
6
Spring
Fall
Winter
B
Top
Middle
Bottom
0
1
2
3
4
5
6
Spring
Fall
Winter
C
0
1
2
3
4
5
6
SWS 5
WS 5
CH
EL

Table 5a. Mean density (#/m^2) of benthic fauna in spring at all sites and levels. S=Surber, T=top basket, M=middle basket, B=bottom basket.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Ameletus	1	0	0	0	12	0	0	6	0	6	0	0	0	45	0	0
Baetis	0	0	0	0	48	0	0	0	109	17	6	6	229	226	6	0
Diphetor	0	0	0	0	0	0	0	0	1	6	6	0	6	23	17	0
Procleon	0	0	0	0	1	0	0	0	1	0	0	0	2	0	0	0
Baetidae	0	0	0	0	191	0	6	0	434	452	28	68	922	994	45	0
Cinygmula	1	0	0	6	1	0	0	0	24	11	0	0	26	119	28	0
Epeorus	0	0	0	0	2	0	0	0	13	0	0	0	28	6	0	0
Heptagenia	0	0	0	0	0	0	0	0	4	0	0	0	2	0	0	0
Leucrocuta	0	0	0	0	19	0	0	0	0	6	0	0	4	6	0	0
Stenonema	3	0	0	0	8	6	0	0	2	0	11	0	0	0	0	0
Heptageniidae	0	0	0	0	28	0	6	11	37	141	45	6	96	277	23	0
Drunnella	0	0	0	0	0	0	0	0	3	0	0	0	18	6	0	0
Ephemerella	0	0	0	0	15	45	17	0	4	17	0	0	3	34	0	0
Eurylophella	206	192	6	45	110	452	90	0	51	0	0	0	18	0	0	0
Ephemerellidae	0	0	0	0	5	90	0	0	4	203	90	136	0	113	0	0
Habrophlebia	1	40	45	11	0	0	0	0	0	0	0	0	0	0	0	0
Habrophlebiodes	31	6	0	0	1	0	0	0	19	107	0	11	7	136	90	11
Paraleptophlebia	145	791	785	237	211	1729	412	328	310	927	780	520	473	4322	1949	1045
Leptophlebiidae	105	175	45	17	39	0	0	0	8	0	0	0	0	0	0	0
Ephemera	63	0	0	0	0	0	0	0	1	68	11	0	15	45	85	68
Litobrancha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lanthus	111	215	73	11	14	40	11	23	0	6	6	11	4	0	0	6
Cordulegaster	9	11	6	0	6	0	0	0	0	0	0	0	0	0	0	0
Pteronarcys	0	0	0	0	1	0	0	0	3	17	6	0	4	6	0	0
Peltoperla	264	169	102	6	91	667	0	6	1	11	0	11	0	6	0	0
Tallaperla	0	0	0	0	0	0	0	0	2	0	0	0	0	6	0	0
Peltoperlidae	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0
Amphinemura	22	17	6	0	37	147	0	11	11	45	0	6	3	164	11	0
Prostoia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Soyedina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nemouridae	398	2169	181	90	12	904	0	0	0	23	0	45	0	0	45	6
Leuctra	573	5220	3294	1090	1760	7712	2633	1814	563	3175	2266	1508	322	2147	1729	791
Allocapnia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracapnia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capniidae	109	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acroneuria	0	0	0	0	0	0	0	0	5	17	90	6	7	6	40	6
Remenus	3	0	6	0	6	124	0	0	0	17	0	0	0	62	0	0
Isoperla	18	11	0	0	10	11	0	0	5	11	0	0	3	11	0	6
Perlodidae	9	0	0	0	86	181	0	6	40	45	0	0	104	333	0	0
Alloperla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0
Haploperla	0	0	0	0	0	51	0	0	0	6	6	0	3	34	11	0
Suwallia	0	0	0	0	0	0	0	0	28	17	17	0	23	23	0	0
Sweltsa	9	6	11	11	35	11	0	11	80	68	90	17	46	11	0	11

Table 5a. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Chloroperlidae	24	11	6	0	185	113	0	102	116	429	11	0	323	186	68	6
Microvelia	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperocorixa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sialis	0	6	11	23	2	0	0	34	0	0	0	17	1	0	0	11
Nigronia	16	17	0	0	5	0	6	6	1	0	11	0	1	0	6	0
Dolophilodes	0	0	0	0	10	0	0	0	228	1164	6	6	232	136	6	0
Wormaldia	4	11	11	0	2	11	0	0	1	0	0	0	0	6	0	0
Lype	2	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
Polycentropus	2	23	11	6	0	6	0	0	16	34	40	23	15	68	62	45
Phylocentropus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplectrona	3	0	0	0	14	40	0	0	29	40	0	6	14	45	17	0
Hydropsyche	0	0	0	0	0	0	0	0	4	0	0	0	9	11	0	0
Rhyacophila	25	45	0	0	32	57	0	6	19	34	6	0	10	23	6	0
Rhyacophila (pupae)	1	0	0	0	6	17	6	0	1	0	0	0	3	0	0	0
Glossosoma	0	0	0	0	16	0	0	0	33	0	0	0	98	0	0	0
Agapetus	0	0	0	0	0	0	0	0	49	0	0	0	20	0	0	0
Lepidostoma	20	51	45	6	13	119	23	17	4	130	102	73	1	57	79	79
Hydatophylax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pycnopsyche	14	40	51	6	4	28	40	11	0	0	17	0	3	17	28	0
Limnophilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	45	0	0
Goera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neophylax	2	0	0	0	2	0	0	0	1	0	0	11	7	11	0	6
Triaenodes	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Archips	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidoptera	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrochus	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pontamalota	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staphylinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psephenus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Ectopria	17	0	0	0	7	11	0	0	13	6	0	6	2	0	0	0
Helichus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prinocyphon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oulimnius	50	0	0	0	48	198	0	0	92	107	0	45	228	395	0	28
Oulimnius (adult)	0	0	0	0	86	90	0	0	33	0	0	0	48	0	0	0
Elmidae	0	90	0	0	164	0	0	0	79	0	0	0	0	0	0	0
Tipula	2	0	0	0	5	0	0	0	0	0	0	0	0	6	0	0
Antocha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranota	200	215	11	17	110	73	17	0	23	62	6	0	24	17	0	0
Hexatoma	65	96	23	11	17	51	23	0	4	23	0	6	8	17	6	0
Limnophila	21	107	23	0	5	57	51	0	3	23	6	11	0	0	6	0
Limonia	20	45	17	0	3	51	11	11	0	6	6	0	0	0	0	0
Ormosia	3	0	11	51	0	0	28	147	0	0	0	6	0	0	0	0
Pedicia	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5a. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Psuedolimnophila	54	203	147	34	10	107	45	17	1	6	0	0	5	0	0	0
Tipulidae	1	17	0	0	0	6	0	0	0	0	0	0	0	0	0	0
Tipulidae (pupae)	5	11	6	0	7	0	0	0	0	0	0	0	0	0	0	0
Bezzia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Probezzia	37	153	119	45	8	11	0	11	0	0	6	0	7	34	0	23
Ceratopogon	3	40	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ceratopogonidae	80	113	0	0	16	45	96	0	0	23	45	45	0	6	45	96
Tanypodinae	220	2232	1339	684	317	1853	994	746	231	2096	514	746	567	5520	2316	1599
Orthocladinae	683	3209	2667	565	564	4588	588	503	299	5373	977	588	732	6113	1740	684
Chironomini	18	23	28	6	10	452	311	192	346	4966	1232	1090	154	8525	5802	3921
Tanytarsini	1831	8994	5068	2989	514	5994	2927	3576	502	6616	4390	3847	323	5944	3718	2661
Chironomidae	23	136	6	0	17	723	107	107	0	559	356	232	9	333	362	339
Chironomidae (pupae)	112	599	237	17	96	712	305	119	104	808	260	316	61	1362	1169	458
Dixa	138	164	0	0	13	158	90	0	30	0	0	0	2	68	0	0
Bittacomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prosimulium	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Chelifera	26	17	0	0	0	0	0	0	1	0	0	6	2	23	17	0
Clinocera	5	0	0	0	0	0	0	0	0	0	0	0	1	6	0	0
Empididae	0	0	0	0	1	45	0	0	0	45	0	0	12	96	0	0
Chrysops	2	11	0	6	2	0	0	6	0	6	6	0	0	0	0	0
Merycomyia	1	0	11	0	1	11	11	0	0	0	0	0	0	0	0	0
Tabanidae	0	6	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Mycetophilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collembola	134	514	90	0	771	6853	0	0	960	791	0	0	27	3045	23	0
Cambarus	0	6	0	6	4	45	6	0	3	11	0	6	3	34	28	11
Isopoda	0	0	6	28	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus	0	6	6	0	0	0	0	0	0	102	0	0	14	68	40	17
Oligochaeta	85	51	6	6	59	147	0	0	3	90	23	0	8	28	68	6
Nematoda	16	90	0	90	0	0	90	0	0	0	45	0	0	0	68	0
Bivalvia	48	6	215	119	16	0	0	0	4	0	0	0	20	0	45	23
Ostrocoda	766	2944	1085	814	8	158	0	0	12	113	11	0	78	407	136	203
Copepoda	95	1898	2802	1446	23	2599	994	633	8	1062	1650	1040	27	3503	2757	1944
Acari	55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terrestrial	0	96	0	0	0	0	0	0	0	0	0	0	0	0	6	0
Salamander	5	6	0	0	2	23	11	0	0	11	0	6	1	28	17	0
Sculpin	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0
Mean total	7015	31356	18616	8497	5939	37621	9955	8461	5014	10153	11181	10480	5504	45367	22734	14107
# samples	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10

Table 5b. Mean density (#/m^2) of benthic fauna in fall at all sites and levels. S=Surber, T=top basket, M=middle basket, B=bottom basket.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Ameletus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetis	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0
Diphetor	0	0	0	0	0	0	0	0	0	0	0	0	4	6	7	0
Procleon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetidae	0	0	0	0	0	0	0	0	8	0	0	0	92	0	57	0
Cinygmula	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Epeorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heptagenia	0	0	0	0	0	0	0	0	2	0	13	0	0	6	0	0
Leucrocuta	0	0	0	0	0	0	0	0	0	0	0	0	2	0	7	0
Stenonema	3	0	6	6	32	19	51	73	8	85	38	13	28	215	0	0
Heptageniidae	0	0	0	0	16	6	6	45	23	34	6	0	37	34	0	6
Drunnella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephemerella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	106	0
Eurylophella	46	40	0	6	62	126	40	11	5	62	69	25	55	107	14	19
Ephemerellidae	0	0	0	0	12	0	0	0	4	0	0	0	0	45	0	0
Habrophlebia	1	68	90	0	0	6	6	0	0	0	0	0	0	0	0	0
Habrophlebiodes	0	0	0	0	0	0	0	0	0	28	57	0	0	40	57	132
Paraleptophlebia	40	0	0	0	28	0	17	0	121	220	100	88	259	333	106	138
Leptophlebiidae	31	503	153	17	35	0	0	45	32	0	13	50	93	90	28	0
Ephemera	0	0	0	0	0	0	0	0	1	90	94	69	24	915	1137	584
Litobrancha	0	0	0	0	0	6	0	0	0	0	0	0	0	0	78	6
Lanthus	47	915	113	11	13	19	119	107	1	57	19	38	2	6	28	31
Cordulegaster	45	57	17	0	4	0	0	45	0	0	0	0	0	0	7	0
Pteronarcys	0	0	0	0	0	6	0	0	1	11	0	0	4	11	7	0
Peltoperla	7	0	0	0	3	19	45	0	0	6	0	0	0	0	0	0
Tallaperla	0	0	0	0	0	0	0	0	0	0	0	0	3	11	0	0
Peltoperlidae	0	23	0	0	0	6	0	0	0	0	0	0	0	0	0	0
Amphinemura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prostoia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Soyedina	53	130	0	6	2	6	0	0	0	6	0	0	0	0	0	0
Nemouridae	1	0	0	0	16	100	45	0	0	0	0	0	0	0	57	0
Leuctra	65	435	158	282	312	408	186	384	97	322	226	213	103	294	184	126
Allocapnia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paracapnia	0	0	0	0	0	0	0	0	6	0	6	0	146	90	0	6
Capniidae	0	0	45	0	94	50	0	0	94	102	13	25	43	158	0	50
Acroneuria	0	0	0	0	1	0	0	0	7	68	31	6	37	90	57	0
Remenus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoperla	1	0	0	0	5	31	0	0	0	0	0	0	1	0	0	0
Perlodidae	5	23	6	0	49	113	0	0	34	17	19	6	210	34	0	0
Alloperla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haploperla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Suwallia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sweltsa	1	45	0	0	14	63	11	6	69	153	38	13	145	271	35	13

Table 5b. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Chloroperlidae	8	0	90	90	156	201	362	0	61	90	75	0	57	68	85	0
Microvelia	0	0	0	0	0	0	0	0	0	40	0	0	0	6	0	0
Hesperocorixa	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Sialis	2	209	119	23	2	370	271	73	0	17	82	138	0	34	64	75
Nigronia	8	90	17	6	3	138	17	0	2	0	0	6	1	6	7	0
Dolophilodes	0	0	0	0	0	6	0	0	0	0	0	0	6	0	0	0
Wormaldia	1	40	11	6	0	0	0	0	0	0	0	0	0	0	0	0
Lype	4	0	0	0	2	0	0	0	0	6	0	0	1	0	0	0
Polycentropus	2	68	119	0	0	13	6	6	68	339	452	182	48	119	184	75
Phylocentropus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplectrona	6	11	0	0	63	226	51	0	35	45	0	0	150	11	7	0
Hydropsyche	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Rhyacophila	6	62	0	0	106	126	0	0	10	153	0	31	18	28	28	0
Rhyacophila (pupae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glossosoma	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Agapetus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidostoma	0	17	0	6	0	6	6	0	0	0	0	0	0	0	0	0
Hydatophylax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pycnopsyche	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limnophilidae	7	0	0	0	17	0	0	0	1	0	0	0	0	0	0	0
Goera	0	0	0	0	1	0	0	0	0	6	6	0	5	0	0	0
Neophylax	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0
Triaenodes	31	11	6	11	0	0	6	0	0	0	0	0	0	0	0	0
Archips	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidoptera	1	0	0	6	3	0	0	0	1	6	0	0	0	6	0	0
Hydrochus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pontamalota	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staphylinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
Psephenus	0	0	0	0	0	0	0	0	0	0	0	0	1	6	0	0
Ectopria	0	0	0	0	36	0	0	0	6	68	0	0	5	6	0	0
Helichus	0	0	0	0	0	0	0	0	0	0	0	0	5	6	0	0
Prinocyphon	0	0	79	23	0	0	0	0	0	0	0	0	0	0	0	0
Oulimnius	1	0	0	0	156	44	0	0	20	102	38	0	43	62	14	6
Oulimnius (adult)	0	0	0	0	28	6	0	0	12	0	25	0	69	0	0	0
Elmidae	0	0	0	0	27	6	0	0	75	68	25	0	254	582	28	0
Tipula	2	0	0	6	0	6	6	0	0	6	0	0	0	0	0	0
Antocha	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
Dicranota	1	23	0	0	18	13	0	0	0	0	0	0	1	0	0	0
Hexatoma	36	271	23	0	18	176	68	45	19	85	19	25	15	51	78	107
Limnophila	19	57	28	0	44	113	68	28	8	73	6	50	5	11	92	6
Limonia	10	271	0	11	5	6	23	0	2	6	0	0	3	40	0	6
Ormosia	27	6	0	11	57	0	11	186	0	6	6	25	0	0	0	0
Pedicia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5b. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Psuedolimnophila	161	2000	192	73	54	452	186	23	2	96	69	6	1	40	35	31
Tipulidae	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae (pupae)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bezzia	0	0	0	0	0	6	6	0	0	0	0	0	0	0	0	0
Probezzia	10	96	17	6	73	408	153	23	24	271	119	94	52	441	473	119
Ceratopogon	364	1226	40	0	248	1224	45	6	20	102	25	6	7	79	0	19
Ceratopogonidae	127	740	226	28	25	910	243	164	4	40	57	57	20	90	14	57
Tanypodinae	582	3627	1045	492	417	2229	842	904	61	655	753	659	110	808	657	515
Orthocladinae	722	2271	424	198	525	3591	1412	373	181	1593	1525	1777	112	1011	367	584
Chironomini	1	712	955	6	52	465	1825	96	123	684	1004	753	110	407	155	502
Tanytarsini	343	4051	458	458	1161	2706	1768	678	626	2266	998	879	217	1299	1165	640
Chironomidae	31	599	768	0	148	552	384	186	35	559	427	465	8	153	374	352
Chironomidae (pupae)	5	11	0	6	23	31	0	6	4	51	38	31	48	266	169	75
Dixa	51	186	0	0	1	0	0	0	11	28	0	0	0	11	0	0
Bittacomorpha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prosimulium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chelifera	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Clinocera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Empididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysops	8	11	6	0	0	0	0	0	0	0	0	0	0	0	0	0
Merycomyia	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tabanidae	12	11	6	0	1	100	6	0	0	0	0	6	0	45	7	0
Mycetophilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Collembola	24	102	6	0	18	0	0	0	9	68	0	0	34	237	0	0
Cambarus	0	0	0	0	0	0	0	0	2	0	0	0	2	17	0	0
Isopoda	1	6	23	6	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus	0	0	0	0	0	0	0	0	0	0	0	0	4	6	0	0
Oligochaeta	55	158	6	6	45	38	17	34	12	45	6	0	27	6	14	19
Nematoda	0	0	0	0	0	0	0	0	0	34	0	0	0	0	0	0
Bivalvia	257	158	554	23	0	50	0	6	0	0	0	0	6	0	0	0
Ostrocoda	79	90	0	0	23	100	0	0	17	23	25	0	0	0	0	25
Copepoda	137	181	90	0	16	50	226	90	48	68	138	276	13	11	28	176
Acari	0	0	0	90	0	0	0	0	0	0	0	0	0	23	0	0
Terrestrial	0	6	0	6	0	0	0	0	0	0	0	0	0	0	0	0
Salamander	0	0	0	0	5	6	6	0	4	34	13	6	2	34	14	13
Sculpin	0	0	0	0	0	0	0	0	0	0	0	0	1	11	0	0
Mean total	3491	19622	5893	1921	4281	15161	8537	3644	2014	8989	6673	6020	2750	8802	6011	4514
# samples	10	10	10	10	10	10(9)	10	10	10	10	10(9)	10(9)	10	10	10(8)	10(9)

Table 5c. Mean density (#/m^2) of benthic fauna in winter at all sites and levels.
S=Surber, T=top basket, M=middle basket, B=bottom basket.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Ameletus	37	11	0	0	109	124	0	0	18	0	0	0	25	0	23	0
Baetis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diphetor	0	0	0	0	6	0	0	0	0	0	0	0	1	0	11	0
Procleon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cinygmula	0	0	0	0	4	0	0	0	13	0	0	0	0	0	11	0
Epeorus	0	0	0	0	24	0	0	0	57	9	0	0	97	0	0	0
Heptagenia	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0
Leucrocuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenonema	0	0	0	0	11	11	0	0	2	0	11	0	1	0	0	0
Heptageniidae	0	0	0	0	34	23	0	0	219	245	0	0	155	34	0	0
Drunnella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephemerella	0	6	0	0	26	34	6	0	7	0	0	0	24	0	0	0
Eurylophella	4	23	0	0	101	96	0	0	19	94	0	160	1	0	0	11
Ephemerellidae	17	0	0	0	10	0	0	90	6	151	0	0	23	11	0	0
Habrophlebia	3	23	362	40	0	0	0	0	0	0	0	0	0	0	0	0
Habrophlebiodes	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	45
Paraleptophlebia	70	215	40	11	63	62	141	96	20	28	57	47	68	0	147	418
Leptophlebiidae	13	107	11	0	24	113	45	0	0	0	0	0	0	203	0	181
Ephemera	0	0	0	0	0	0	0	0	0	0	0	38	1	23	45	282
Litobrancha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lanthus	11	62	51	0	8	57	45	23	6	0	23	9	2	0	23	11
Cordulegaster	4	6	28	0	1	0	0	0	0	0	0	0	0	0	0	0
Pteronarcys	0	0	0	0	0	0	0	0	12	160	0	0	14	0	0	0
Peltoperla	75	0	136	0	130	96	68	0	15	0	0	0	1	0	0	0
Tallaperla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peltoperlidae	12	11	0	0	0	0	0	0	57	0	0	0	55	45	181	0
Amphinemura	51	0	0	0	38	0	0	0	23	0	0	0	0	0	0	0
Prostoia	9	102	0	6	8	0	0	0	2	0	0	0	36	0	0	0
Soyedina	0	34	0	0	0	51	0	0	0	0	0	0	1	11	0	0
Nemouridae	256	102	0	6	100	367	0	90	65	0	0	0	161	0	0	0
Leuctra	126	345	215	124	390	1107	847	237	43	226	983	621	62	249	316	373
Allocapnia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Paracapnia	13	23	0	0	14	17	6	0	14	9	11	0	27	0	0	0
Capniidae	4	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0
Acroneuria	0	0	0	0	0	0	0	0	3	19	11	9	7	0	23	45
Remenus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoperla	0	6	0	0	6	23	0	0	9	19	0	0	19	0	23	0
Perlodidae	24	0	0	0	36	51	0	6	26	9	0	0	39	11	11	11
Alloperla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haploperla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Suwallia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sweltsa	5	28	6	6	88	17	68	0	20	47	34	47	26	23	90	68

Table 5c. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Chloroperlidae	12	0	0	0	59	497	23	0	6	603	90	0	20	0	0	0
Microvelia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hesperocorixa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sialis	1	11	28	17	0	28	17	17	0	0	11	19	0	0	0	11
Nigronia	3	85	23	0	6	23	6	0	0	0	0	0	1	0	11	0
Dolophilodes	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Wormaldia	16	96	0	0	40	141	102	0	4	0	0	9	5	0	11	0
Lype	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Polycentropus	0	62	169	6	4	17	6	0	2	9	0	28	1	0	0	34
Phylocentropus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplectrona	4	6	0	0	18	34	11	0	33	19	11	0	33	57	45	11
Hydropsyche	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Rhyacophila	9	51	0	0	32	169	11	0	10	57	23	151	16	0	90	0
Rhyacophila (pupae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glossosoma	0	0	0	0	4	0	0	0	0	0	0	0	4	0	0	0
Agapetus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidostoma	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hydatophylax	6	23	23	0	3	23	0	0	0	0	0	9	6	0	0	0
Pycnopsyche	12	0	0	6	6	11	6	0	3	9	11	0	1	0	0	0
Limnophilidae	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Goera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neophylax	6	0	0	0	58	0	45	0	33	19	0	0	34	0	305	0
Triaenodes	0	11	17	6	1	0	0	0	0	0	0	0	0	0	0	0
Archips	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lepidoptera	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0
Hydrochus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophilidae	0	0	6	0	0	0	0	0	0	0	0	0	2	0	0	0
Pontamalota	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Staphylinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psephenus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ectopria	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0
Helichus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prinocyphon	1	0	28	6	0	0	0	0	0	0	0	0	0	0	0	0
Oulimnius	0	0	0	0	9	11	0	0	4	19	0	0	2	11	23	0
Oulimnius (adult)	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0
Elmidae	0	0	0	0	8	6	0	0	1	151	0	75	16	23	0	0
Tipula	0	6	0	6	0	11	0	0	0	0	0	0	2	0	0	0
Antocha	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Dicranota	4	158	0	0	46	124	34	11	20	19	0	0	0	23	0	0
Hexatoma	9	57	11	6	3	11	11	11	8	38	57	28	7	11	23	34
Limnophila	0	102	0	0	5	6	17	6	4	0	34	28	0	11	0	79
Limonia	6	0	0	0	17	0	6	6	0	0	0	0	0	0	0	0
Ormosia	8	0	0	17	4	23	11	119	1	28	11	0	4	0	11	181
Pedicia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5c. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Psuedolimnophila	23	678	254	45	7	79	57	17	1	85	23	0	0	0	23	0
Tipulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae (pupae)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bezzia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Probezzia	45	96	11	11	6	124	11	90	0	9	34	9	5	45	181	11
Ceratopogon	123	322	209	23	23	107	23	0	0	160	11	9	1	0	0	0
Ceratopogonidae	23	0	96	6	0	0	136	0	0	0	0	0	0	192	0	0
Tanypodinae	63	1469	514	266	132	864	695	51	6	207	328	574	11	192	395	2147
Orthocladinae	458	5186	2706	723	155	1712	2367	339	72	1102	2418	1318	100	486	2000	3345
Chironomini	0	28	6	6	1	107	102	23	20	19	203	94	9	0	825	655
Tanytarsini	151	6977	6096	2655	217	4198	5972	2266	85	3569	2949	5245	185	1853	14655	3057 6
Chironomidae	1	226	181	316	0	181	57	226	5	151	452	311	0	181	542	1627
Chironomidae (pupae)	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0
Dixa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bittacomorpha	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
Prosimulium	22	0	0	0	40	130	0	0	42	9	0	0	63	23	0	11
Chelifera	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clinocera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Empididae	1	6	0	0	5	271	45	0	0	0	0	151	1	0	0	0
Chrysops	0	6	0	0	0	0	6	0	0	0	0	0	0	0	0	0
Merycomyia	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0
Tabanidae	3	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Mycetophilidae	8	11	0	6	9	17	0	0	1	0	0	0	0	0	0	0
Collembola	6	90	0	0	42	90	0	0	18	75	0	0	47	0	0	181
Cambarus	0	0	0	0	0	0	0	0	2	0	0	9	0	0	0	0
Isopoda	1	45	17	6	1	0	0	0	0	0	0	0	0	0	0	0
Gammarus	0	0	0	6	0	0	0	6	0	9	0	0	5	0	11	0
Oligochaeta	23	277	62	0	41	164	175	0	2	151	11	9	10	0	23	0
Nematoda	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0
Bivalvia	0	893	215	356	8	0	68	0	0	0	0	0	0	0	0	0
Ostrocoda	117	271	271	0	71	226	68	23	0	0	0	0	0	181	0	362
Copepoda	29	90	226	90	4	90	136	90	8	301	0	452	35	0	0	1627
Acari	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terrestrial	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salamander	0	0	0	0	0	0	6	0	2	9	23	19	1	0	11	11
Sculpin	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Mean total	1928	18458	12023	4774	2338	11791	11452	3847	1045	7863	7831	9492	1482	3898	20090	42350
# samples	10	10	10	10	10	10	10	10	10	10(6)	10(5)	10(6)	10	10(5)	10(5)	10(5)

Table 6a. Longitudinal and vertical relative abundance of taxa in spring; unshaded =0% of total, light grey=0-5% of total, dark grey=5-10% of total, black>10%of total

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Ameletus	░				░			░		░				░		
Baetis					░				░	░	░	░	░	░	░	
Diphetor									░	░	░		░	░	░	
Procleon					░				░				░			
Baetidae					░		░		▒	░	░	░	█	░	░	
Cinygmula	░			░	░				░	░			░	░	░	
Epeorus					░				░				░	░		
Heptagenia									░				░			
Leucrocuta					░					░			░	░		
Stenonema	░				░	░			░		░					
Heptageniidae					░		░	░	░	░	░	░	░	░	░	
Drunella									░				░	░		
Ephemerella					░	░	░		░	░			░	░		
Eurylophella	░	░	░	░	░	░	░		░				░			
Ephemerellidae					░	░			░	░	░	░		░		
Habrophlebia	░	░	░	░												
Habrophlebiodes	░	░			░				░	░		░	░	░	░	░
Paraleptophlebia	░	░	░	░	░	░	░	░	▒	░	▒	░	▒	▒	▒	▒
Leptophlebiidae	░	░	░	░	░				░							
Ephemera	░								░	░	░		░	░	░	░
Litobrancha																
Lanthus	░	░	░	░	░	░	░	░		░	░	░	░			░
Cordulegaster	░	░	░	░	░											
Pteronarcys					░				░	░	░		░	░		
Peltoperla	░	░	░	░	░	░		░	░	░		░		░		
Tallaperla									░					░		
Peltoperlidae														░		
Amphinemura	░	░	░		░	░		░	░	░		░	░	░	░	
Prostoia																
Soyedina																
Nemouridae	░	░	░	░	░	░				░		░			░	░
Leuctra	░	█	█	█	█	█	█	█	█	█	█	█	░	░	▒	▒
Allocapnia																
Paracapnia																
Capniidae	░															
Acroneuria									░	░	░	░	░	░	░	░
Remenus	░		░		░	░				░				░		
Isoperla	░	░			░	░			░	░			░	░		░
Perlodidae	░				░	░		░	░	░			░	░		
Alloperla															░	
Haploperla						░				░	░		░	░	░	
Suwallia									░	░	░		░	░		
Sweltsa	░	░	░	░	░	░		░	░	░	░	░	░	░		░
Chloroperlidae	░	░	░	░	░	░		░	░	░	░		░	░	░	░
Microvelia		░														
Hesperocorixa																
Sialis		░	░	░	░			░				░	░			░
Nigronia	░	░			░		░	░	░		░		░		░	
Dolophilodes					░				░	░	░	░	░	░	░	
Wormaldia	░	░	░		░	░			░					░		
Lype	░												░			
Polycentropus	░	░	░	░		░			░	░	░	░	░	░	░	░
Phylocentropus																
Diplectrona	░				░	░			░	░		░	░	░	░	
Hydropsyche									░				░	░		
Rhyacophila	░	░			░	░		░	░	░	░		░	░	░	
Rhyacophila (pupae)	░				░	░	░		░				░			
Glossosoma					░				░				░			
Agapetus					░				░				░			
Lepidostoma	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░
Hydatophylax																
Pycnopsyche	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	

Table 6a. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Limnophilidae														░		
Goera																
Neophylax	░				░				░			░	░	░		░
Triaenodes	░	░														
Archips																
Terristrial Lepidoptera		░														
Hydrochus		░														
Hydrophilidae	░															
Pontamalota																
Staphylinidae																
Psephenus													░			
Ectopria	░				░	░			░	░		░	░			
Helichus																
Prinocyphon																
Oulimnius	░				░	░			░	░		░	░	░		░
Oulimnius (adult)					░	░			░				░			
Elmidae		░			░				░							
Tipula	░				░									░		
Antocha																
Dicranota	░	░	░	░	░	░	░		░	░	░		░	░		
Hexatoma	░	░	░	░	░	░	░		░	░		░	░	░	░	
Limnophila	░	░	░		░	░	░		░	░	░	░			░	
Limonia	░	░	░		░	░	░	░	░	░	░					
Ormosia	░		░	░			░	░				░				
Pedicia	░	░														
Psuedolimnophila	░	░	░	░	░	░	░	░	░	░			░			
Tipulidae	░	░				░										
Tipulidae (pupae)	░	░	░		░											
Bezzia	░															
Probezzia	░	░	░	░	░	░		░			░		░	░		░
Ceratopogn	░	░			░											
Ceratopognidae	░	░			░	░	░			░	░	░		░	░	░
Tanypodinae	░	▒	▒	▒	▒	░	▒	▒	░	▒	░	▒	█	█	█	█
Orthocladinae	▒	█	█	▒	▒	█	▒	▒	▒	█	▒	▒	█	█	▒	░
Chironomini	░	░	░	░	░	░	░	░	▒	█	▒	█	░	█	█	█
Tanytarsini	█	█	█	█	░	█	█	█	█	█	█	█	░	█	█	█
Chironomidae	░	░	░		░	░	░	░		░	░	░	░	░	░	░
Chironomidae (pupae)	░	░	░	░	░	░	░	░	░	░	░	░	░	░	▒	░
Dixa	░	░			░	░	░		░				░	░		
Bittacomorpha																
Prosimulium													░			
Chelifera	░	░							░			░	░	░	░	
Clinocera	░												░	░		
Empididae					░	░				░			░	░		
Chrysops	░	░		░	░			░		░	░					
Merycomyia	░		░		░	░	░									
Tabanidae		░						░								
Mycetophlidae																
Collembola	░	░	░		█	█			█	░			░	▒	░	
Cambarus		░		░	░	░	░		░	░		░	░	░	░	░
Isopoda			░	░												
Gammarus		░	░							░			░	░	░	░
Oligochaeta	░	░	░	░	░	░			░	░	░		░	░	░	░
Nematoda	░	░		░			░				░				░	
Bivalvia	░	░	░	░	░				░				░		░	░
Ostrocoda	█	▒	▒	▒	░	░			░	░	░		░	░	░	░
Copepoda	░	▒	█	█	░	▒	▒	▒	░	░	█	▒	░	▒	█	█
Acari	░															
Terrestrial		░													░	
Salamander	░	░			░	░	░			░		░	░	░	░	
Sculpin																

Table 6b. Longitudinal and vertical relative abundance of taxa in fall; unshaded= 0% of total, light grey=0-5% of total, dark grey=5-10% of total, black>10% of total

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Ameletus																
Baetis									░				░			
Diphetor													░	░	░	
Procleon																
Baetidae									░				░		░	
Cinygmula									░							
Epeorus																
Heptagenia									░		░			░		
Leucrocuta													░		░	
Stenonema	░		░	░	░	░	░	░	░	░	░	░	░	░		
Heptageniidae					░	░	░	░	░	░	░	░	░	░		░
Drunnella																
Ephemerella															░	
Eurylophella	░	░		░	░	░	░	░	░	░	░	░	░	░	░	░
Ephemerellidae					░				░					░		
Habrophlebia	░	░	░			░	░									
Habrophlebiodes										░	░			░	░	░
Paraleptophlebia	░				░		░		▒	░	░	░	▒	░	░	░
Leptophlebiidae	░	░	░	░	░			░	░		░	░	░	░	░	
Ephemera									░	░	░	░	░	█	█	█
Litobrancha						░									░	░
Lanthus	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░	░
Cordulegaster	░	░	░		░			░							░	
Pteronarcys						░			░	░			░	░	░	
Peltoperla	░				░	░	░			░						
Tallaperla													░	░		
Peltoperlidae		░				░										
Amphinemura																
Prostoia																
Soyedina	░	░		░	░	░				░						
Nemouridae	░				░	░	░								░	
Leuctra	░	░	░	█	░	░	░	█	░	░	░	░	░	░	░	░
Allocapnia																
Paracapnia									░		░		▒	░		░
Capniidae			░		░	░			░	░	░	░	░	░		░
Acroneuria					░				░	░	░	░	░	░	░	
Remenus																
Isoperla	░				░	░							░			
Perlodidae	░	░	░		░	░			░	░	░	░	▒	░		
Alloperla																
Haploperla																
Suwallia																
Sweltsa	░	░			░	░	░	░	░	░	░	░	▒	░	░	░
Chloroperlidae	░		░	░	░	░	░		░	░	░		░	░	░	
Microvelia										░				░		
Hesperocorixa													░			
Sialis	░	░	░	░	░	░	░	░		░	░	░		░	░	░
Nigronia	░	░	░	░	░	░	░		░			░	░	░	░	
Dolophilodes						░							░			
Wormaldia	░	░	░	░												
Lype	░				░					░			░			
Polycentropus	░	░	░			░	░	░	░	░	▒	░	░	░	░	░
Phylocentropus	░															
Diplectrona	░	░			░	░	░	░	░	░			▒	░	░	
Hydropsyche													░			
Rhyacophila	░	░			░	░			░	░		░	░	░	░	
Rhyacophila (pupae)																
Glossosoma													░			
Agapetus																
Lepidostoma		░		░		░	░									
Hydatophylax																
Pycnopsyche																

Table 6b. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Limnophilidae	▨				▨				▨							
Goera					▨					▨	▨		▨			
Neophylax					▨											
Triaenodes	▨	▨	▨	▨			▨									
Archips	▨															
Terristrial Lepidoptera	▨		▨	▨					▨	▨				▨		
Hydrochus																
Hydrophilidae																
Pontamalota																
Staphylinidae														▨		
Psephenus													▨	▨		
Ectopria					▨				▨	▨			▨	▨		
Helichus													▨	▨		
Prinocyphon			▨	▨												
Oulimnius	▨				▨	▨			▨	▨	▨		▨	▨	▨	▨
Oulimnius (adult)					▨	▨			▨		▨		▨			
Elmidae					▨	▨			▨	▨	▨		■	■	▨	
Tipula	▨			▨		▨	▨			▨						
Antocha														▨		
Dicranota	▨	▨			▨	▨							▨			
Hexatoma	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Limnophila	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Limonia	▨	▨	▨	▨	▨	▨	▨		▨	▨			▨	▨		▨
Ormosia	▨	▨		▨	▨		▨	■		▨	▨	▨				
Pedicia																
Psuedolimnophila	▨	■	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Tipulidae		▨														
Tipulidae (pupae)	▨															
Bezzia						▨	▨									
Probezzia	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▩	▩	▨
Ceratopogn	■	▨	▨		▩	▩	▨	▨	▨	▨	▨	▨	▨	▨		▨
Ceratopognidae	▨	▨	▨	▨	▨	▩	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Tanypodinae	■	■	■	■	▩	■	▩	■	▨	▩	▩	■	▨	■	■	■
Orthocladinae	■	■	▨	■	■	■	■	■	▩	■	■	■	▨	■	▩	■
Chironomini	▨	▨	■	▨	▨	▨	■	▨	▩	▩	■	■	▨	▨	▨	■
Tanytarsini	▩	■	▨	■	■	■	■	■	■	■	■	■	▩	■	■	■
Chironomidae	▨	▨	■		▨	▨	▨	▩	▨	▩	▩	▩	▨	▨	▩	▩
Chironomidae (pupae)	▨	▨		▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨
Dixa	▨	▨			▨				▨	▨				▨		
Bittacomorpha																
Prosimulium																
Chelifera					▨											
Clinocera																
Empididae																
Chrysops	▨	▨	▨													
Merycomyia	▨															
Tabanidae	▨	▨			▨	▨	▨					▨		▨	▨	
Mycetophlidae																
Collembola	▨	▨	▨		▨				▨	▨			▨	▨		
Cambarus									▨				▨	▨		
Isopoda	▨	▨	▨	▨												
Gammarus													▨	▨		
Oligochaeta	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Nematoda										▨						
Bivalvia	▩	▨	▩	▨		▨		▨					▨			
Ostrocoda	▨	▨			▨	▨			▨	▨	▨					▨
Copepoda	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Acari				▨										▨		
Terrestrial		▨		▨												
Salamander					▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨
Sculpin													▨	▨		

Table 6c. Longitudinal and vertical relative abundance of taxa in winter; unshaded = 0% of total, light grey = 0-5% of total, dark grey = 5-10% of total, black > 10% of total

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Ameletus	░	░			░	░			░				░		░	
Baetis																
Diphetor					░								░		░	
Procleon																
Baetidae																
Cinygmula					░				░						░	
Epeorus					░				░	░			▒			
Heptagenia					░											
Leucrocuta																
Stenonema					░	░			░		░		░			
Heptageniidae					░	░			█	░			█	░		
Drunnella																
Ephemerella		░			░	░	░		░				░			
Eurylophella	░	░			░	░			░	░		░	░			░
Ephemerellidae	░				░			░	░	░			░	░		
Habrophlebia	░	░	░	░												
Habrophlebiodes																░
Paraleptophlebia	░	░	░	░	░	░	░	░	░	░	░	░	░		░	░
Leptophlebiidae	░	░	░		░	░	░							▒		░
Ephemera												░	░	░	░	░
Litobrancha																
Lanthus	░	░	░		░	░	░	░	░		░	░	░		░	░
Cordulegaster	░	░	░		░											
Pteronarcys									░	░			░			
Peltoperla	░		░		▒	░	░		░				░			
Tallaperla																
Peltoperlidae	░	░							▒				░	░	░	
Amphinemura	░				░				░							
Prostoia	░	░		░	░				░				░			
Sovedina		░				░							░	░		
Nemouridae	█	░		░	░	░		░	▒				█			
Leuctra	░	▒	░	░	█	▒	▒	▒	░	░	█	▒	░	▒	░	░
Allocapnia									░							
Paracapnia	░	░			░	░	░		░	░	░		░			
Capniidae	░									░						
Acroneuria									░	░	░	░	░		░	░
Remenus																
Isoperla		░			░	░			░	░			░		░	
Perlodidae	░				░	░		░	░	░			░	░	░	░
Alloperla																
Haploperla																
Suwallia																
Sweltsa	░	░	░	░	░	░	░		░	░	░	░	░	░	░	░
Chloroperlidae	░				░	░	░		░	▒	░		░			
Microvelia																
Hesperocorixa																
Sialis	░	░	░	░		░	░	░			░	░				░
Nigronia	░	░	░		░	░	░						░		░	
Dolophilodes													░			
Wormaldia	░	░			░	░	░		░			░	░		░	
Lype	░				░											
Polycentropus		░	░	░	░	░	░		░	░		░	░			░
Phylocentropus																
Diplectrona	░	░			░	░	░		░	░	░		░	░	░	░
Hydropsyche	░								░				░			
Rhyacophila	░	░			░	░	░		░	░	░	░	░		░	
Rhyacophila (pupae)																
Glossosoma					░								░			
Agapetus																
Lepidostoma													░			
Hydatophylax	░	░	░		░	░						░	░			
Pycnopsyche	░			░	░	░	░		░	░	░		░			

Table 6c. Continued.

Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Limnophilidae		▨														
Goera																
Neophylax	▨				▨		▨		▨	▨			▨		▨	
Triaenodes		▨	▨	▨	▨											
Archips																
Terristrial Lepidoptera						▨										
Hydrochus																
Hydrophilidae			▨										▨			
Pontamalota		▨														
Staphylinidae																
Psephenus																
Ectopria					▨								▨			
Helichus																
Prinocyphon	▨		▨	▨												
Oulimnius					▨	▨			▨	▨			▨	▨	▨	
Oulimnius (adult)						▨										
Elmidae					▨	▨			▨	▨		▨	▨	▨		
Tipula		▨		▨		▨							▨			
Antocha													▨			
Dicranota	▨	▨			▨	▨	▨	▨	▨	▨				▨		
Hexatoma	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Limnophila		▨			▨	▨	▨	▨	▨		▨	▨		▨		▨
Limonia	▨				▨		▨	▨								
Ormosia	▨			▨	▨	▨	▨	▨	▨	▨	▨		▨		▨	▨
Pedicia																
Psuedolimnophila	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨				▨	
Tipulidae																
Tipulidae (pupae)																
Bezzia																
Probezzia	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨
Ceratopogn	▨	▨	▨	▨	▨	▨	▨			▨	▨	▨	▨			
Ceratopognidae	▨		▨	▨			▨							▨		
Tanypodinae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Orthocladinae	■	■	■	■	▨	■	■	▨	▨	■	■	▨	▨	■	▨	▨
Chironomini		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨
Tanytarsini	▨	■	■	■	▨	■	■	■	▨	■	■	■	■	■	■	■
Chironomidae	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨		▨	▨	▨
Chironomidae (pupae)						▨										
Dixa																
Bittacomorpha			▨													
Prosimulium	▨				▨	▨			▨	▨			▨	▨		▨
Chelifera		▨														
Clinocera																
Empididae	▨	▨			▨	▨	▨				▨	▨	▨			
Chrysops		▨					▨									
Merycomyia						▨										
Tabanidae	▨							▨								
Mycetophilidae	▨	▨		▨	▨	▨			▨							
Collembola	▨	▨			▨	▨			▨	▨			▨			▨
Cambarus									▨			▨				
Isopoda	▨	▨	▨	▨	▨											
Gammarus				▨				▨		▨			▨		▨	
Oligochaeta	▨	▨	▨		▨	▨	▨		▨	▨	▨	▨	▨		▨	
Nematoda					▨											
Bivalvia		▨	▨	▨	▨		▨									
Ostrocoda	▨	▨	▨		▨	▨	▨	▨						▨		▨
Copepoda	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨			▨
Acari																
Terrestrial																
Salamander							▨		▨	▨	▨	▨	▨		▨	▨
Sculpin													▨			

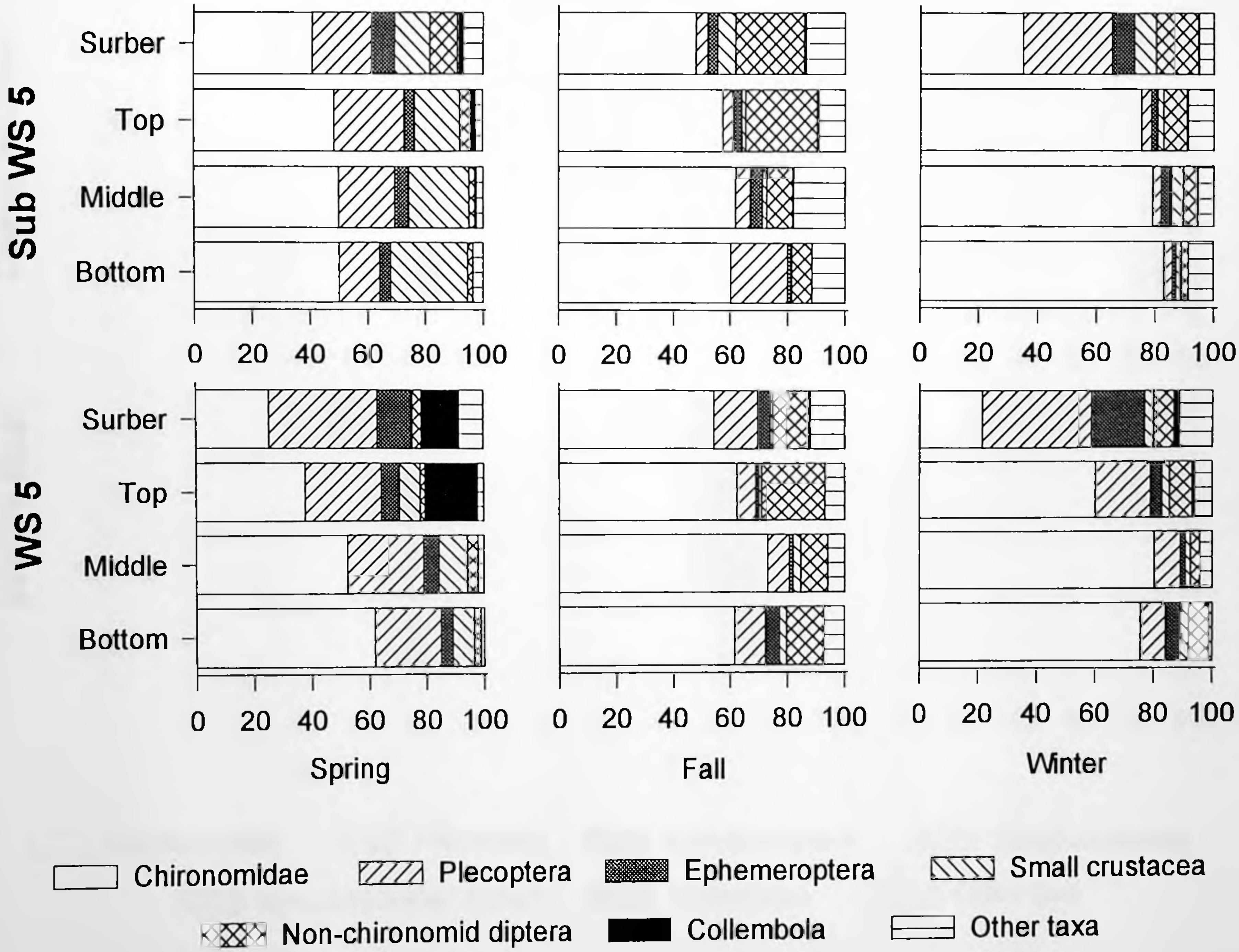
Table 7. Occurrence of taxa vertically and longitudinally across all seasons; unshaded =not present, grey=present

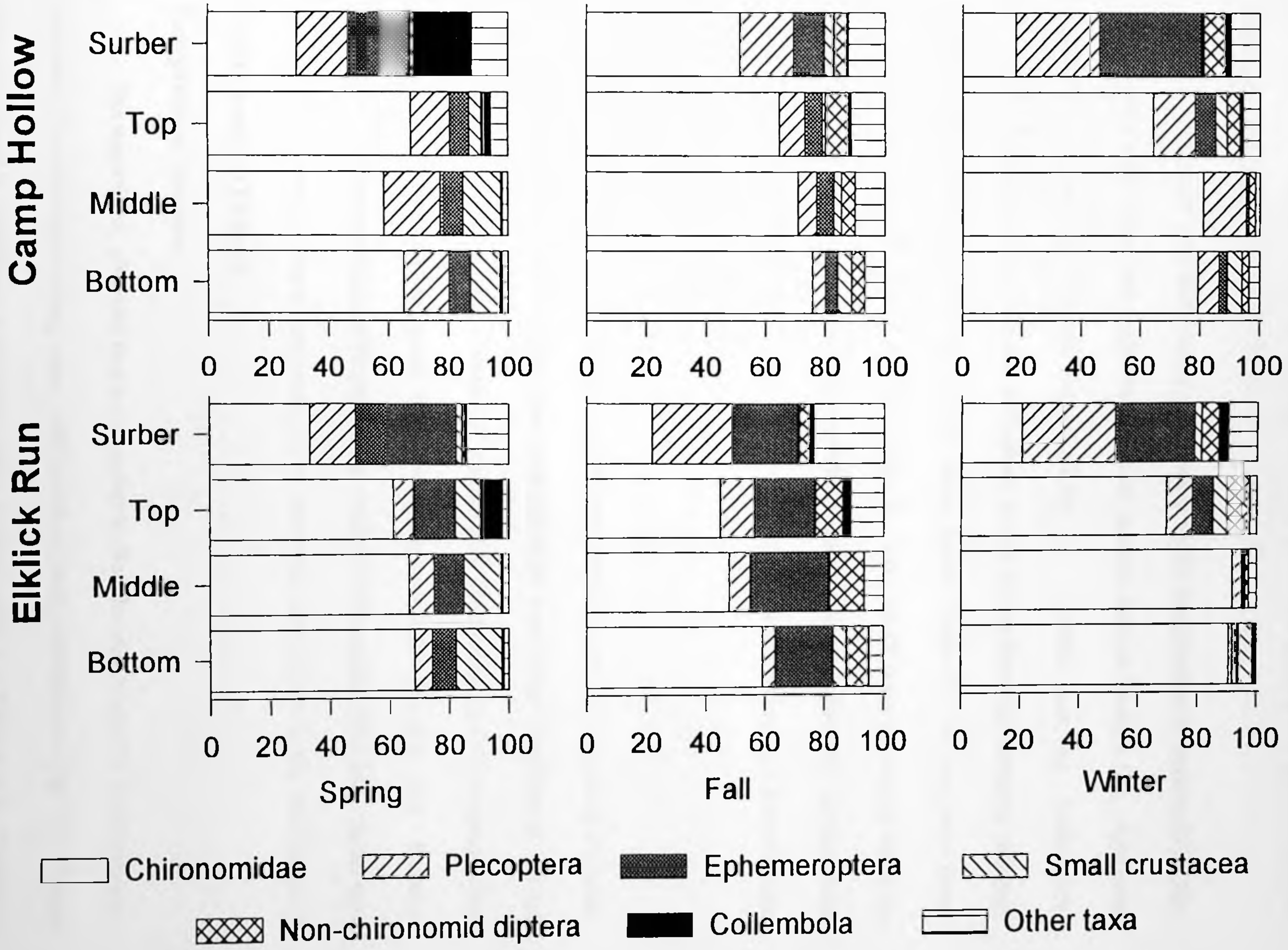
Seasons	All Seasons															
Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Ameletus	▨	▨			▨			▨	▨	▨			▨	▨	▨	
Baetis					▨				▨	▨	▨	▨	▨	▨	▨	
Diphetor					▨				▨	▨	▨		▨	▨	▨	
Procleon					▨				▨				▨			
Baetidae					▨		▨		▨	▨	▨	▨	▨	▨	▨	
Cinygmula	▨			▨	▨				▨	▨			▨	▨	▨	
Epeorus					▨				▨	▨			▨	▨		
Heptagenia					▨				▨		▨		▨	▨		
Leucrocuta					▨					▨			▨	▨	▨	
Stenonema	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		
Heptageniidae					▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	
Drunella									▨				▨	▨		
Ephemerella		▨			▨	▨	▨		▨	▨			▨	▨	▨	
Eurylophella	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Ephemerellidae					▨	▨			▨	▨	▨	▨		▨		
Habrophlebia	▨	▨	▨	▨		▨	▨									
Habrophlebiodes	▨	▨			▨				▨	▨	▨	▨	▨	▨	▨	▨
Paraleptophlebia	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Leptophlebiidae	▨	▨	▨	▨	▨	▨	▨	▨	▨							
Ephemera	▨								▨	▨	▨	▨	▨	▨	▨	▨
Litobrancha						▨										
Lanthus	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Cordulegaster	▨	▨	▨	▨	▨			▨							▨	
Pteronarcys					▨	▨			▨	▨	▨		▨	▨	▨	
Peltoperla	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨		
Tallaperla									▨				▨	▨		
Peltoperlidae	▨	▨				▨			▨				▨	▨	▨	
Amphinemura	▨	▨	▨		▨	▨		▨	▨	▨		▨	▨	▨	▨	
Prostoia	▨	▨		▨	▨				▨				▨			
Soyedina	▨	▨		▨	▨	▨	▨			▨			▨	▨		
Nemouridae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨		▨	▨
Leuctra	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Allocapnia									▨							
Paracapnia	▨	▨			▨	▨	▨		▨	▨	▨		▨	▨		▨
Capniidae	▨		▨		▨	▨			▨	▨	▨	▨	▨	▨		▨
Acroneuria					▨				▨	▨	▨	▨	▨	▨	▨	▨
Remenus	▨		▨		▨	▨				▨				▨		
Isoperla	▨	▨			▨	▨			▨	▨			▨	▨	▨	▨
Perlodidae	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨
Alloperla															▨	
Haploperla						▨				▨	▨		▨	▨	▨	
Suwallia									▨	▨	▨		▨	▨		
Sweltsa	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Chloroperlidae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨
Microvelia		▨								▨				▨		
Hesperocorixa													▨			
Sialis	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨
Nigronia	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨		▨	▨	▨	
Dolophilodes					▨				▨	▨	▨	▨	▨	▨	▨	
Wormaldia	▨	▨	▨	▨	▨	▨	▨		▨			▨	▨	▨		▨
Lype	▨				▨	▨				▨			▨			
Polycentropus	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨
Phylocentropus	▨															
Diplectrona	▨	▨			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Hydropsyche	▨								▨				▨	▨		
Rhyacophila	▨	▨			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
Rhyacophila (pupae)	▨				▨	▨	▨		▨				▨			
Glossosoma					▨				▨				▨			
Agapetus					▨				▨				▨			
Lepidostoma	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Hydatophylax	▨	▨	▨		▨	▨						▨	▨			

Table 7. Continued.

Seasons	All Seasons															
Site	Subwatershed 5				Watershed 5				Camp Hollow				Elklick Run			
Level	S	T	M	B	S	T	M	B	S	T	M	B	S	T	M	B
Pycnopsyche	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
Limnophilidae	▨	▨							▨					▨		
Goera					▨					▨	▨		▨			
Neophylax	▨				▨		▨		▨	▨		▨	▨	▨	▨	▨
Triaenodes	▨	▨	▨	▨	▨		▨									
Archips	▨															
Terristrial Lepidoptera	▨	▨		▨	▨	▨			▨	▨				▨		
Hydrochus		▨														
Hydrophilidae	▨		▨										▨			
Pontamalota		▨														
Staphylinidae														▨		
Psephenus													▨	▨		
Ectopria	▨				▨	▨			▨	▨		▨	▨	▨		
Helichus													▨	▨		
Prinocyphon	▨		▨	▨												
Oulimnius	▨				▨	▨			▨	▨	▨	▨	▨	▨	▨	▨
Oulimnius (adult)					▨	▨			▨		▨		▨			
Elmidae		▨			▨	▨			▨	▨		▨	▨	▨	▨	
Tipula	▨	▨		▨	▨	▨	▨			▨			▨	▨		
Antocha													▨	▨		
Dicranota	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨		
Hexatoma	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Limnophila	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Limonia	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨		▨	▨		▨
Ormosia	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨
Pedicia	▨	▨														
Psuedolimnophila	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Tipulidae	▨	▨				▨										
Tipulidae (pupae)	▨	▨	▨		▨											
Bezzia	▨				▨	▨										
Probezzia	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Ceratopogn	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨
Ceratopognidae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Tanypodinae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Orthocladinae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Chironomini	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Tanytarsini	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Chironomidae	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Chironomidae (pupae)	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Dixa	▨	▨			▨	▨	▨		▨	▨			▨	▨		
Bittacomorpha			▨													
Prosimulium	▨				▨	▨			▨	▨			▨	▨		▨
Chelifera	▨	▨			▨				▨			▨	▨	▨	▨	
Clinocera	▨												▨	▨		
Empididae	▨	▨			▨	▨	▨			▨	▨	▨	▨	▨		
Chrysops	▨	▨		▨	▨		▨	▨		▨	▨					
Merycomyia	▨		▨		▨	▨	▨									
Tabanidae	▨	▨						▨								
Mycetophlidae	▨	▨		▨	▨	▨			▨							
Collembola	▨	▨	▨		▨	▨			▨	▨			▨	▨	▨	▨
Cambarus		▨		▨	▨	▨	▨		▨	▨		▨	▨	▨	▨	▨
Isopoda	▨	▨	▨	▨												
Gammarus		▨	▨	▨				▨		▨			▨	▨	▨	▨
Oligochaeta	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Nematoda	▨	▨		▨	▨		▨			▨	▨				▨	
Bivalvia	▨	▨	▨	▨	▨		▨	▨	▨				▨		▨	▨
Ostrocoda	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨
Copepoda	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Acari	▨			▨										▨		
Terrestrial		▨		▨											▨	
Salamander	▨	▨		▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨
Sculpin													▨	▨		

Figure 20. Relative abundance of Chironomidae, Plecoptera, Ephemeroptera, small crustacea (Copepoda and Ostrocoda), Non-chironomid diptera, Collembola, and other taxa at all levels, sites, and season.


Sub WS 5
Surber
Top
Middle
Bottom
WS 5
Surber
Top
Middle
Bottom
0
20
40
60
80
100
Spring
Fall
Winter
Chironomidae
Plecoptera
Ephemeroptera
Small crustacea
Non-chironomid diptera
Collembola
Other taxa


Camp Hollow
Elklick Run
Surber
Top
Middle
Bottom
0
20
40
60
80
100
Spring
Fall
Winter
Chironomidae
Plecoptera
Ephemeroptera
Small crustacea
Non-chironomid diptera
Collembola
Other taxa

in relative abundance with depth except for small Crustacea (Copepods and Ostrocods) (Table 8, Fig. 20).

Taxa groups were more evenly distributed in Surber samples than in baskets (Fig. 20). There were also more taxa exclusive to Surber samples than to baskets (eg., *Agapetus*, *Glossoma*), across all sites and seasons (Table 7). Certain taxa (eg., Collembola, Heptageniidae) were most abundant at (Surber) or near the surface (top baskets), although small numbers of these taxa were found in lower depths (Table 7). No taxa were found exclusivly in middle or bottom baskets (Table 7). Taxa which were present at all levels throughout the study include: *Paraleptophlebia*, *Lanthus*, *Leuctra*, *Sweltsa*, *Lepidostoma*, *Hexatoma*, *Limnophila*, *Pseudolimnophila*, *Probezzia*, Ceratopogonidae, all Chironomidae, Oligochaeta, and Copepods (Table 7).

Seasonal Patterns

Tanytarsini was the most abundant taxon across seasons and also was most abundant in winter (Fig. 21). Diptera other than Chironomidae were most abundant in the fall including; *Pseudolimnophila*, *Ormosia*, *Ceratopogon*, *Probezzia*, and Ceratopogonidae (Table 6b). Tanypodinae increased in relative abundance in the fall (Fig. 21). Relative abundance of Ephemeroptera and Plecoptera were highest in the spring (Fig. 20). Some taxa may have been absent in one or more seasons, or were only identified to family level because of early instars. (Table 5).

Longitudinal patterns

The majority of abundant taxa were present at all of the sites (Table 7). Chironomidae dominated in abundance among sites, with variation among subfamilies (Fig. 21). Some groups increased in abundance downstream from Subwatershed 5 to Elklick (e.g., Baetidae,

Table 8a. Most abundant taxa in spring samples for all sites and levels. Values are the percent of total density.

Surber	%	Top basket	%	Middle basket	%	Bottom basket	%
				Sub-watershed 5			
Tanytarsini	26	Tanytarsini	29	Tanytarsini	27	Tanytarsini	35
Ostrocoda	11	*Leuctra*	17	*Leuctra*	18	Copepoda	17
Orthocladinae	10	Orthocladinae	10	Copepoda	15	*Leuctra*	13
Leuctra	8	Ostrocoda	9	Orthocladinae	14	Ostrocoda	10
Nemouridae	6	Tanypodinae	7	Tanypodinae	7	Tanypodinae	8
Peltoperla	4	Nemouridae	7	Ostrocoda	6	Orthocladinae	7
Cumulative %	65		79		87		90
				Watershed 5			
Leuctra	30	*Leuctra*	21	Tanytarsini	29	Tanytarsini	42
Collembola	13	Collembola	18	*Leuctra*	26	*Leuctra*	21
Orthocladinae	10	Tanytarsini	16	Copepoda	10	Tanypodinae	9
Tanytarsini	9	Orthocladinae	12	Tanypodinae	10	Copepoda	7
Tanypodinae	5	Copepoda	7	Orthocladinae	6	Orthocladinae	6
Paraleptophlebia	4	Tanypodinae	5	*Paraleptophlebia*	4	*Paraleptophlebia*	4
Cumulative %	71		79		85		89
				Camp Hollow Run			
Collembola	19	Tanytarsini	22	Tanytarsini	33	Tanytarsini	37
Leuctra	11	Orthocladinae	18	*Leuctra*	17	*Leuctra*	14
Tanytarsini	10	Chironomini	16	Copepoda	13	Chironomini	10
Baetidae	9	*Leuctra*	11	Chironomini	9	Copepoda	10
Chironomini	7	Tanypodinae	7	Orthocladinae	7	Tanypodinae	7
Paraleptophlebia	6	Dolophilodes	4	*Paraleptophlebia*	6	Orthocladinae	6
Cumulative %	62		78		85		84
				Elklick Run			
Baetidae	21	Chironomini	19	Chironomini	26	Chironomini	28
Orthocladinae	13	Orthocladinae	13	Tanytarsini	16	Tanytarsini	19
Tanypodinae	10	Tanytarsini	13	Copepoda	12	Copepoda	14
Paraleptophlebia	9	Tanypodinae	12	Tanypodinae	10	Tanypodinae	11
Chloroperlidae	7	*Paraleptophlebia*	10	*Paraleptophlebia*	9	*Paraleptophlebia*	7
Tanytarsini	6	Copepoda	8	Orthocladinae	8	*Leuctra*	6
Cumulative %	66		75		81		85

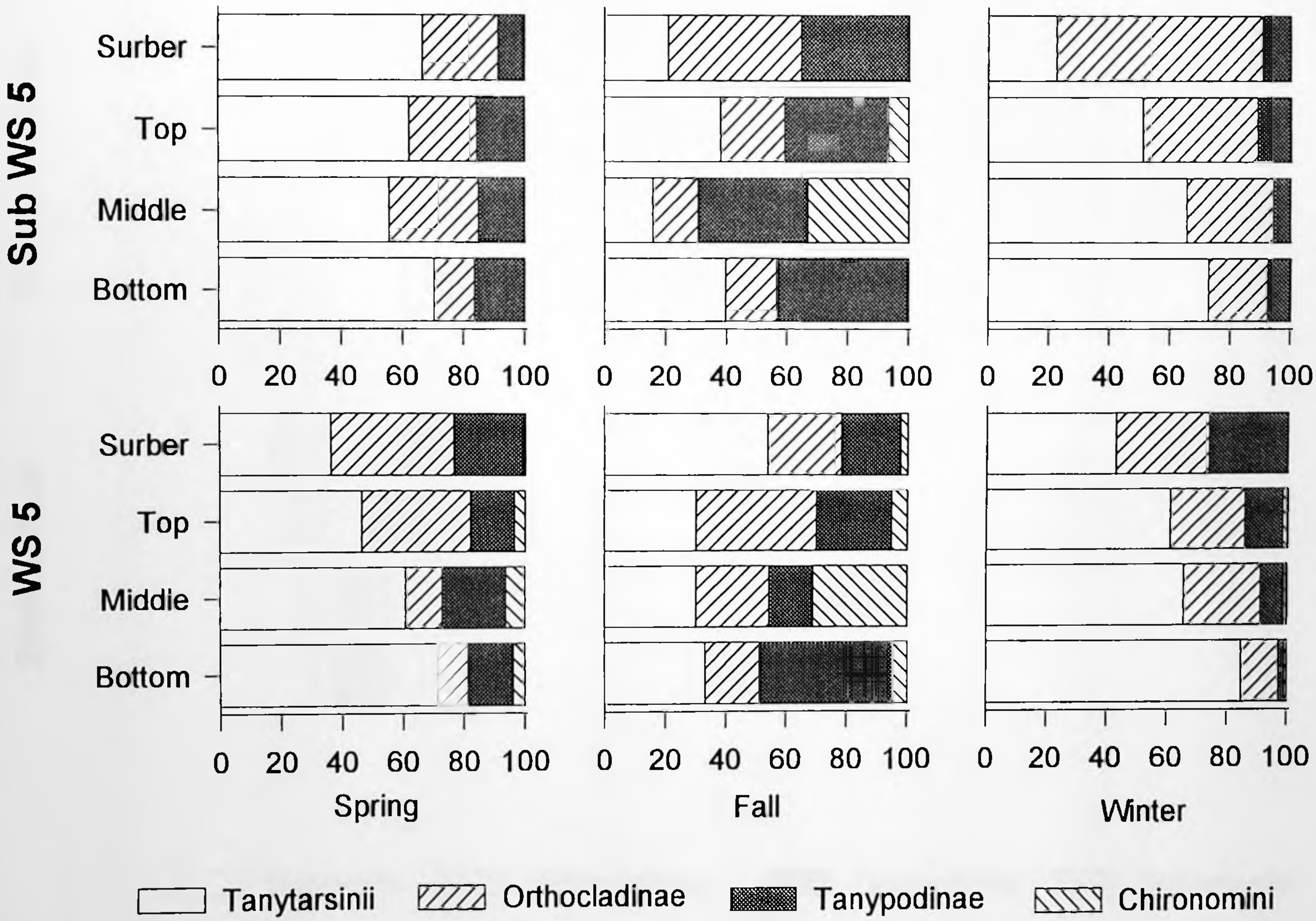
Table 8b. Most abundant taxa in fall samples for all sites and levels. Values are the percent of total density.

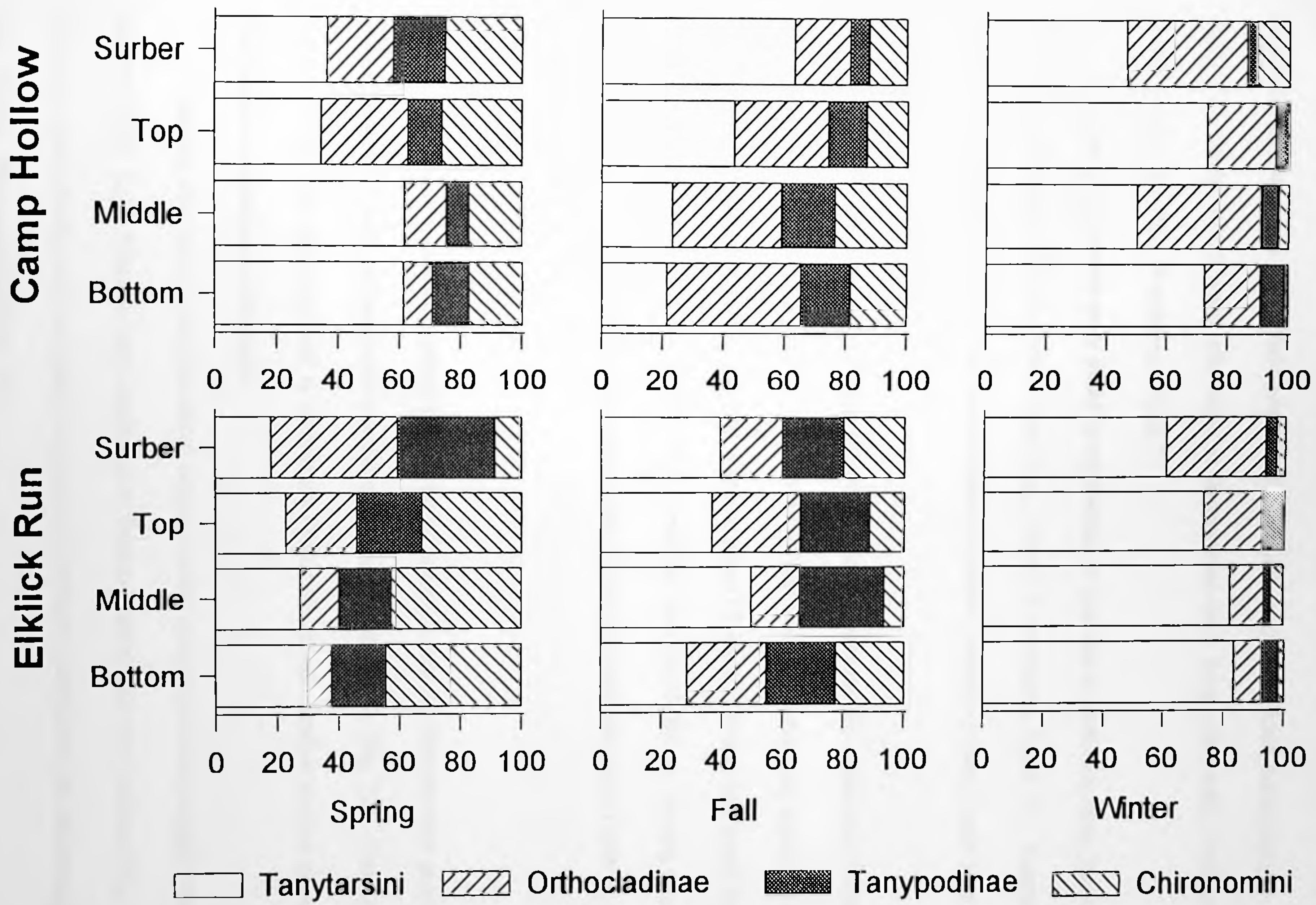
Surber	%	Top basket	%	Middle basket	%	Bottom basket	%
			Sub-watershed 5				
Orthocladinae	21	Tanytarsini	21	Tanypodinae	18	Tanypodinae	26
Tanypodinae	17	Tanypodinae	18	Chironomini	16	Tanytarsini	24
Ceratopogon	10	Orthocladinae	12	Chironomidae	13	*Leuctra*	15
Tanytarsini	10	*Pseudolimnophila*	10	Bivalve	9	Orthocladinae	10
Bivalve	7	*Ceratopogon*	6	Tanytarsini	8	Acari	5
Pseudolimnophila	5	*Lanthus*	5	Orthocladinae	7	Chloroperlidae	5
Cumulative %	70		72		71		85
			Watershed 5				
Tanytarsini	27	Orthocladinae	23	Chironomini	21	Tanypodinae	25
Orthocladinae	12	Tanytarsini	17	Tanytarsini	21	Tanytarsini	19
Tanypodinae	10	Tanypodinae	15	Orthocladinae	17	*Leuctra*	11
Leuctra	7	Ceratopogonidae	10	Tanypodinae	10	Orthocladinae	10
Ceratopogon	6	Chironomini	3	Chironomidae	5	Chironomidae	5
Oulimnius	4	Chironomidae	3	Chloroperlidae	4	*Ormosia*	5
Cumulative %	66		71		78		75
			Camp Hollow Run				
Tanytarsini	31	Tanytarsini	25	Orthocladinae	23	Orthocladinae	30
Orthocladinae	9	Orthocladinae	17	Chironomini	15	Tanytarsini	15
Chironomini	6	Chironomini	8	Tanytarsini	15	Chironomini	13
Paraleptohlebia	6	Tanypodinae	7	Tanypodinae	11	Tanypodinae	11
Leuctra	5	Chironomidae	6	*Polycentropus*	7	Chironomidae	8
Capniidae	5	*Polycentropus*	4	Chironomidae	6	Copepoda	5
Cumulative %	62		67		77		82
			Elklick Run				
Elmidae	11	Tanytarsini	15	Tanytarsini	19	Tanytarsini	14
Paraleptohlebia	9	Orthocladinae	11	*Ephemera*	19	Orthocladinae	13
Tanytarsini	8	*Ephemera*	10	Tanypodinae	11	*Ephemera*	13
Perlodidae	7	Tanypodinae	9	*Probezzia*	8	Tanypodinae	11
Diplectrona	5	Elmidae	8	Chironomidae	6	Chironomini	11
Paracapnia	5	*Probezzia*	5	Orthocladinae	6	Chironomidae	8
Cumulative %	45		58		69		70

Table 8c. Most abundant taxa in winter samples for all sites and levels. Values are the percent of total density.

Surber	%	Top basket	%	Middle basket	%	Bottom basket	%
				Sub-watershed 5			
Orthocladinae	24	Tanytarsini	38	Tanytarsini	51	Tanytarsini	56
Nemouridae	16	Orthocladinae	28	Orthocladinae	23	Orthocladinae	15
Tanytarsini	8	Tanypodinae	8	Tanypodinae	4	Bivalve	7
Leuctra	7	Bivalve	5	*Habrophlebia*	3	Chironomidae	7
Ceratopogon	6	*Pseudolimnophila*	4	Ostrocoda	2	Tanypodinae	6
Ostrocoda	6	*Leuctra*	2	*Pseudolimnophila*	2	*Leuctra*	3
Cumulative %	67		85		85		94
				Watershed 5			
Leuctra	17	Tanytarsini	36	Tanytarsini	52	Tanytarsini	59
Tanytarsini	9	Orthocladinae	15	Orthocladinae	21	Orthocladinae	9
Orthocladinae	7	*Leuctra*	9	*Leuctra*	7	*Leuctra*	6
Tanypodinae	6	Tanypodinae	7	Tanypodinae	6	Chironomidae	6
Peltoperla	6	Chloroperlidae	4	Oligochaeta	2	*Ormosia*	3
Ameletus	5	Nemouridae	3	*Paraleptophlebia*	1	*Paraleptophlebia*	3
Cumulative %	50		74		89		86
				Camp Hollow Run			
Heptageniidae	27	Tanytarsini	45	Tanytarsini	38	Tanytarsini	55
Nemouridae	8	Orthocladinae	14	Orthocladinae	31	Orthocladinae	14
Tanytarsini	8	Chloroperlidae	9	*Leuctra*	13	*Leuctra*	7
Orthocladinae	7	Copepoda	4	Chironomidae	6	Tanypodinae	6
Peltoperlidae	6	Heptageniidae	3	Tanypodinae	4	Copepoda	5
Leuctra	4	*Leuctra*	3	Chironomini	3	Chironomidae	3
Cumulative %	60		78		95		90
				Elklick Run			
Heptageniidae	17	Tanytarsini	48	Tanytarsini	73	Tanytarsini	72
Nemouridae	13	Orthocladinae	12	Orthocladinae	10	Orthocladinae	8
Tanytarsini	13	Ceratopogonidae	6	Chironomini	4	Tanypodinae	5
Orthocladinae	7	*Leuctra*	6	Chironomidae	3	Copepoda	4
Paraleptophlebia	5	Leptophlebidae	5	Tanypodinae	2	Chironomidae	4
Prosimulium	4	Tanypodinae	5	*Leuctra*	2	Chironomini	2
Cumulative %	59		82		94		95

Figure 21. Relative abundance within Chironomidae including Tanytarsini, Orthocladinae, Tanypodinae, and Chironomini at all levels, sites, and seasons.


Sub WS 5
WS 5
Surber
Top
Middle
Bottom
0
20
40
60
80
100
Spring
Fall
Winter
Tanytarsinii
Orthocladinae
Tanypodinae
Chironomini


Camp Hollow
Elklick Run
Surber
Top
Middle
Bottom
0
20
40
60
80
100
Spring
Fall
Winter
Tanytarsini
Orthocladinae
Tanypodinae
Chironomini

Heptageniidae, *Habrophlebiodes*, *Ephemera*, *Polycentropus*) (Table 7). Some taxa were only found at upstream sites (e.g., *Habrophlebia*, *Triaenodes*, some Tipulidae, *Merycomyia*, and Isopoda), while others were only found at downstream sites (e.g., *Drunella*, *Tallaperla*, *Acroneuria*, *Suwallia*, *Psephenus*, Table 7).

Some groups were only found in top baskets or Surbers at upstream sites, but were found at all depths at downstream sites (e.g., *Baetis*, *Leucrocuta*, Table 7). Copepods increased in abundance downstream and increased in relative abundance with depth (Fig. 20, Table 8).

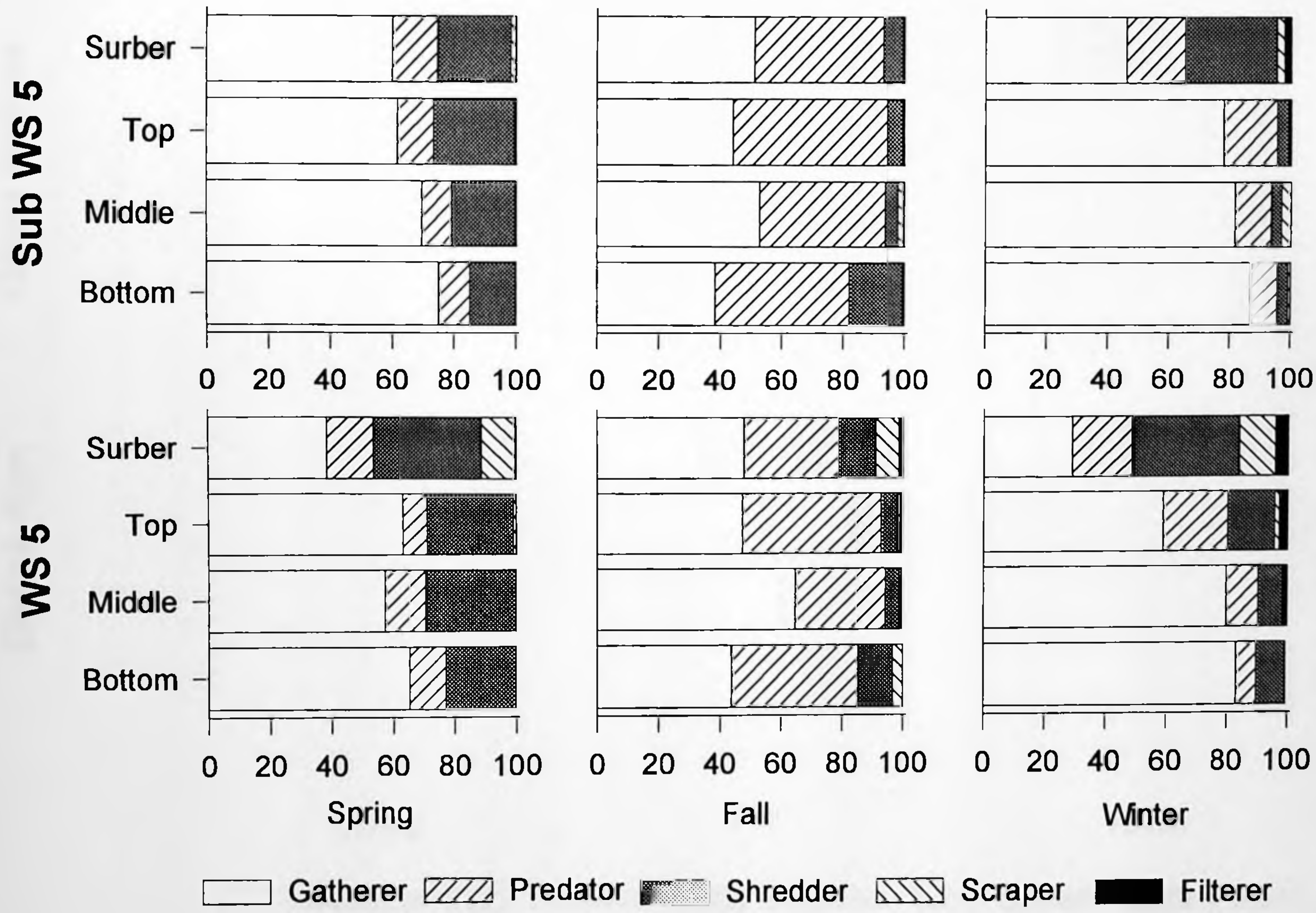
The distribution of taxa among sites varied among seasons for some taxa (Table 5, Table 7). For example, certain Heptageniidae and Baetidae were not present at upstream sites in the fall, but were present in spring and winter samples (Table 5). Some taxa were absent at all four sites during one season or more (e.g., *Drunella*, *Suwallia*,Table 5). Spring samples had a high abundance of Tanytarsini upstream and Chronomini downstream (Table 5a).

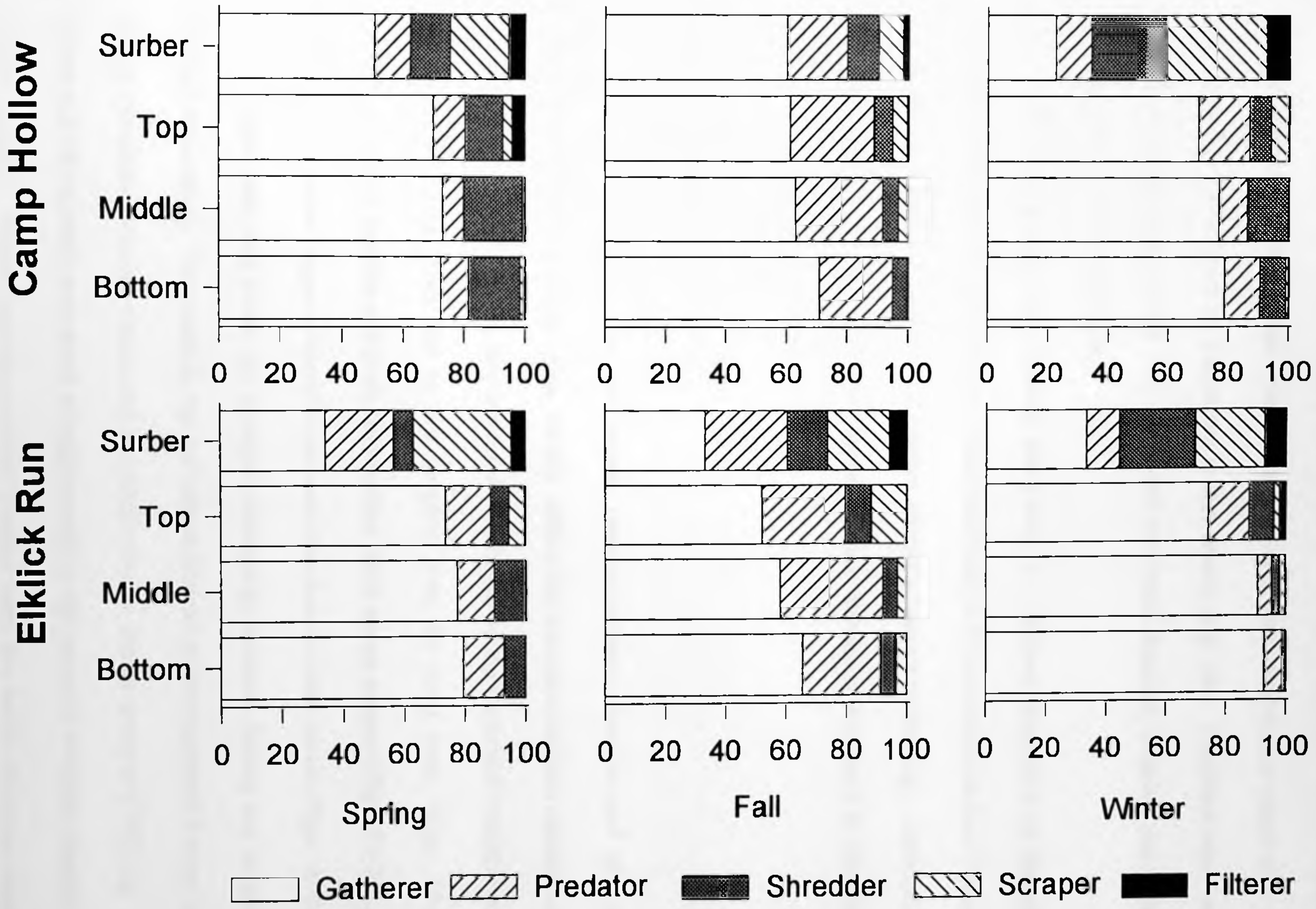
Functional feeding groups

Relative abundance of feeding groups varied among levels. Gatherers were generally most abundant overall and increased in relative abundance with depth (Fig. 22). Tanytarsini was the main taxa that increased in abundance (Table 8). Other feeding groups generally decreased in abundance with depth.

Density was more evenly distributed among feeding groups in Surber samples than in baskets (Fig. 22). Filterers were restricted to Surber samples and top baskets (Fig. 22). Scrapers were present in lower baskets suggesting facultative detritivory for some scrapers (eg., *Baetis*, Heptageniidae)(Fig. 22).

Figure 22. Functional feeding group relative abundance including, gatherers, predators, shredders, scrapers, and filterers at all levels, sites, and seasons. Functional group assignments given in Appendix I.


Sub WS 5
WS 5
Surber
Top
Middle
Bottom
0
20
40
60
80
100
Spring
Fall
Winter
Gatherer
Predator
Shredder
Scraper
Filterer


Camp Hollow
Elklick Run
Surber
Top
Middle
Bottom
0
20
40
60
80
100
Spring
Fall
Winter
Gatherer
Predator
Shredder
Scraper
Filterer

Abundance of various feeding groups varied seasonally. Gatherers were consistently more abundant than other groups across seasons but were most abundant in winter (Fig. 22) due to a high abundance of Tanytarsini in that season (Fig. 20). Predators were most abundant in fall (Table 5, Fig. 22). Shredders were most abundant in spring due to high abundance of *Leuctra* (Table 8).

Feeding groups varied among sites (Table 5). Highest abundance of shredders including *Leuctra*, *Peltoperla*, and Nemouridae was found in the upstream reaches (Table 8). Filterers and scrapers increased in relative abundance downstream (eg., *Diplectrona*, *Prosimulium*) (Table 5). Within the hyporheic zone, shredders decreased in abundance downstream and with depth (Fig. 22).

Underlying factors

In general, across sites and seasons, macroinvertebrate densities and interstitial velocities decreased with depth (Figs. 23-26). Elklick Run macroinvertebrate densities were the exception in winter when they increased with depth, but no interstitial velocities were measured for comparison due to lost samplers from the flood event (Figs. 25-26). Macroinvertebrate densities and interstitial velocities varied among seasons (Figs. 23-26). Top baskets had broader ranges of densities and velocities than did other levels (Figs. 23-26).

Some sites and levels had stronger relationships between density and interstitial velocity than others. For example, top and bottom baskets at Subwatershed 5 there was a strong correlation between density and interstitial velocity during spring and fall (Fig. 23). Spring and fall velocities were more strongly correlated with macroinvertebrate density than winter samples. Winter macroinvertebrate densities were low while velocities remained

Figure 23. Plots of macroinvertebrate densities and interstitial velocities from calibration model (cm/s) at Subwatershed 5, in top, middle, and bottom baskets.

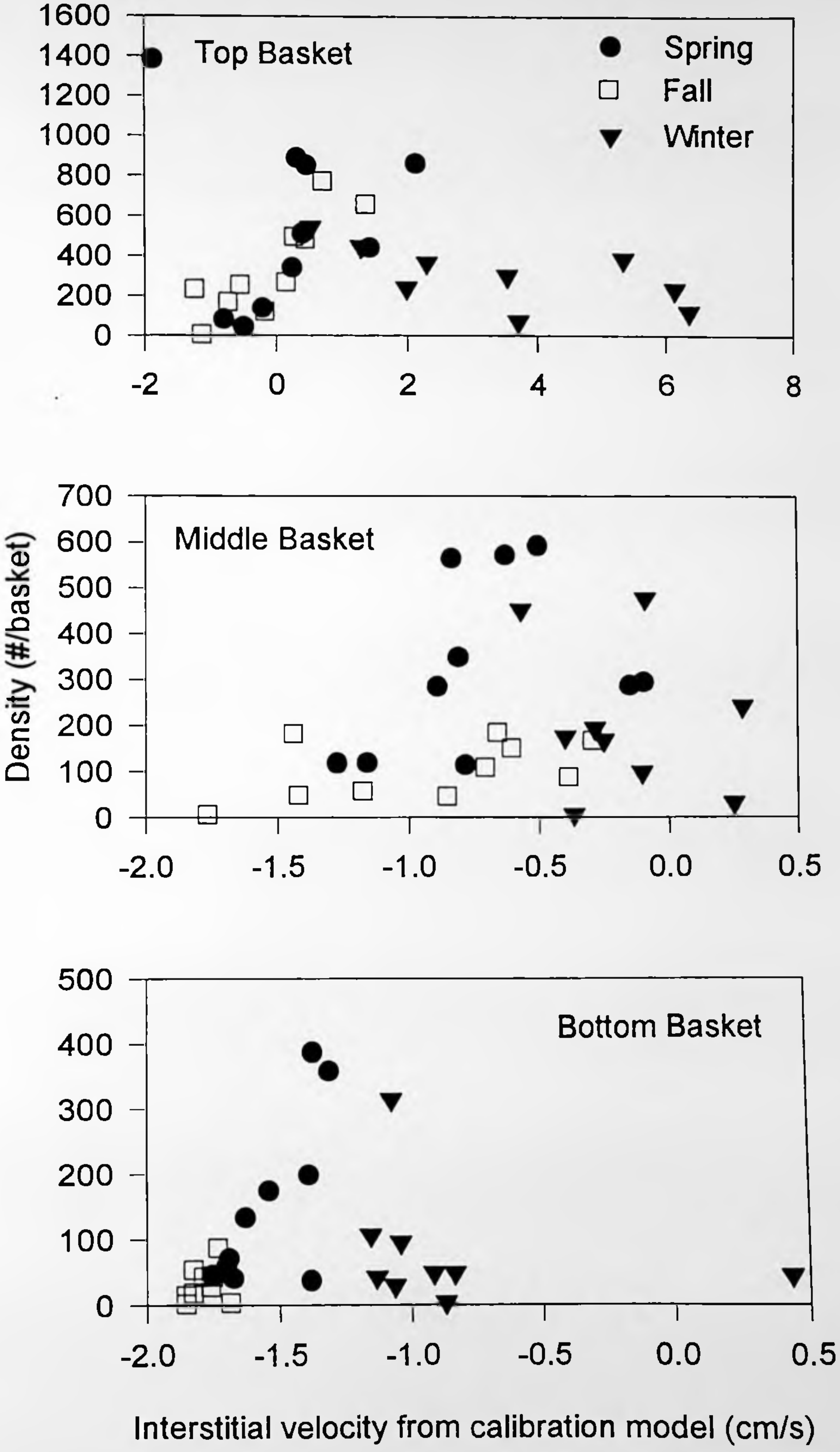

Top Basket
● Spring
□ Fall
▼ Winter
1600
1400
1200
1000
800
600
400
200
0
-2
0
2
4
6
8
Middle Basket
700
600
500
400
300
200
100
0
-2.0
-1.5
-1.0
-0.5
0.0
0.5
Density (#/basket)
Bottom Basket
500
400
300
200
100
0
-2.0
-1.5
-1.0
-0.5
0.0
0.5
Interstitial velocity from calibration model (cm/s)

Figure 24. Plots of macroinvertebrate densities and interstitial velocities from calibration model (cm/s) at Watershed 5, in top, middle, and bottom baskets.

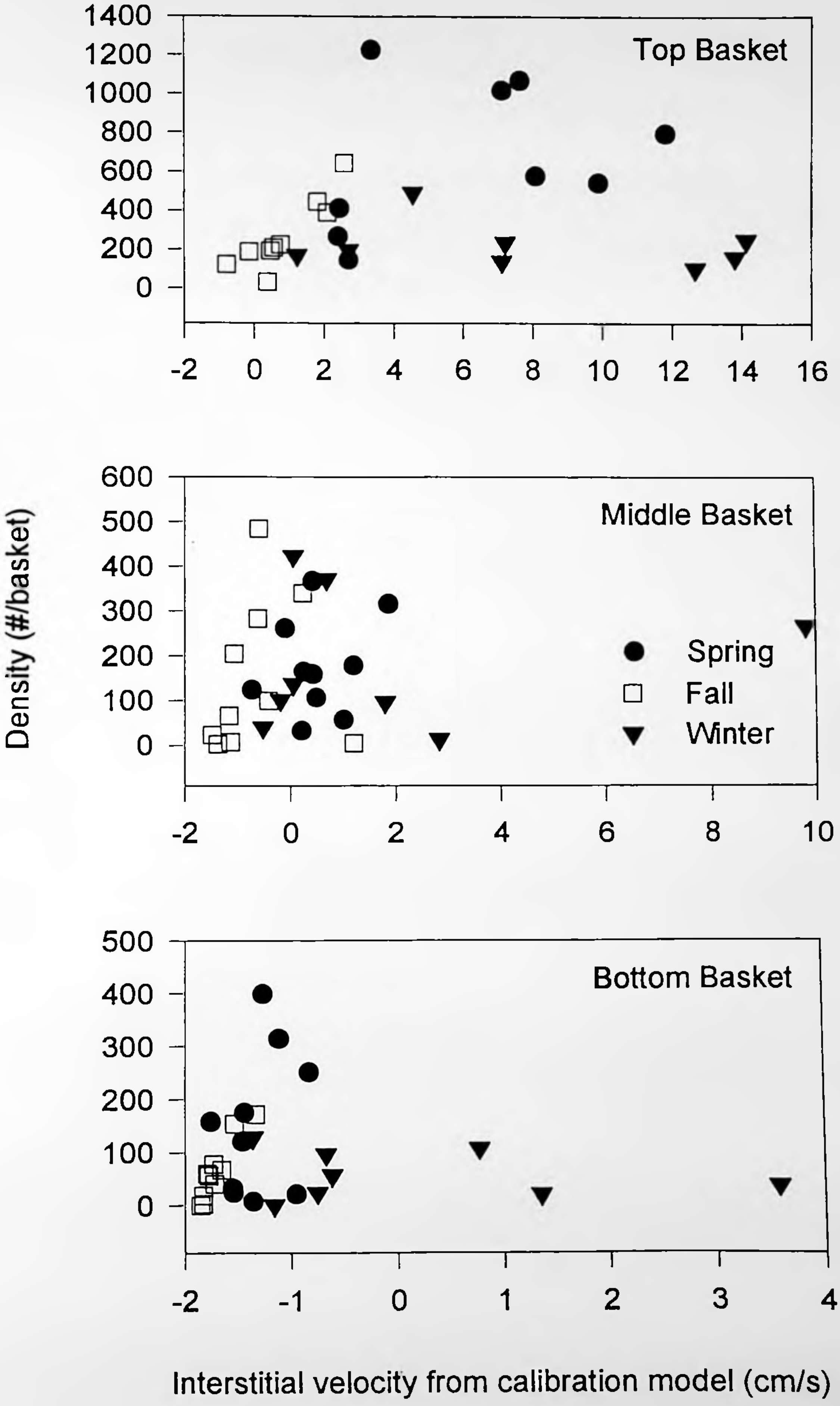

Top Basket
1400
1200
1000
800
600
400
200
0
-2
0
2
4
6
8
10
12
14
16
Middle Basket
600
500
400
300
200
100
0
● Spring
□ Fall
▼ Winter
-2
0
2
4
6
8
10
Bottom Basket
500
400
300
200
100
0
-2
-1
0
1
2
3
4
Density (#/basket)
Interstitial velocity from calibration model (cm/s)

Figure 25. Plots of macroinvertebrate densities and interstitial velocities from calibration model (cm/s) at Camp Hollow, in top, middle, and bottom baskets.

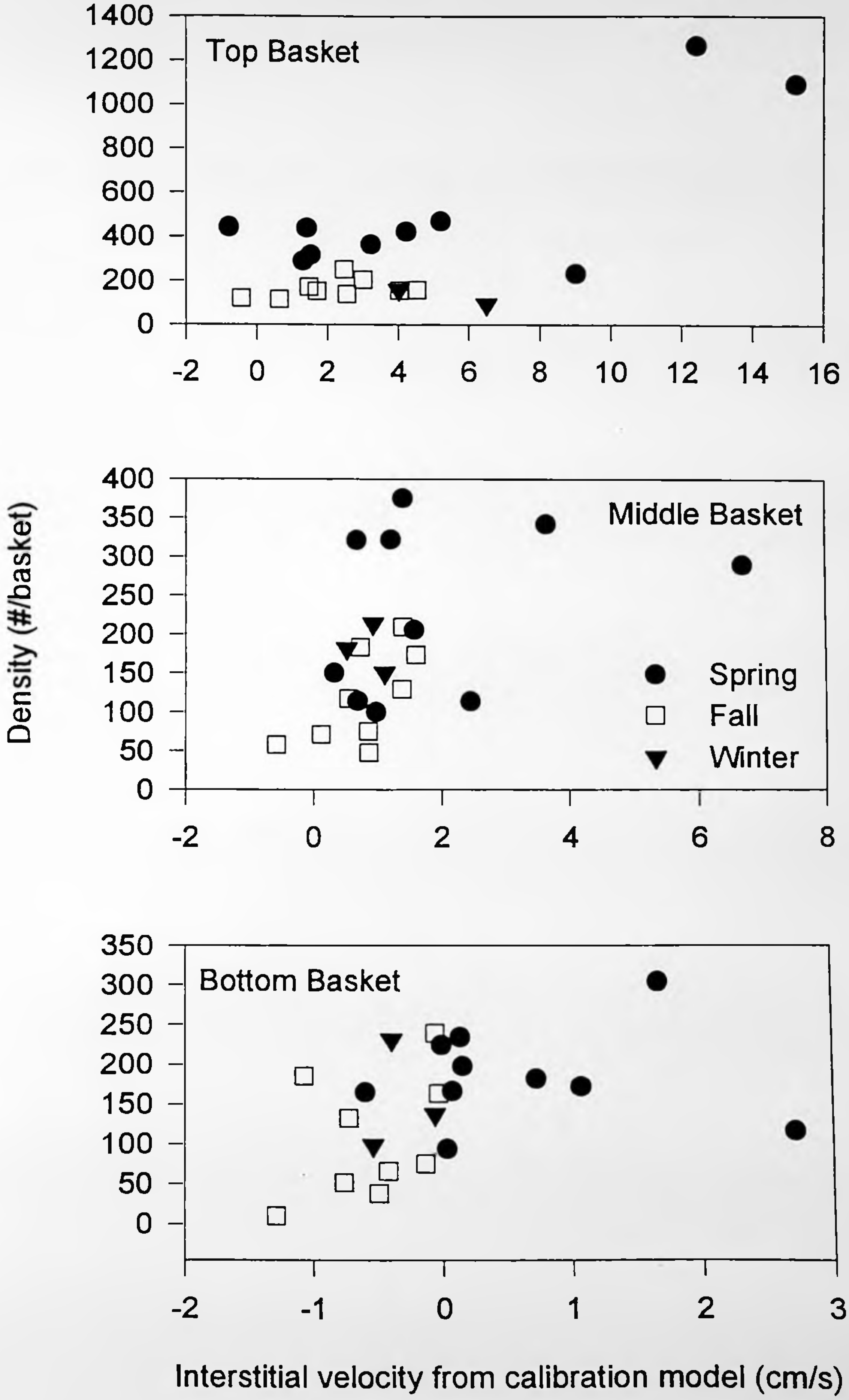
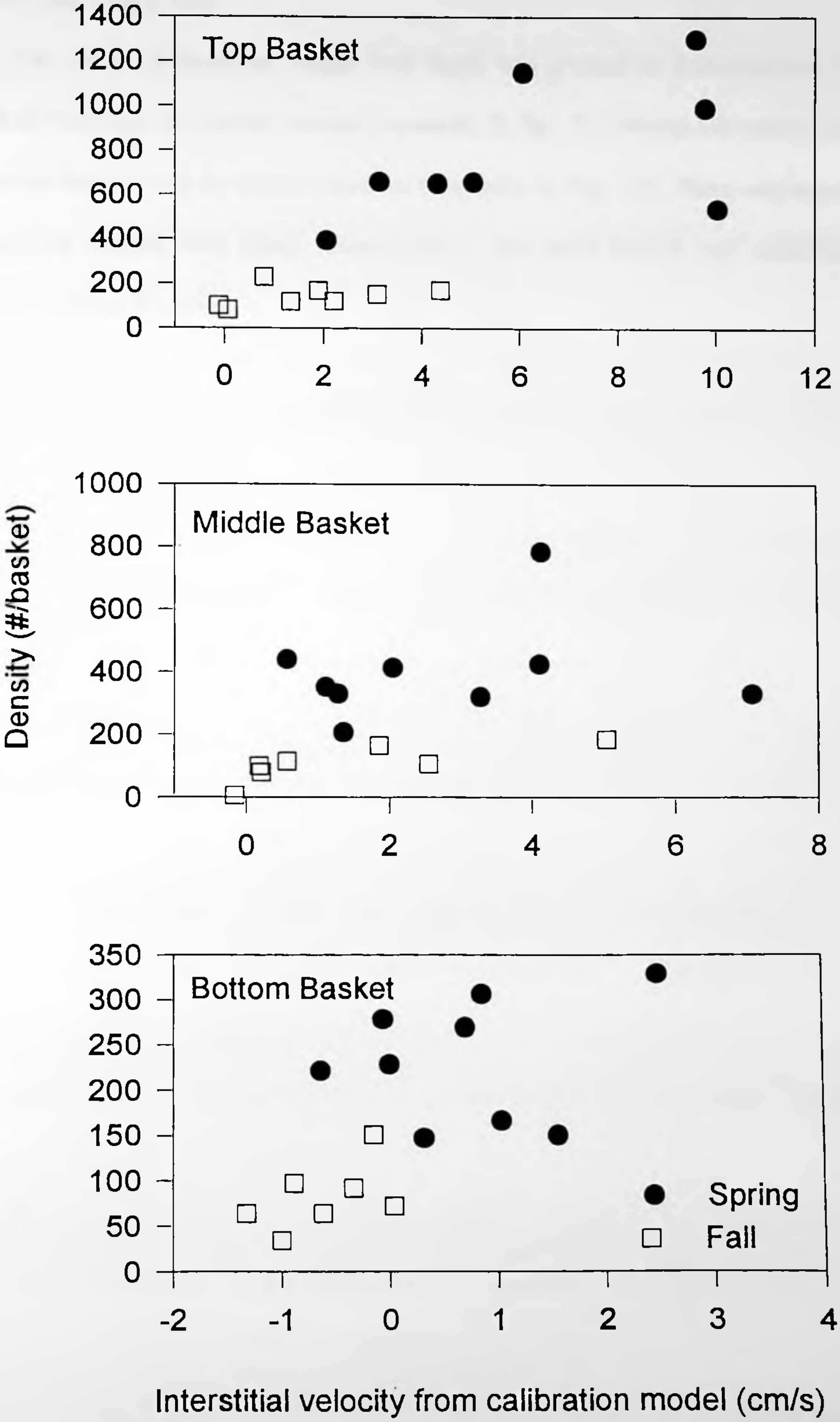

Top Basket
1400
1200
1000
800
600
400
200
0
-2
0
2
4
6
8
10
12
14
16
Middle Basket
400
350
300
250
200
150
100
50
0
-2
0
2
4
6
8
Spring
Fall
Winter
Bottom Basket
350
300
250
200
150
100
50
0
-2
-1
0
1
2
3
Density (#/basket)
Interstitial velocity from calibration model (cm/s)

Figure 26. Plots of macroinvertebrate densities and interstitial velocities from calibration model (cm/s) at Elklick Run, in top, middle, and bottom baskets.


Top Basket
1400
1200
1000
800
600
400
200
0
0
2
4
6
8
10
12
Middle Basket
1000
800
600
400
200
0
0
2
4
6
8
Bottom Basket
350
300
250
200
150
100
50
0
-2
-1
0
1
2
3
4
● Spring
□ Fall
Density (#/basket)
Interstitial velocity from calibration model (cm/s)

relatively high (Fig 23-26).

The effect of dissolved oxygen with depth was greatest at Subwatershed 5 and watershed 5 through the summer months (Appendix II, Fig. 5). During this period, middle and bottom baskets had the lowest velocities (Appendix II, Fig. 12). There was less effect of dissolved oxygen with depth downstream. The same pattern was observed for macroinvertebrate densities.

CHAPTER VI

DISCUSSION

Underlying factors

The primary factors underlying variation in hyporheic macroinvertebrate assemblages in this study were flow regime and substrate permeability. These two factors affect abiotic and biotic variations in the hyporheic environment (Poole and Stewart 1976, Allan 1995). Both factors affect dissolved oxygen stratification in the substrate which probably has a strong influence on the stratification of hyporheic fauna. In this study, as flow increased downstream, porosity of substrate and levels of dissolved oxygen increased within the substrate (Appendix II). The greatest effect of depth on hyporheic macroinvertebrate densities occurred at upstream sites, which also had the lowest flow, porosity, and dissolved oxygen (Appendix II).

Studies have reported lower concentrations of dissolved oxygen with depth due to low advective mixing and more groundwater influence (Hynes 1983, Hendricks and White 1991). Evidence of groundwater influence was most apparent at Subwatershed 5, where low dissolved oxygen levels are characteristic of groundwater. Groundwater influence downstream was less apparent as the effect of depth on dissolved oxygen was less. Downstream differences were probably due to greater mixing of surface waters, with higher dissolved oxygen content (Appendix II, Fig. 5).

The correlation coefficient for macroinvertebrate density versus interstitial velocity was highest in the fall when oxygen saturation was lowest (Fig. 27, Table 9). This was also the period of lowest flows. During periods of low flow and high temperature when dissolved

Figure 27. Correlation coefficient for macroinvertebrate density verses interstitial velocity from calibration model in relation to percent Dissolved oxygen saturation and discharge at Watershed 5 (L/s) during each season.

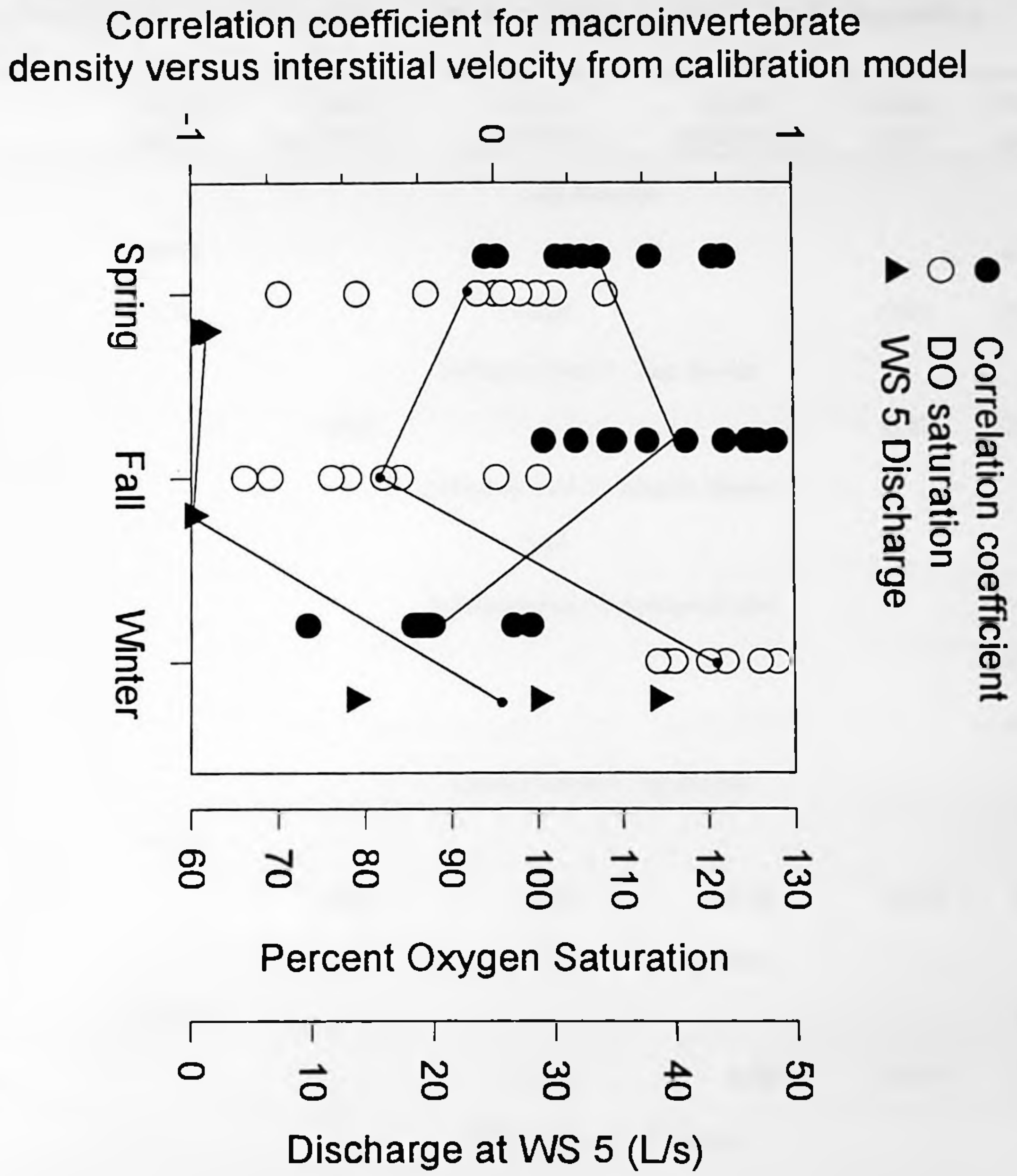

Correlation coefficient for macroinvertebrate density versus interstitial velocity from calibration model
-1
0
1
● Correlation coefficient
○ DO saturation
▶ WS 5 Discharge
Spring
Fall
Winter
60
70
80
90
100
110
120
130
Percent Oxygen Saturation
0
10
20
30
40
50
Discharge at WS 5 (L/s)

Table 9. Significant (P<0.05) correlations between macroinvertebrate density (#/m^2) and taxa richness (#/sample)and physical variables. Values are Pearson product moment correlation coefficients.

	Velocity (cm/s)	CPOM (gAFDM/m^2)	FPOM (gAFDM/m^2)	TPOM (gAFDM/m^2)	CPash (g/m^2)	FPash (g/m^2)
All Samples						
Density	0.48					-0.12
Richnesss	0.51		-0.26		-0.14	-0.27
Subwatershed 5 - Top Basket						
Density		-0.43			-0.47	-0.45
Subwatershed 5 - Middle Basket						
Density			0.41			
Subwatershed 5 - Bottom Basket						
Density						-0.41
Richness						-0.39
Camp Hollow - Top Basket						
Density	0.72					
Richness		-0.70	-0.68	-0.70	-0.69	-0.71
Camp Hollow - Middle Basket						
Density	0.47					-0.48
Richness			-0.47	-0.48	-0.49	-0.44
Elklick Run - Top Basket						
Density	0.68					
Richness	0.48		-0.45		-0.56	-0.56
Elklick Run - Bottom Basket						
Density	0.66		0.62	0.46		0.71

oxygen saturation was low, variation in velocity among baskets was correlated with to macroinvertebrate density because velocity decreases the renewal rate of oxygen within baskets. In winter, when higher discharge was observed, the correlation coefficients were weak or negative suggesting less of an effect of velocity and oxygen on macroinvertebrates (Fig. 27).

Density and taxa richness

Density of macroinvertebrates was highest in the top baskets (0-10 cm) throughout the study, comprising 51% of the hyporheic density overall. Middle baskets comprised 29% of total hyporheic density, and bottom baskets composed 20% of total hyporheic density. Estimated density in top baskets was approximately 6 times greater than density estimated from Surber samples. The mean annual density for hyporheic fauna from 0-30 cm in this study was 41,484 m^2, which is low compared to other studies. While a few studies have reported similarly low densities (Radford and Hartland-Rowe 1971; Poole and Stewart 1976), more studies have reported higher densities (Coleman and Hynes 1970; Godbout and Hynes 1982; Giberson and Hall 1988; McElravey and Resh 1991). Densities were lowest in the fall probably due to water levels dropping below the top of samplers, resulting in a smaller submerged volume within the samplers for colonization.

Taxa richness was highest in Surbers probably due to the greater heterogeneity of the sampling environment. Large cobbles and flat rocks at the stream surface provide a diverse habitat for a variety of functional groups which is not available in hyporheic samplers. Top baskets could be considered as transitional habitats into the shallow hyporheic zone combining both streambed surface and interstitial habitat. Taxa richness was highest in the spring, partly because taxonomy was most complete, with most instars being relatively mature.

Physical parameters

Particulate organic matter varied with level, season, and site. VCPOM was almost exclusively found in top baskets, primarily because descent of large particles to lower baskets was limited. Both CPOM and FPOM biomass were greater in bottom baskets than in middle baskets, which may result from the way the artificial samplers fill with organic matter. The bottom baskets probably fill first, from the gap between the baskets and cylinder, until the top spaces of the gap clog, thereby and preventing organic matter/sediment from filling the middle basket. The greater amounts of organic matter in the lower baskets may also be due to decending into lower levels during retrieval of baskets.

The addition of fine sediments to streams can significantly affect macroinvertebrate assemblages, including hyporheic fauna (Richards and Bacon 1994). Inorganic sediment deposits were highest in bottom baskets and lowest in middle baskets, which may again have to do with the way these artificial samplers fill (similar to organic matter). Upstream sites had the strongest effects of sediment with depth: more sediment in the deeper baskets; this may have had a limiting effect on the number of macroinvertebrates deeper in the hyporheos. Sandy bottom streams, which also have lower porosity with depth, usually also display stronger effects of depth on macroinvertebrate densities than cobble and gravel bed streams (Strommer and Smock 1989). My results are similar to Richards and Bacon (1994) where macroinvertebrate habitat was impaired because of increased fine sediment in the hyporeos. Maridet et al. (1992) also reported that higher amounts of sediment had a negative effect on macroinvertebrate density by lowering the porosity of the substrate.

Temperatures did not vary much with depth, except for upstream sites during the summer months. Temperatures varied a few degrees from the surface to -25 cm at times during the summer (Appendix II) similar to Pennak and Ward (1986). White et al. (1987) reported greater differences between surface and deep substrate temperatures, probably due to a greater influence of groundwater.

Community structure

Chironomidae was the dominant taxa at all depths, as reported in most hyporheic studies (Table 10). Within Chironomidae, Tanytarsini increased in relative abundance with depth. Most groups other than Chironomidae decreased in relative abundance with depth while small Crustaceans increased in relative abundance with depth. During retrieval of baskets, escape of small fauna could be caused by timing of retrieval and/or the flushing out during removal. Finally, some taxa were exclusive to the surface such as *Agapetus* and *Glossosoma* which may be obligate scrapers. Some macroinvertebrates were only identified to family in fall and winter because of a large number of small instars. Therefore, total taxa richness was probably underestimated.

Some taxa were found exclusively at upstream or downstream sites. *Habrophlebia* was common only at Subwatershed 5 and has not been previously documented on the Fernow. Subwatershed 5 was comparable to debris pools, relatively stable environments that accumulate large amounts of coarse particulate organic matter (Grubaugh et al 1996). Subwatershed 5 also has a constant source of surface water throughout the year probably due to the influence of springs, unlike other intermittent first/second order streams on the rare, along with *Habrophlebiodes* which also has not been previously documented on the

Table 10. Summary of selected hyporheic studies. See Table 2 for details on techniques.

Study	Mean density in Surbers (#/m²)	Mean density in hyporheos (#/m²)	# taxa and / or total #	Most abundant taxa	Effect of depth	Seasonal effect
Coleman and Hynes 1970	n.a.	163,074	200	Chironomidae, *Paraleptophlebia*, Copepoda, Oligochaeta, Hydracarina	Even density distribution with depth	Normal life history variations
Poole and Stewart 1976	n.a.	13,486	25	Chironomidae, *Simulium*, *Cheumatopsyche*, *Neochoroterpes*, *Stenelmis*	Density decreased with depth	Normal life history variations
Godbout and Hynes 1982	75,355	161,076	?	Chironomidae, *Stenelmis*, *Sphaerium*, *Optioservis*, *Baetis*	Density decreased with depth	Normal life history variations
Giberson and Hall 1988	n.a.	>600,000	?	Chironomidae, Copepoda, Simulidae, Ostrocoda, Oligochaeta	Density decreased with depth	Spring snow melt caused surface fauna decrease
McElravey and Resh 1991	<densities of hyporheos	97,800	55	Chironomidae, Oligochaeta, Brachycentridae, Odontoceridae, *Paraleptophlebia*	Density decreased with depth	Normal life history variations
Griffith and Perry 1993	n.a.	?	70	Chironomidae, Oligochaeta, *Paraleptophlebia*, *Leuctra*, *Peltoperla*	Density decreased with depth	Drought effect on fauna
this study	3,567	41,484	102	Chironomidae, *Leuctra*, *Paraleptophlebia*, Ceratopogonidae, Copepoda	Density decreased with depth	Flood, drought, and seasonal effect on fauna

Fernow and was found at all study sites. Diversity of non-Chironomidae Diptera was highest at upstream sites. These sites are similiar to debris pool-like conditions, which may possibly explain why taxa tend to be more semi aquatic. *Tallaperla*, *Suwallia*, and *Psephenus* were found only at downstream sites. *Tallaperla* has been documented as a downstream taxa on the Fernow, due primarily to higher alkalinity at downstream reaches (Yokum et al. 1996).

Copepods also increased downstream and with depth possibly because of an increase in porosity downstream, but numbers may have been underestimated due to large basket mesh. Gatherers (eg., Tanytarsini, Chironomini, Orthocladinae) were the dominant feeding group within the hyporheos probably because of the abundance of FPOM in the hyporheic environment. Surface dwelling scrapers (e.g., *Baetis*, many Heptageniidae) increased downstream probably reflecting downstream increases in periphyton, which are an important food resource for scrapers (Merrit and Cummins 1996). In this study, as in Strommer and Smock (1989), few if any macroinvertebrates were found to be unique to the shallow hyporheos, most likely because of limited vertical groundwater influence, and the shallow depth of the hyporheic zone. For example, large alluvial river systems often yield taxa that spend the majority of their life deep in extensive substrate (Stanford and Ward 1988).

Other Studies

Though there have been decades of research conducted on hyporheic fauna, it is difficult to directly compare results due to the different sampling techniques and many different regions sampled. Few hyporheic studies have been conducted in Appalachian headwater streams (Griffith and Perry 1993).

Estimates of hyporheic densities of macroinvertebrates ranged from 1000 m^2 in a Czechoslovakian river to over 500,000 m^2 in the Speed River, Ontario (Pugsley and Hynes 1983). Most studies report densities lower than 100,000 individuals m^2 and 2/3 of the studies have reported hyporheic densities less than 50,000 individuals m^2 (McElravy and Resh 1991).

Some studies have reported greater densities of fauna 10-20 cm below the surface, than at the surface (Williams and Hynes 1974), but the majority of studies are in agreement that the highest density of invertebrates occurs within the first 15 cm of substrate (Poole and Stewart 1976, Godbout and Hynes 1982, Pugsley and Hynes 1983, Giberson and Hall 1988, Strommer and Smock 1989, McElravy and Resh 1991, Maridet et al. 1992, Griffith and Perry 1993, Table 10). Various parameters have been explored that affect vertical variation in the fauna of the hyporheic environment including; interstitial flow, porosity of substrate, dissolved oxygen, and life history of organisms (e.g., Williams 1984, Maridet et al. 1992)

In Fernow streams, the majority of macroinvertebrates were within the first 0-10 cm during base flow conditions. In fall, maximum density often shifted to the middle basket because the top basket was dewatered. Density increased with depth downstream following a winter flood. This increase of macroinvertebrate densities with depth was probably caused by the scouring and replacement of gravel from many of the top baskets at Elklick Run and Camp Hollow. Macroinvertebrates may also have retreated to lower baskets in response to flooding.

The majority of studies of hyporheic fauna have reported Chironomidae as constituting 60% or more of the total number of animals collected (McElravy and Resh 1991). Williams (1984) suggested that invertebrates that inhabit the substrate habitat must possess certain characteristics, such as a small body size and vermiform bodies which allow them to colonize interstitial habitat. Chironomidae, Oligochaeta, and *Leuctra* which are all common in the hyporheos share these characteristics. Chironomidae are more abundant within the hyporheic environment than at the surface. Griffith and Perry (1993) found high abundances of *Paraleptophlebia* and *Leuctra*, in the hyporheos in all seasons as in this study. Often, large *Paraleptophlebia* were found at the lowest levels which seems unusual for a taxa with such fragile gills.

Few studies have looked at hyporheic fauna from a longitudinal perspective. Grubaugh (1994) reported that along a southern Appalachian stream continuum of second through seventh order streams, major changes in functional group assemblage were not evident until the fifth-order reach (Wohl et al. 1995). I detected some changes in functional organization from 1st through 4th order reaches. The relative abundance of scrapers increased greatly downstream, as the stream widens and the canopy opens just below the 4th order site which may allow extra colonization of periphyton on flat rocks and cobbles (Grubaugh et al. 1996). Taxonomic structure was most different between the upstream sites, Subwatershed 5 & Watershed 5, and the downstream sites, Camp Hollow and Elklick Run. The two upstream sites shared unique taxa including *Habrophlebia*, *Trienodes*, *Merycomyia*, Isopoda and a few rare taxa, while downstream reaches had unique taxa including *Drunella*, *Talloperla*, *Suwallia*, and a few rare taxa. Some taxa including *Baetis* and *Paraleptophlebia*, were only found at the surface at upstream sites, but were found at all depths at downstream reaches.

Surber versus substrate sampler

Macroinvertebrate density in the hyporheos as estimated from substrate baskets was much higher than surface density as estimated from Surber samplers. Radford and Hartland-Rowe (1971) reported about five times as many benthic invertebrates in substrate samplers versus Surbers in a gravel-bottom stream, in Alberta, Canada. In this study, top baskets had 10 times as many macroinvertebrates as Surber samples. During Surber sampling, I attempted to disturb the substrate 0-10 cm below the surface, in order to compare with top baskets. Actual volume sampled with Surbers certainly varied among samples complicating comparisons based on volume. Artificial samplers may give more precise densities but are also artificially alter environments. Differences in density and taxa richness can be summarized by considering Surbers as sampling above top baskets but including both surface and hyporheic fauna.

Taxa richness was higher on the surface of the stream bottom because of the cobbles that serve as foraging sites for many taxa (eg., scrapers and filterers). These cobbles can divert currents, serve as substrate for periphyton and bryophyte growth, and retain coarse organic matter. These larger cobbles that are typical of the stream bottom were not included in or on top of baskets, therefore eliminating or underestimating fauna associated with large cobbles.

Limitations of artificial samplers

Artificial substrate samplers give good estimations of the location of animals and also the volume and surface sampled (Tabacchi 1990), but there are limitations with these samplers. Dynamics of the colonization period are often unknown, removal of baskets can be a delicate procedure, loss of fauna and/or samplers may occur during flood events, and ideal colonization time may vary with site and season (Tabacchi 1990). After the initial disturbance during placement, three months was likely adequate time for colonization. Such sampling is only feasible for long term studies. Although an effort was made in this study to match the surrounding substrate with clean gravel mixtures, it may have created an "island" effect with respect to particulate organic matter and sediment. Another shortcoming of an artificial hyporheic substrate is that it does not reveal the true stratigraphy of biota and sediment as does freeze coring (Tabacchi 1990).

Artificial substrate samplers can be convenient during retrieval but sample size and placement can be difficult. Placement within the coarse substrate of headwater streams is difficult and large sample sizes are needed in case of catastrophic events.

Drought effects

Saturated hyporheic environments may serve as a potential refuge for surface organisms that are small enough to fit in interstitial spaces during times of drought (Williams and Hynes 1977, Boulton 1989, Cooling and Boulton 1993, Boulton and Stanely 1995). Griffith's and Perry's (1993) study on the Fernow showed that the hyporheic zone acts as a refuge for the lotic macroinvertebrate community during droughts.

In this study there was an effect of drought on macroinvertebrate densities in top baskets during the fall. This may have more to due with the level of water in the baskets than anything else. Top baskets were often above the water's surface, resulting in movement of fauna to lower depths.

Flood effects

Floods in steep gradient streams are quick, powerful events that keep benthic fauna in a constant state of change (Allan 1995). The strongest effects of a flood event were most evident at the downstream sites. The higher numbers of fauna with depth may have been due to a combination of high velocities at the surface, and scouring of gravel from the top baskets. How many fauna retreated to lower levels is unknown.

A flood response study by Angradi (in press) suggests that even though densities dropped 70% on the surface following a flood, there were only small effects on community structure. Angradi reported that rapid recovery of macroinvertebrates after flood events was due to abundant refugia, including organic debris dams, deep interstitial habitat, and 1st-order tributaries. Many studies support this idea that hyporheic habitat serves as a potential source of recolonization for the stream bed surface after flood events (William and Hynes 1974, Palmer et al. 1992, Griffith and Perry 1993, Angradi in press).

Management implications

Is it necessary for managers to quantify hyporheic fauna? Can managers afford to sample the hyporheic environment? Surber samplers, which are among the most common type used for monitoring macroinvertebrate communities, adequately quantify taxa richness, but may greatly underestimate total benthic density.

How does anthropogenic stress (e.g., sediment, acid rain, pollution) affect hyporheic fauna assemblages? There have been numerous studies relating sediment particle size and distribution of macroinvertebrates (Allan 1975, Ward 1975, Minshall 1984, Richards and Bacon 1994). Substrates composed of smaller size particles typically have fewer taxa and productivity than substrates with more heterogeneous substrates (Allan 1975, Ward 1975, Richards and Bacon 1994). Fine sediment loads may alter vertical distribution of fauna. If fine sediment load is a problem in streams, it could fill deep interstitial spaces essential for many early instars, small meiofauna, and as deep refugia from predation and spates for surface benthos. Depending on the timing of disturbances the hyporheic zone may function in different ways. During slower disturbances (drought), macroinvertebrates may have time to take refuge in the hyporheic zone. If the disturbance is rapid (flooding, pH depressions), macroinvertebrates that remain in the hyporheic zone may potentially recolonize surface areas.

CHAPTER VII

SUMMARY AND CONCLUSIONS

(1) Vertical, longitudinal, and seasonal variations of benthic and hyporheic fauna were examined from March 1995 to January 1996 in first through fourth order streams of the Fernow Experimental Forest. Various physical and chemical parameters of the hyporheic environment were measured including surface velocity, interstitial velocity, dissolved oxygen, temperature, water chemistry, particulate organic matter, and sediment.

(2) Fauna were sampled with Surber samplers and artificial substrate samplers. Surber samples collected stream bed surface fauna while artificial substrate samplers were used to collect hyporheic fauna.

(3) One hundred and two taxa were identified, and annual mean densities were estimated at 41,484/m^2 in the hyporheic environment across site and depth. Surber sample estimates were approximately 3,556/m^2 on the stream bed surface. Of the total hyporheic density, 51% was from the 0-10 cm level, 29% were from the 10-20 cm level, and 20% were from the 20-30 cm level.

(4) Taxa richness was higher in Surber samples than artificial substrate samples. Density was higher in artificial substrate samples than in Surber samples.

(5) Chironomidae was the dominant taxa at all depths. Tanytarsini was the dominant taxa within Chironomidae. Most other taxa groups decreased in relative abundance with depth into the hyporheos with the exception of Copepods. Few if any macroinvertebrates were found unique to the hyporheos.

(6) An application of the clod card method for quantifying water velocity within the artificial substrate sampler was used. Interstitial velocity decreased with depth and increased downstream.

(7) Flow regime and substrate porosity were probably the two primary underlying factors shaping hyporheic fauna assemblages. These two factors affect flow, dissolved oxygen, temperature, water chemistry, particulate organic matter, and sediment distribution.

(8) In general, relative abundance of macroinvertebrates decreased with depth, except during a drought and following a flood event. During drought conditions in the fall, water levels decreased within samplers, resulting in higher densities in lower levels. During flood conditions in winter, high surface velocities and scouring in top baskets probably resulted in higher densities in lower levels.

(9) There were longitudinal differences in functional feeding groups and restriction of some taxa to upstream or downstream sites. Scrapers and filterers increased in relative

abundance downstream. *Habrophlebia* and a few other rare taxa were restricted to upstream sites while *Tallaperla*, *Suwallia*, *Psephenus* and a few other rare taxa were restricted to downstream sites.

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Appendix I. Taxa collected in this study.

Taxa	Functional Group
Arthropoda	
Insecta	
Collembola	
Ephemeroptera	
Ameletidae	
Ameletus	scraper
Baetidae	
Baetis	scraper
Diphetor	scraper
Procleon	scraper
Heptageniidae	
Cinygmula	scraper
Epeorus	scraper
Heptagenia	scraper
Leucrocuta	scraper
Stenonema	scraper
Ephemerellidae	
Drunnella	scraper
Ephemerella	gatherer
Eurylophella	shredder
Leptophlebiidae	
Habrophlebia	scraper
Habrophlebiodes	scraper
Paraleptophlebia	gatherer
Ephemeridae	
Ephemera	gatherer
Litobrancha	gatherer
Odonata	
Gomphidae	
Lanthus	predator
Cordulegasteridae	
Cordulegaster	predator
Plecoptera	
Pteronarcyidae	
Pteronarcys	shredder
Peltoperlidae	
Peltoperla	shredder
Tallaperla	shredder
Nemouridae	
Amphinemura	shredder
Prostoia	shredder
Soyedina	shredder
Leuctridae	
Leuctra	shredder
Taxa	**Funtional Group**
Limnophilidae	
Hydatophylax	shredder
Pycnopsyche	shredder
Goera	scraper
Uenoidae	
Neophylax	scraper
Leptoceridae	
Triaenodes	shredder
Lepidoptera	
Tortiidae	
Archips	shredder
Coleoptera	
Hydrophilidae	
Hydrochus	shredder
Staphylinidae	
Pontamalota	predator
Psephenidae	
Psephenus	scraper
Ectopria	scraper
Dryoidae	
Helichus	scraper
Scirtidae	
Prinocyphon	na[1]
Elmidae	
Oulimnius	scraper
Diptera	
Tipulidae	na[1]
Tipula	shredder
Antocha	gatherer
Dicranota	predator
Hexatoma	predator
Limnophila	predator
Limonia	shredder
Ormosia	gatherer
Pedicia	predator
Psuedolimnophila	predator
Ceratopognidae	predator
Bezzia	predator
Probezzia	predator
Ceratopogon	predator
Chironomidae	na[1]
Tanypodinae	predator
Orthocladinae	gatherer
Chironomini	gatherer

Appendix I. Continued.

Taxa	Functional Group
Capniidae	
Allocapnia	shredder
Paracapnia	shredder
Perlidae	
Acroneuria	predator
Perlodidae	
Remenus	predator
Isoperla	predator
Chloroperlidae	
Alloperla	predator
Haploperla	predator
Suwallia	predator
Sweltsa	predator
Hemiptera	
Veliidae	
Microvelia	predator
Corixidae	
Hesperocorixa	predator
Megaloptera	
Sialidae	
Sialis	predator
Corydalidae	
Nigronia	predator
Trichoptera	
Philopotamidae	
Dolophilodes	filterer
Wormaldia	filterer
Psychomyiidae	
Lype	scraper
Polycentropodidae	
Polycentropus	predator
Phylocentropus	gatherer
Hydropsychidae	
Diplectrona	filterer
Hydropsyche	filterer
Rhyacophilidae	
Rhyacophila	predator
Glossosomatidae	
Glossosoma	scraper
Agapetus	scraper
Lepidostomatidae	
Lepidostoma	shredder
Tanytarsini	gatherer
Dixidae	
Dixa	gatherer
Ptychopteridae	
Bittacomorpha	gatherer
Simuliidae	
Prosimulium	filterer
Empididae	
Chelifera	predator
Clinocera	predator
Tabanidae	
Chrysops	predator
Merycomyia	predator
Mycetophlidae	
Collembola	
Crustacea	
Decapoda	
Cambaridae	
Cambarus	na[1]
Isopoda	gatherer
Amphipoda	
Gammaridae	
Gammarus	shredder
Copepoda	gatherer
Podocopa	gatherer
Hydrachnidia	
Acari	predator
Mollusca	
Bivalvia	gatherer
Oligochaeta	gatherer
Nematoda	gatherer
Chordata	
Amphibia	
Urodela	
Plethodontidae	
*Desmognathus**	na[1]
*Eurycea**	na[1]
*Gyrinophilus**	na[1]
*Plethodon**	na[1]
Actinopterygii	
Teleostei	
Cottidae	
Cottus	na[1]

[1] na=not assigned to a functional group. * Listed as Salamanders in other tables. Majority were larval *Eurycea*

Appendix II

An application of the clod card method for quantifying water velocity in the shallow hyporheic zone of an Appalachian stream system

TED ANGRADI*
United States Forest Service, Northeastern Forest Experiment Station, Timber and Watershed Laboratory, Parsons, WV 26287, U.S.A.

ROBERT HOOD
Department of Biology, Marshall University, Huntington, WV, U.S.A.

*Author to whom correspondence should be sent

Running head: Quantifying hyporheic water velocity

SUMMARY

1. A method for quantifying interstitial water velocity based on the dissolution of plaster of Paris standards (clod cards) was developed as part of a study of vertical, longitudinal (1-4 order sites), and seasonal variation in the biotic and physical characteristics of the shallow hyporheic zone (0-30 cm) of a headwater stream system in West Virginia, USA.
2. A calibration model was developed using a water velocity simulation tank to relate mass loss of clod cards to water velocity and temperature. The model was then used to calculate water velocity through artificial substrates in the shallow hyporheic zone based on in situ mass loss of clod cards.
3. Water velocity in the hyporheic zone increased with stream order, was highest in early spring and winter during high stream base flows, and decreased with depth into the substrate. There was a strong interaction between depth and season: during periods of high stream discharge, water velocity through the upper level of the shallow hyporheic zone (0-10 cm into the substrate) increased disproportionately more than velocity in lower levels. Mean interstitial velocity in March ranged from 0 cm/s in the lowest level (20-30 cm) to 3.5 cm/s in the upper level (0-10 cm) at the first order site and from 2.5 cm/s (20-30 cm) to 9.5 cm/s (0-10 cm/s) at the fourth order site. Gradients in stream discharge and sediment permeability accounted for treatment effects.
4. Use of calibrated data improved the ability to resolve among-season differences in interstitial water movement over use of uncalibrated mass loss data. For some clod card applications, empirical calibration may not be necessary.

Mention of a proprietary product in this article does not constitute or imply an endorsement or recommendation for its use by the USDA or Forest Service.

Introduction

Factors likely to influence the structure and function of lotic interstitial macroinvertebrate assemblages and biotic processes include water velocity, particulate organic matter content, temperature, dissolved oxygen, nutrient availability, and sediment structure (Godbout and Hynes, 1982; Pennak and Ward, 1986; Pennak, 1988; Williams, 1989; Palmer, 1990; Boulton, Valett, and Fisher, 1992; Dole-Olivier and Marmonier, 1992; Sterba et al., 1992). Of these, interstitial water velocity is probably the most difficult to measure. Water velocity through sediment as upwelling, infiltration of surface-water (advection) or underflow is, however, a key factor since it exerts considerable influence on the magnitude and variation in all other factors (Williams and Hynes, 1974; Munn and Meyer, 1988; Triska et al., 1989; White, 1990; Stanley and Boulton, 1993; Jones, Fisher, and Grimm, 1995).

During a study of longitudinal, seasonal, and vertical variation in lotic macroinvertebrate assemblages at the Fernow Experimental Forest in West Virginia, USA, we installed artificial substrates in the shallow hyporheic zone (SHZ, 0-30 cm into the substrate) of connected first through fourth order streams in each of three seasons, and allowed them to colonize for three months. Because interstitial flow is likely to exert an influence on hyporheic macroinvertebrate assemblages, we sought a method to quantify water movement through the substrates in order to better understand observed variation in biotic variables.

Methods are available for indirect measurements of hyporheic (sensu White, 1993) water velocity. These include dye and chemical tracers (e.g., Williams and Hynes, 1974; Bencala et al., 1983; Munn and Meyer, 1990), mini-piezometers (Lee and Cherry, 1978) and seepage meters (methods reviewed by Boulton, 1993). Because of the low spatial resolution of these measurements (tens of meters, Palmer, 1993; but see Williams and Hynes, 1974), values are typically extrapolated to the reach scale. Using these methods it is difficult to quantify water velocity through a particular patch of substrate at a specific depth -- the contents of an artificial substrate buried in the SHZ, for example. Boulton (1993) recommended a partial solution: stratification of treatments or samples among reaches with known surface - subsurface hydrologic exchange rates. While this approach provides some control of relative interstitial velocities at the reach scale, it does not provide a covariate measure of interstitial water velocity for each SHZ sample location, which is critical for understanding how interstitial velocity influences hyporheic macroinvertebrates assemblages which often vary over spatial scales of < 1 m.

There have been a few attempts at quantifying interstitial water velocity using water soluble materials that can be imbedded within substrates, exposed to flow, retrieved, and the resultant mass loss used as an integrated index of water movement. This approach has the advantage that an interstitial measure of water velocity can be obtained for a specific location within the substratum. Rabeni and Minshall (1977) used calibrated salt (NaCl) tablets to estimate water velocity through 5 cm deep trays filled with substrate in an Idaho, USA, stream. Poole and Stewart (1976) attempted similar measurements within the SHZ of a Texas, USA, stream. In both studies, the salt tablets were weighed, exposed to flow for 2 minutes, dried and reweighed. This approach is rapid and easily replicatable, and has the advantage that if the tablets can be inserted and retrieved without disturbing the substrate, measurements of water velocity can be made simultaneously with macroinvertebrate colonization (Rabeni and Minshall, 1977).

Because of the design and placement of most hyporheic artificial substrates (including ours, described below) we feel that successful recovery of salt tablets before they are completely dissolved is unlikely. Furthermore, with an integration period of only a few minutes, variation in mass loss associated with handling loss might easily overwhelm treatment effects. For these reasons we rejected the salt tablet method for our application.

An analogous approach, the so-called plaster "clod card" method, has been used to quantify water motion in the marine environment (Muus, 1968; Doty, 1971; Howerton and Boyd, 1992; Jokiel and Morrissey, 1993; Thompson and Glenn, 1994). In a typical application of the clod card method (e.g., Jokiel and Morrissey, 1993), blocks or "clods" of $CaSO_4$ (plaster of Paris) are weighed, attached to coral reefs for one or more days or tide-cycles, retrieved, and reweighed. Water velocity across the plaster clod can be determined from standard curves relating water velocity to mass loss adjusted for temperature and salinity derived empirically in a calibration tank (e.g., Thompson and Glenn, 1994). We conducted preliminary experiments which convinced us that dissolution of plaster clods might successfully be used to quantify water velocity within SHZ substrates. So far as we are aware, the only previous use of a plaster dissolution method in a stream was Peckarsky and Penton (1990) who described the use of 1-cm diameter plaster hemispheres to compare flow conditions inside and outside of enclosures in streams.

The objective of this paper is to describe our application of the plaster clod card method. Specifically, we (1) developed an empirical calibration model in the laboratory to relate mass loss in situ to water velocity; we (2) examined two dependent variables derived from in-situ mass loss data for quantifying water velocity: uncalibrated mass loss data which are relatively easy to obtain, and interstitial velocity data which requires a calibration model; and (3) using in situ clod card data we tested the hypotheses that (a) water velocity in the SHZ varies longitudinally in a Fernow stream system (first through fourth order reaches) and among seasons, (b) water velocity varies with depth into the SHZ, and (c) that the effect of depth depends on site and season. The season factor is a surrogate for stream flow which varies greatly among seasons in Fernow streams. Based on our observations of the substrate and flow regimes in Fernow streams and in accordance with a spatial (downstream) model of hyporheic flow (White, Elzinga, and Hendricks, 1987; White, 1993: fig. 4) we predicted that the water velocity through the SHZ would be greatest at the fourth-order site. We predicted that water velocity in the SHZ would be positively correlated with stream flow and would be greatest in winter/spring and least in fall, during the maxima and minima, respectively, of the annual hydrograph of Fernow streams (Adams et al., 1994). We also surmised that the effect of depth into the SHZ on interstitial water velocity would be least at the first order site and in fall where surface water advection was least likely. This paper is concerned with methodology and field measurements of SHZ water velocity and related physical and chemical variables. In a subsequent paper we will relate water velocity and other treatment effects to macroinvertebrate assemblages of the SHZ in streams at the Fernow

Experimental Forest.

Study Site

The Fernow Experimental Forest lies on the unglaciated Allegheny Plateau of the central Appalachian Mountains in north central West Virginia (39°3'N, 79°41'W). The area is characterized by steep slopes (>20%), narrow valleys, and high annual precipitation (≈145 cm, Adams et al., 1994). Forest vegetation of the Fernow consists mainly of mature second growth stands of mesophytic Appalachian hardwoods. Experimental watersheds are primarily underlain by sedimentary rock of the Hampshire formation.

Our four 100 m long study reaches were located on connected tributaries (first - third order) of Elklick Run or on Elklick Run itself (fourth order). Physical, chemical, and sedimentological characteristics of study reaches are summarized in Table 1. Noteworthy differences among reaches are the higher alkalinity of Elklick Run caused by a limestone-influenced tributary that enters Elklick downstream from its confluence with Camp Hollow, and the finer substrate in the Subwatershed 5 reach (Table 1, Fig. 1a), probably due to low stream competence.

We attempted to determine depth to bedrock in each reach by excavation with a backhoe (Camp Hollow and Elklick Run) or with a shovel. At Subwatershed 5 (first - order) we encountered a heavy clay layer at 27-38 cm (Table 1). At Watershed 5, bedrock outcrops were common; between outcrops, we excavated to at least 50 cm without encountering bedrock. At Camp Hollow and Elklick Run, bedrock was encountered at about 1 m or was not reached (one site at Elklick Run).

Watershed 5 is gauged just downstream from the study reach (Fig. 2). Using several years of flow records for Watershed 5 and several other gauged Fernow watersheds (unpublished data), we estimated mean annual flow for each reach during the study (Table 1) by regression of watershed area versus mean annual flow ($r^2 = 0.94$). Except during storms, stream flow in Fernow streams is dominated by groundwater inputs, seasonal variation in which is linked to the evapotranspirational demand of forest vegetation (Fernow flow regimes were reviewed by Adams et al. 1994, and Angradi, in press). Surface flow is seasonally discontinuous in study streams except in the Subwatershed 5 reach where an extremely low but continuous baseflow is maintained by seeps adjacent to the channel.

Methods

Plaster clod cards

Using plastic ice-cube trays as molds, we prepared plaster clods from the formulation of 470 mg $CaSO_4$ calcined powder (Fisher Scientific, Pittsburgh, PA): 1 L tap water. After filling the trays, we tapped the trays on the bench top to release trapped air bubbles. After about 30 minutes, cubes were removed from trays and allowed to dry at room temperature for at least a week. Dried cubes were sanded on the bottom (the face with the largest dimension) to a final weight of 29-31 g. Dried and sanded cubes were glued to the inside of 60 mm diameter polystyrene petri dish covers (Fisher Scientific) with silicone sealant. The dish covers served as a base for the clods; their purpose was twofold: they provided a surface for labeling, and they protected the base of the clod from chipping during handling. Total height of the finished clod cards was about 3 cm. The raised rim of the base shielded the bottom 5-7 mm of the clod from lateral water movement. However, since we constructed every clod card identically, we considered this effect negligible.

Field studies

Shallow hyporheos samplers were comprised of two components, a perforated section of pipe (hereafter called the sampler) installed vertically in the substrate with the top flush with the stream bottom, and a set of three baskets that fit inside the pipe. The sampler was constructed of a 30 cm section of 15.5-cm internal diameter PVC pipe through which 2-cm holes were drilled such that ≈50% of the total surface area of the sampler was removed. Baskets were constructed of 11-mm mesh galvanized hardware cloth fastened to 14.5 cm diameter bases of 9 mm plywood.

We used relatively coarse mesh for the baskets to reduce clogging by organic matter and to avoid excluding larger taxa (e.g., crayfish, salamanders, Pteronarcys) from the baskets.

The base of each basket had an 11-cm diameter opening covered with 0.25-mm mesh nitex cloth. Each 10 cm high basket thus sampled a different SHZ level: top (≈0-10 cm), middle (≈10-20cm), and bottom (≈20-30cm). The middle and bottom baskets had wire bails to facilitate removal. Because of the fine mesh bases and snug fit of the baskets within the samplers, we speculated that water velocity through the baskets would be least restricted in the horizontal direction. Similar samplers have been used elsewhere (Gilpin and Brusven, 1976; Griffith and Perry, 1993)

We attempted to match the particle size distribution of the standardized substrate used within the baskets to ambient conditions. Based on shovel sampling (Grost, Hubert, and Wesche, 1991) we estimated the mean composition of the gravel for the four study reaches (Fig. 1b). The use of a one standardized mixture based on a mean distribution across sites is a compromise of accuracy in favor of precision since substrates at the first-order site (Subwatershed 5) were finer than elsewhere. We reasoned that over the 3 month macroinvertebrate colonization periods, fine particle content of substrate baskets would become adjusted to ambient conditions, and the standardized mix would not greatly effect macroinvertebrate assemblages. Bulk substrate samples were collected along Elklick Run, dried, and sorted using a mechanical sieve shaker. We selected four size classes of gravel between 8 and 64 mm for use within the baskets, and we remixed the sorted bulk particles to match the mean distribution (Fig. 1b). Larger particles (cobbles) were not feasible to use in the baskets, and finer fractions would escape from the baskets and possibly cause them to jam within the samplers.

In each study reach at the beginning of each season, we installed 10 samplers at random locations within riffles and shallow runs. Although stream bed profile, water depth, and depth to bedrock influence surface water advection (Hendricks and White, 1991; Harvey and Bencala, 1993; White, 1993), we installed samplers without reference to these factors (except that samplers were inundated). Reasons for this were 1) depth to bedrock could not be determined at the surface, 2) pools (typically sites of advection, White, 1993) were limited to a few small plunge pools formed below boulders or debris, and three, and 3) water depth is highly flow dependent. Installation of samplers was very laborious, especially during high stream base flows in spring and winter, often requiring excavation of a 0.5 m diameter pit to install the samplers at the proper depth followed by backfilling around the sampler.

For clod card trials we placed a preweighed clod card in the center of each basket (e.g., at ≈ 5 , 15, and 25 cm depth) surrounded by the gravel mix. An extra sampler was installed at each site with an electronic thermograph at the top and bottom basket position. We also placed baskets with clod cards in the weir pond at the base of Watershed 5 (second-order) to estimate mass loss of the clods in still water. To allow correction of final mass for clod handling loss we transported extra baskets containing substrates and clod cards to and from the field for every set of clods installed. After three days --a period determined in preliminary tests to result in measurable mass at low velocities, but to not result in complete clod dissolution at high velocities-- we retrieved the clod cards and allowed them to dry at room temperature for at least a week before reweighing. Because of space limitations, we opted for air drying rather than oven drying. Potential small effects of variation in ambient humidity on mass loss determinations was ignored (after Thompson and Glenn, 1994; Jokiel and Morrissey, 1993; and Howerton and Boyd, 1992).

After the clod cards were retrieved we refilled the baskets with clean standardized gravel mix and allowed macroinvertebrates to colonize them for about three months undisturbed (Fig. 2). After retrieving the baskets, we removed the gravel and invertebrates and we again refilled the baskets with clean gravel and ran post-colonization clod card trials. After the post-colonization clod card field trials we excavated the samplers, reinstalled them at new random locations and started the process over. Because of a January, 1996 spate which buried samplers at Elklick Run (Fig. 2a), we had to remove most of the Elklick Run samplers to retrieve the baskets at the end of the colonization period. Consequently, we collected no winter post-colonization clod card data at Elklick Run. We reiterate that since an objective for the overall study was to describe the macroinvertebrate assemblages of the SHZ, we could not disturb the substrates with samplers during the three month colonization by macroinvertebrates. We therefore used the clod card method to estimate water velocity through the SHZ at each sample location before (pre-colonization trials) and after each three month macroinvertebrate colonization period (post-colonization trials). This compromise allows us to test hypotheses regarding seasonal (discharge-related) variation in interstitial velocity, and to relate macroinvertebrate assemblages to interstitial flow conditions just after the end of the colonization period (post-colonization trials).

Near the upstream end, midway , and near the downstream end of each study reach, we installed a set of access pipes for collecting water for chemical analyses. Each set consisted of three lengths of 2.6-cm diameter PVC pipe aligned vertically in the substrate and extending about 20 cm above the stream bottom. The buried portions of the pipe were drilled to admit water from either the top (0-10 cm), middle (10-20 cm) or bottom (20-30 cm) level of the SHZ. For sampling, access pipes were evacuated with a peristaltic pump; the tubes allowed to refill and water samples were collected using the pump. Samples from each site were pooled by level for analysis. Water chemistry analyses were conducted at the US Forest Service, Timber and Watershed Lab, Parsons, WV (Edwards and Wood, 1993). Dissolved oxygen measurements were made by inserting a probe into each access pipe after initial pumping (YSI Inc. model 57, Yellow Springs, OH). Water velocity at the sediment surface above each sampler was measured with a turbo-prop velocity meter (Global Water, Fair Oaks, CA).

Calibration Experiments

We conducted calibration trials in a rotating-arm water motion simulation tank, so called because the clod cards, or in this case, baskets containing clod cards, were moved through the water rather the water being forced through the baskets as in a flume. Similar tanks have been described elsewhere (Doty, 1971; Thompson and Glenn,1994; Howerton and Boyd, 1992).

Our tank was constructed of wood (1.2 m wide x 1.2 m long x 0.28 m deep) and held about 390 L of water. A beam across the top of the tank supported a gear-motor (McMaster-Carr, Inc., New Brunswick, NJ). A vertical drive shaft supported on bearings was connected to a 1.1 m rotating aluminum arm on which six baskets could be placed, three on each side of the shaft. A sheet-metal liner was placed in the tank to isolate a circular area within the square tank to reduce eddies. Because clod dissolution rate increases with water temperature (Thompson and Glenn, 1994), water temperature in the tank was varied within the ambient range for Fernow streams using an aquarium chiller placed in a corner of the tank. Speed of arm rotation was controlled by the use of three different gear motors nominally rated at 1, 3, or 5 rotations per minute (RPM).

For each trial, baskets containing gravel and a clod were placed on the rotating arm within a 10 cm high section of sampler drilled as described above. The rotating arm could accommodate 6 baskets, but with the 3 and 5 RPM motors only 4 or 2 baskets were used to avoid problems with eddy formation near the shaft. We calculated the arm velocity for each basket arm position from the radius and true RPMs of the rotating arm which we measured with a stop watch (Fig. 3). We estimated the induced velocity of the water in the tank by measuring with a stopwatch the speed of nearly neutrally buoyant particles (table-tennis balls filled with water) for several arm radii marked on the bottom of the tank. We used regression to determine the arm velocity and induced velocity for the position (radius) of each basket, and we determined the actual velocity of the baskets by subtraction (Fig. 3, after Thompson and Glenn, 1993). Trials were each run for three days at a range of temperatures from 0 - 20°C. However, because of logistical problems, we were unable run trials at all temperature and motor combinations. Water from Camp Hollow was used in all trials. According to the recommendation of Thompson and Glenn (1994), we never allowed the ratio of clod cards: tank volume (L) to exceed 1:20. In most cases we used a fresh tank of stream water for each trial.

Due to space limitations within the tank, we were unable to expose clods to zero velocity conditions simultaneously with rotating arm calibration trials. Instead we ran trials identical to those described above except with the motor turned off. Mass loss at zero velocity was determined from regression (described below).

We performed two experiments to determine if there was likely to be a difference in dissolution rate among sites based on water chemistry. For each site except Subwatershed 5, we placed 1 clod in each of 5 20 L buckets filled with stream water from that site. Water chemistry at Watershed 5 was similar to Subwatershed 5 (Table 1) which was inaccessible for obtaining water in necessary quantity. We ran bucket trials for 3 days at two temperatures.

Data analysis

Development and application of calibration model

To correct for dissolution of clods in the tank at zero velocity, we subtracted the mass loss at zero velocity determined by linear regression (mass loss as a function of temperature) from the mass loss in all non-zero-velocity calibration trials. We used linear regression to model corrected mass loss (g/day) as a function of temperature (C) and velocity (cm/s). We rearranged the calibration model to predict velocity in the SHZ from in situ mass loss data.

Hypothesis testing

To determine if calibrated data produce different results from uncalibrated date, we used two dependent variables for hypotheses testing: raw mass loss values from in situ clod cards (uncorrected for mass loss at zero velocity, temperature or velocity), and velocity values determined from the calibration model. We used a factorial ANOVA (SAS, 1990) with a repeated-measures factor (level) and between groups factors (site and season). To test hypotheses involving level and interactions including level, we used MANOVA (SAS, 1990) Test criteria for Wilks' Lambda (multivariate exact F). Because they were conducted in different seasons and because of the potential confounding effect of changes in sediment structure surrounding the samplers during the macroinvertebrate colonization period, we conducted separate analyses for pre- and post-colonization in situ clod card trials. We evaluated the difference between pre- and post-colonization interstitial velocity by comparing regressions of interstitial velocity against stream flow at Watershed 5 for the two sets of field experiments. To reduce heteroscedasticity, mass loss and velocity data were transformed prior to analysis: $\log_{10}$(mass loss +1), $(\text{velocity}+2)^{0.5}$. We conducted a similar analysis for percent saturation of dissolved oxygen determined from access pipes in each reach.

Results

Calibration model

Calibration trials showed clearly that there was a strong effect of simulated water velocity on mass loss of clod cards, and that the relationship depended on water temperature (Fig. 4a). Using the tank we were able to achieve simulated velocities from near zero to about 8 cm/s. A linear regression model of mass loss (corrected for mass loss at zero velocity, Fig. 4b) versus simulated water velocity and water velocity * temperature explained 93 percent of the variation in the data (Fig. 4c).

At zero velocity, the slope of the regression between temperature and mass loss was nearly identical for the calibration tank and the weir pond (Fig. 4b) indicating a consistent relationship between temperature and mass loss of clod cards. However, more mass was lost per day in the weir pond than in the calibration tank. We reasoned that there was enough water circulation in the weir pond caused by stream inflow and seepage through the weir walls to cause the difference. Therefore, to correct for dissolution of clods in the field at "true" zero velocity, we subtracted the mass loss at zero velocity determined by the calibration tank regression from the actual mass loss of clods from the SHZ. We saw no indication on any clods of scraping or burrowing by organisms during the 3 d exposure period.

Application of the calibration model to corrected mass loss data from the field revealed that the range of data used to generate the calibration model (Fig. 4d, surface) overlapped with most of the field data (Fig. 4d, points). However, some clod cards from the field lost more mass than any clod cards during calibration trials. Also, many modeled velocity values were negative due to the zero velocity correction value based on temperature (i.e. the mass lost at zero velocity at a given temperature from Fig. 4b: calibration tank regression) exceeding the mass actually lost in the field. This result is discussed further below.

Water temperature, chemistry and sediment

Compared to an 18 °C annual range in water temperature (Fig. 5), variation in temperature with depth and site were small (Fig. 5, Table 2). Water in the top level was warmer in summer and slightly cooler in winter than the bottom level. The effect was greatest at Subwatershed 5, the most upstream site. At Elklick Run, the most downstream site, there was very little difference in temperature between levels.

Mean percent saturation of dissolved oxygen in the SHZ was lower at Subwatershed 5 and Watershed 5 than at Camp Hollow and Elklick (Repeated measures ANOVA, site effect: $F_{3,208}=67.54$, $P<0.01$; Fig. 5) and in summer (date effect: $F_{25,208}=24.51$, $P<0.01$). The Seasonal effect was least at Elklick Run (date * site effect $F_{75,208}=2.4$, $P<0.01$).

Dissolved oxygen concentration decreased with depth (MANOVA, level effect: $F_{2,207}=191.8$, $P<0.01$, Fig. 5), and the effect was greatest at Subwatershed 5 and Watershed 5 (level * site effect: $F_{6,414}=26.5$, $P<0.01$), and in summer (level * date effect, $F_{50,414}= 2.9$, $P<0.01$) . For two water chemistry parameters that might have an effect on mass loss of plaster clods, pH and conductivity (Thompson and Glen, 1994), the effect of depth was small relative to seasonal or longitudinal differences (Fig. 6). There was a slight tendency for pH to be higher in the top (0-10 cm) level.

There was no effect of site on mass loss in either the March (one-way ANOVA: $F_{2,12}=1.6$, $P=0.25$) or August ($F_{2,11}=0.2$, $P=0.83$) bucket trials despite a 0.7 - 0.9 unit range in pH and a 17-103 µS/cm range in conductivity among sites (Fig. 7). Based on these results, we concluded that across the four sites and three levels we sampled, there was unlikely to be an important confounding effect of water chemistry on mass loss of plaster clods.

Hypothesis testing: effects of site, season, and level on SHZ water velocity

For both dependent variables (uncorrected and uncalibrated mass loss, and modeled velocity), the effects of season, site, and level (depth) were significant for pre- and post-colonization clod card trials (Fig. 8, 9, Table 3). Water velocity through the SHZ was greatest in the top level (0-10 cm) at all sites in all seasons (Fig. 10b). Across sites, SHZ water velocity increased from first through fourth order reaches (Fig. 10c). Across sample dates, SHZ water velocity was highest in March and January and least in October (Fig. 10b). Among-site and among-date variability decreased with depth into the substrate (Fig. 10b-c).

Among sample date variation in interstitial velocity is explained by variation in stream flow. There was a positive linear relationship between mean interstitial velocity from the calibration model (all depths combined) and streamflow from Watershed 5 for pre- and post-colonization clod card trials (Fig. 11). At Camp Hollow, SHZ velocity during the highest flows was lower than would be expected based on data from other seasons. Of this set of samplers, only 4 were available following a storm that occurred at the end of the macroinvertebrate colonization period (Fig. 2a): four samplers were washed away, and two samplers had to be removed to retrieve the baskets. Presumably, the baskets that were not washed away were located in areas of lower than average velocity for the reach, hence the lower than expected interstitial velocities. The slopes of the regression lines were similar between pre- and post-colonization clod card trials, evidence that there was little difference in the relationship between stream flow and interstitial velocity before and after macroinvertebrate colonization.

There was a significant interaction between level and season and between level and site (Table 3). In winter and spring the water velocity through the top level was proportionately much higher than in summer and fall (Fig. 9, 10b). At the first order reach, Subwatershed 5, there was less of an effect of level than at other sites, especially in post-colonization trials (Fig. 9, 10c). There was also a weak but significant interaction between season and site in pre- and post-colonization trials (Fig 10a).

Many clods lost more mass than would be predicted from zero-velocity calibrations or weir pond data (Fig. 8), especially at Subwatershed 5 and in bottom baskets at Watershed 5.

Consequently, application of the calibration model to field data resulted in some negative values for velocity (Fig. 4d, 9). Our interpretation of this phenomenon is that for clod card locations for which the calibration model indicated interstitial velocities < 0 cm/s, water movement through the baskets, if it occurred, which we doubt, was undetectable relative to mass loss at zero velocity. Variation among samples and levels within the negative velocity range was probably related to the volume of interstitial water available for clod dissolution. Where flow and sediment permeability are low as at upstream sites, the volume of water available for dissolution for each clod may have been limited to the few liters of pore space within each sampler, less than the 20 L/clod recommended by Howerton and Boyd (1992) as necessary for avoiding volume effects.

Inferences regarding the effects of level and site did not depend on which dependent variable was used (Table 3, 4; compare F values for mass loss and velocity). This was as expected since the calibration model computes velocity directly from mass loss with an adjustment for temperature, and among-level and among-site differences in temperature were always small (Fig. 5, Table 2). Inferences regarding effects of season do depend on which dependent variable was used since temperature varies greatly among seasons. Although the overall effect of season was significant for both dependent variables, the F values for uncalibrated mass loss were smaller than F values for modeled velocity for pre- and post-colonization clod card trials (Table 3). In comparisons between dates for specific sites, the interpretation may be different when using calibrated versus uncalibrated data. For example, uncalibrated mass loss data (Fig. 8) indicated that in the post-colonization sample from Camp Hollow, water velocity through the top (0-10) level in June was greater than in January; the calibrated data (Fig. 9) indicates the opposite pattern.

During periods of surface flow, velocity at the substrate surface was much higher than in the SHZ (Compare figs. 2b and 9). We do not have direct surface measurements which correspond directly to clod card trials. However, based on seasonal patterns (Fig. 2b), we estimate that surface velocity was about 3-5 times higher than velocity in the top of the SHZ.

Discussion

Sources of variation in water velocity in the SHZ: hydrology and sediment

From our in situ clod card data can be seen the effects of two of the factors that control hyporheic water velocity: flow regime and sediment structure (Bretschko, 1992; Sterba et al., 1992; Vervier et al., 1992; Hakenkamp, Valent, and Boulton, 1993; Naegeli, Huggenberger, and Uelinger, 1996). In all sites and seasons, water velocity decreased with depth (Fig. 9), for which we consider there to be three plausible explanations: (1) decreased influence of advected surface water with depth in all seasons, (2) decreased sediment permeability with depth that was independent of stream discharge and water source (i.e., ground water underflow or advected surface water)or (3), most likely, a combination of sediment permeability and advection of surface water.

Because hyporheic and groundwater generally have a much lower concentration of dissolved oxygen than overlying stream water (Hynes, 1983; Hendricks and White, 1991; Creuz des Chatelliers et al., 1992), dissolved oxygen has been used to identify groundwater inputs to hyporheic zones (e.g., Fortner and White, 1988; Williams, 1989), or infiltration of aerated surface water into the oxygen-depleted hyporheic zone (Williams and Hynes, 1974; Woods, 1980; Whitman and Clark, 1982, Valett, Fisher and Stanley, 1990). Findlay (1995) showed that hyporheic dissolved oxygen content decreased with increasing sediment contact time -- a function of interstitial velocity.

Our dissolved oxygen data suggest a contribution of groundwater to SHZ flow at Subwatershed 5 and Watershed 5 (Fig. 5). However, maximum vertical variation in dissolved oxygen content occurred in June and July during periods of maximum stream temperature (Fig. 5) rather than in September or October when surface flows were least (Fig. 2). Also, dissolved oxygen near the surface (0-10 cm, Fig. 5) was similar at upstream and downstream sites during summer. This suggests that high biological oxygen demand and long contact times (sensu Findlay, 1995) at upstream sites probably accounts for most of the among-site variation in hyporheic dissolved oxygen.

Water within the SHZ is generally a mixture of ground water and surface water (Whitman and Clark, 1982; Hynes, 1983; Castro and Hornberger, 1991). The fact that the disproportionate increase in interstitial water velocity during high base flow periods was restricted to the top level (e.g., Fig. 11) indicates that seasonal variation in flow through the SHZ was dampened with depth; probably because displacement of interstitial water by unmixed advected surface water during high flows only occurs in the top few cm of the substrate (see also White, 1993:65). This reduced seasonal variation in SHZ flow with depth is likely to influence temporal variation in SHZ macroinvertebrate assemblages and biotic processes -- a hypothesis we will explore in a subsequent paper.

Interstitial velocity increased downstream with increasing stream flow and depth to bedrock (Table 1, Fig. 2b and 10c), supporting the qualitative spatial model of White (1993). However, not all of the variation between sites in SHZ flow can be attributed to increases in stream discharge with increasing watershed area. A plot of SHZ velocity versus estimated annual discharge (Fig. 12) shows that SHZ water velocity at Subwatershed 5 and in the bottom level at Watershed 5 was less than would be expected based on mean annual discharge (as estimated from watershed area). Most likely, the lower permeability of sediments at Subwatershed 5 (Fig. 1a) partially accounts for the extremely limited water velocity through the SHZ at that site. Also, although not reflected in surface shovel samples (Fig 1a), and unlike more downstream sites, subsurface sediments at Watershed 5 and Subwatershed 5 are finer than surface sediments (T. Angradi, personal observation) -- probably because depth of scour during floods is shallow in small Fernow headwaters and increases in the downstream direction.

Few published interstitial velocity data are available for comparison with our findings (Palmer, 1993). Perhaps most comparable are dye-tracer data from the Speed River, Ontario (Williams and Hynes, 1974). As in our study, Williams and Hynes (1974) found that interstitial velocity was much less than surface velocity and that variability in velocity decreased with depth into the substrate. However, they reported interstitial velocities much lower than we calculated for Fernow streams. For example, they reported an interstitial velocity of about 0.08 cm/s at a depth of 15 cm (Williams and Hynes, 1974:fig. 3), compared to values of 1-5 cm/s for the middle level (10-20 cm) at Elklick Run. The difference can probably be explained in large part by the finer substrates at

Speed River (Stocker and Hynes, 1972). Also, our method may slightly overestimate true interstitial velocity (i.e., outside samplers and during colonization) due to the low amount of fine sediment within baskets during clod card trials (Table 1b).

Dependent variables

Our conclusions were not strongly affected by which dependent variable we used. In general, only comparisons between samples of contrasting temperature were affected. We originally undertook our calibration trials to allow us to correct for the temperature effect, and because we did not know if the effect of velocity on mass loss would be linear over the typical range of interstitial velocities. On theoretical grounds (Thompson and Glenn, 1994), mass loss versus water motion is expected to be a decreasing rather than a linear function because the exposed area of the clod diminishes with dissolution. In our calibration trials, clods rarely lost more than 30% of their original weight, and we did not detect a non linear effect (e.g., Fig. 4a)

Our original intention in conducting calibration trials was to improve the precision of the clod card method by calibrating in situ mass loss data for temperature and velocity, and that the resulting velocity values would be accurate and comparable to velocity estimates derived by other methods. Because our methods for estimating mass loss at zero velocity did not adequately represent in situ conditions for all treatment groups, negative velocities were generated for certain clod cards, particularly at upstream sites and during low base flow periods where water volume available for dissolution probably limited dissolution rate. However, during high base flow periods and at downstream reaches (Camp Hollow and Elklick Run), we feel our interstitial velocities are accurate because, as in the calibration tank or in the weir pond, mass loss was not likely to have been limited by the volume of water available for clod dissolution. Despite the negative velocity artefact, the calibrated velocity data is useful as a relative measure of variation in water velocity or circulation which can be correlated with other biotic variables to help explain among- and within-treatment-group variability in interstitial macroinvertebrate assemblages.

Generating a calibration model for clod cards is a labor intensive endeavor. Whether it is needed for every study using clod cards will depend of course on the objectives of the study (also see Thompson and Glen, 1994). A calibration model will be most useful under the following conditions: large variation in water temperature or ionic strength among treatment groups, large variation in mass loss among treatment groups (where the non-linear effect might become important), and variation among treatment groups in the method of clod card deployment (e.g, surficial vs. subsurficial). Where only water temperature is a concern, a satisfactory temperature correction might be obtained simply by expressing mass loss per degree day rather than per unit time as has been done for mass loss of leaf packs (Boulton and Boon, 1991).

Interstitial velocity as an environmental covariate for interpreting faunal assemblages

We have compared mean velocity among treatment groups to test hypotheses regarding treatment effects. The velocity value determined for each level in each sampler is useful as a covariate for examining treatment effects on biotic parameters. Although we did not estimate SHZ water velocity simultaneously with macroinvertebrate colonization, individual profiles for each sampler in post-colonization trials (Fig. 13) reveal considerable within-treatment-group (i.e., for a given season, site, and level) variability likely to influence the structure of the macroinvertebrate assemblages inhabiting substrate baskets. For example, we found significant relationships between interstitial velocity and abundance of hyporheic macroinvertebrates in individual baskets, particularly in fall, when interstitial dissolved oxygen concentrations were lowest (R. Hood, unpublished data).

The range in environmental conditions may matter as much as the mean condition to benthic fauna (Palmer and Poff, 1997). Our data show (Fig. 14) that there was much overlap in total (annual) variability in interstitial velocity among sites and depths. Therefore, if variation among hyporheic taxa in environmental tolerances (e.g., to temperature, dissolved oxygen, resource renewal rate) which are linked to variation in interstitial velocity account for most of the spatial variation in hyporheic assemblages, we would not expect a unique hyporheic fauna at each site or depth, except perhaps in bottom baskets (20-30 cm) at upstream sites. We predict that spatial (among site and vertical) variation in hyporheic assemblages will be season-specific, because overlap depends on stream flow (e.g., Fig 11), and will be most strongly linked to factors other than interstitial velocity such as conditions at the substrate surface (e.g. relative amounts of organic detritus and periphyton which influence longitudinal variation), and biotic interactions (e.g., predation risk which influences vertical variation) (Palmer, 1990; McElravey and Resh, 1991).

Comments on the clod card method

Palmer (1993) felt that the development of methods for measuring subsurface flows at small spatial scales was a major challenge in hyporheic research. The clod card method may fill this need in some situations. We stress that our approach to using clod cards to measure water velocity in streams is only that, an approach. Other researchers attempting to use clod cards will need to modify our methodology to suit their needs. Our experience has suggested several refinements and alternate applications of the method for other researchers to consider:

1. Where maximum accuracy is desired, zero-velocity trials should be conducted under conditions as comparable to all treatment groups as possible. For example, in our study we might have attempted to conduct zero-velocity trials with different water volumes to improve the accuracy of velocity calibrations where water movement is very low.
2. Our clod card design may be suboptimal because it has a non-dissolving component (the plastic base) that may interfere with dissolution in some situations . Our clods do not, for example present a dissolvable surface downward. A plaster sphere would be ideal (Muss, 1968).
3. Where possible, calibration should be conducted such that an accuracy check can be made using a standard flow meter. For example, clod cards within substrates might be associated with exposed clod at the surface cards during calibration and _in situ_ so that field velocity data can be related to interstitial flow.
4. Clod size and exposure time should be adjusted such that enough mass is lost

from inundated clods to render unimportant any variation caused by handling loss and measurement error, and enough mass is retained to avoid complex non-linear effects with decreasing surface area (although these effects can be modeled, see Thompson and Glen, 1994).

6. Other possible lotic applications for clods or clod cards include (1) quantifying small spatial scale variation in water circulation in stream pools or springs where water velocity is too low to be metered; (2) making integrated measurements of inundation where other instrumentation is not feasible as in a wave-washed or regulated environment; and (3) as an alternate method for obtaining integrated estimates of water velocity where a velocity meter can not be used (e.g., Peckarsky and Penton, 1990).

Conclusion

We have demonstrated the feasibility of the clod card method for interstitial use in lotic systems. We used a laboratory-calibrated application of clod cards to test hypotheses regarding vertical, seasonal, and longitudinal variation in water velocity through the shallow hyporheic zone of a headwater stream system. Consideration of seasonal, longitudinal and vertical variation in velocity or mass loss data in the context of the annual hydrograph and other data (sediment structure, dissolved oxygen) allow some preliminary inferences regarding the ultimate sources of reach and patch-scale variation in SHZ water velocity: hydrology and bedsediment characteristics. Interstitial velocity measurements can be useful for interpreting patterns of variation in hyporheic fauna. We have suggested ways in which our approach to using clod cards might be modified and improved so that other researches might successfully employ the method.

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We thank Kevin Yokum and the staff of the Timber and Watershed Laboratory for their help in the laboratory and field. Frederica Wood and Thomas Jacob assisted with data analysis. Christine Hakenkamp provided many useful comments on the ms.

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Figure Captions

Fig. 1. Sediment characteristics of study reaches. (a) Cumulative sediment particle size distributions of study reaches from shovel samples. (b) Mean percentage composition of shovel samples across reaches, and actual percentage composition of substrate mix used in samplers. Shaded particle size categories were used in samplers. Particles larger than 64 mm were omitted from the analysis.

Fig. 2. (a) Stream flow from Watershed 5 during the study. Dashed reference line is mean flow during study. Symbols at baseline indicate dates of clod card trials; filled symbols = pre-colonization trials; open symbols = post-colonization trials; arrows indicate three month macroinvertebrate colonization periods. (b) Mean velocity at sampler locations during the study.

Fig. 3. Example of actual velocity calculation from calibration tank. Regression models: arm velocity = 0.056 +0.106 (arm radius), $\underline{r}^2 = 0.99$ (value for $\underline{r}^2$ of regression for arm velocity < 1 because arm speed varied slightly during trial); induced velocity (from neutrally buoyant particles) = 0.394 + 0.131 (arm radius) - 0.00095 (arm radius)^2, $\underline{r}^2 = 0.95$. Points for actual velocity are for basket positions on rotating arm.

Fig. 4. Development of calibration model for determining velocity from in situ clod card mass loss data. (a) Mass loss data from calibration tank uncorrected for mass loss at zero velocity. (b) Mass loss at zero velocity in the calibration tank and the WS 5 weir pond. Regression models: mass loss in weir pond = 0.56 + 0.025 (temperature), $\underline{r}^2$=0.92; mass loss in calibration tank = 0.45 + 0.026 (temperature), $\underline{r}^2$ 0.83). (c) Model fit to mass loss data from calibration tank corrected for mass loss at zero velocity. Regression model: corrected mass loss = -0.0544 + 0.263 (simulated velocity) + 0.0079(simulated velocity * temperature); $\underline{r}^2$=0.93. (d) Model (as in c) rearranged (surface) to allow prediction of velocity from mass loss data, and in situ clod card loss data fit to model (points).

Predictive model shown for range of original calibration data.

Fig. 5. Variation in SHZ water temperature (from thermographs) and dissolved oxygen (from access pipes) during the study. Missing temperature data due to malfunctioning or lost thermographs.

Fig. 6. Variation in pH and conductivity during the study. Values are means from three sets of access pipes in each reach (see text for details). Combined values are for three occasions when samples were inadvertently pooled across levels. Note different vertical scales.

Fig. 7. Results of trials testing for an effect of water quality on mass loss in 20 L buckets.

Fig. 8. Mean mass loss from in situ clod card trials. Filled symbols are for pre-colonization trials; open symbols are for post-colonization trials. Clod card data was not collected at Elklick Run in January. Vertical axis is level of the SHZ: top = 0-10 cm; middle = 10-20 cm; bottom = 20-30 cm.

Fig. 9. Mean velocity calculated from calibration model for in situ clod card trials. Otherwise as in Fig. 8.

Fig. 10. Graphic depiction of main effects and interactions from hypotheses tests. (a) Mean velocity at each site in each season. Error bars show within-site variability across levels. (b) Mean velocity at each level in each season. Error bars show among-sample variability across sites. (c) Mean velocity at each level at each site; legend as in (b). Error bars show among-sample variability across dates. Filled symbols are for pre-colonization trials; open symbols are for post-colonization trials. Post colonization clod card data from Elklick Run and Camp Hollow was omitted from the analysis.

Fig. 11. Relationship between mean interstitial velocity from calibration model and streamflow from Watershed 5 (the gaged watershed) for pre- and post-colonization clod card trials (filled and open symbols respectively). Symbol type indicates basket level. Slopes and r^2 values for pre-colonization trials: Subwatershed 5, 1.52, 0.56; Watershed 5, 2.13, 0.62; Camp Hollow, 1.18, 0.25; Elklick Run, 2.08, 0.39. Slopes and r^2 values for pre-colonization trials: Subwatershed 5, 1.07, 0.28; Watershed 5, 1.94, 0.22; Camp Hollow, 2.18, 0.22; Elklick Run, 2.4, 0.31. January (high flow) data not included in regression for Camp Hollow; see text for explanation. Flow varies among sites because clod card trials were not conducted simultaneously at each site. Note log scale for flow.

Fig. 12. Mean velocity at each site in pre-colonization trials versus estimated mean flow during the study (from Table 1 as estimated by regression from watershed area). Open symbols as in Fig. 10b. Filled symbols show expected mean velocity at Subwatershed 5 based on relationship between mean flow and velocity for other sites.

Fig. 13. Velocity profiles for individual samplers in post-colonization clod card trials. Clod card data was not collected at Elklick Run in January. Vertical axis as in Fig. 8

Fig. 14. Total variation (mean and range pooled across seasons) in interstitial velocity from pre-colonization clod card trials. For each site and depth, _n_=30. Vertical axis as in Fig. 8

Table 2. Mean water temperature for field measurements of clods. Data used in calibration model to calculate velocity from temperature and mass loss. Replacement values for missing data (see Fig. 5) shown in italics. Values were derived from regression of top vs. bottom level temperature using other data in table (r^2=0.99). March 10 and June 16 are the ending dates for spring pre- and post-colonization clod card trials at Subwatershed 5.

Site	Ending date	Top (0-10 cm)	Bottom (20-30 cm)
Subwatershed 5	March 10	4.8	5.4
	June 16	12.6	12.3
	June 23	15.5	14.3
	October 6	14.3	13.3
	October 11	11.5	12.1
	January 25	4.1	*4.5*
Watershed 5	March 9	5.8	5.9
	June 15	13.1	13.2
	June 20	14.8	14.4
	October 5	13.7	13.4
	October 11	11.9	12.3
	January 26	4.0	4.3
Camp Hollow	March 8	6.6	6.8
	June 12	15.9	15.4
	June 19	14.3	13.8
	October 4	13.1	*12.8*
	October 10	12.4	*12.2*
	January 27	*3.2*	3.7
Elklick Run	March 7	5.7	5.5
	June 9	15.3	15.1
	June 17	13.8	13.7
	October 3	*12.7*	12.5
	October 10	*12.3*	12.1
Watershed 5 weirpond	March 10	4.4	na
	June 16	13.3	na
	June 20	14.8	na
	October 5	13.7	na
	October 11	11.9	na
	January 26	4.0	na

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Table 3. Repeated measures ANOVA tests for between-subjects (season, site) effects and MANOVA tests for level effects. Variables tranformed prior to analysis (see text). Post-colonization clod-card data could not be collected in January at Elklick Run and several samples were missing at Camp Hollow in January. We therefore omitted Camp Hollow and Elklick Run from post-colonization hypothesis testing.

Dependent variable	Effect	df	F	P
	Pre-colonization clod-cards			
Mass loss (g/day)	Season	2,107	32.8	<0.01
	Site	3,107	68.2	<0.01
	Season * Site	6,107	2.9	<0.05
	Level	2,106	259.7	<0.01
	Level * Season	4,212	16.8	<0.01
	Level * Site	6,212	2.9	<0.01
Velocity from calibration (cm/s)	Season	2,107	60.4	<0.01
	Site	3,107	67.9	<0.01
	Season * Site	6,107	3.3	<0.01
	Level	2,106	258.9	<0.01
	Level * Season	4,212	16.5	<0.01
	Level * Site	6,212	3.8	<0.01
	Post-colonization clod-cards			
Mass loss (g/day)	Season	2,49	17.3	<0.01
	Site	1,49	37.1	<0.01
	Season * Site	2,49	5.1	<0.01
	Level	2,48	230.5	<0.01
	Level * Season	4,96	4.6	<0.01
	Level * Site	2,48	17.0	<0.01
Velocity from calibration (cm/s)	Season	2,49	38.2	<0.01
	Site	1,49	35.3	<0.01
	Season * Site	2,49	4.4	<0.05
	Level	2,48	226.6	<0.01
	Level * Season	4,96	4.5	<0.01
	Level * Site	2,48	15.7	<0.01

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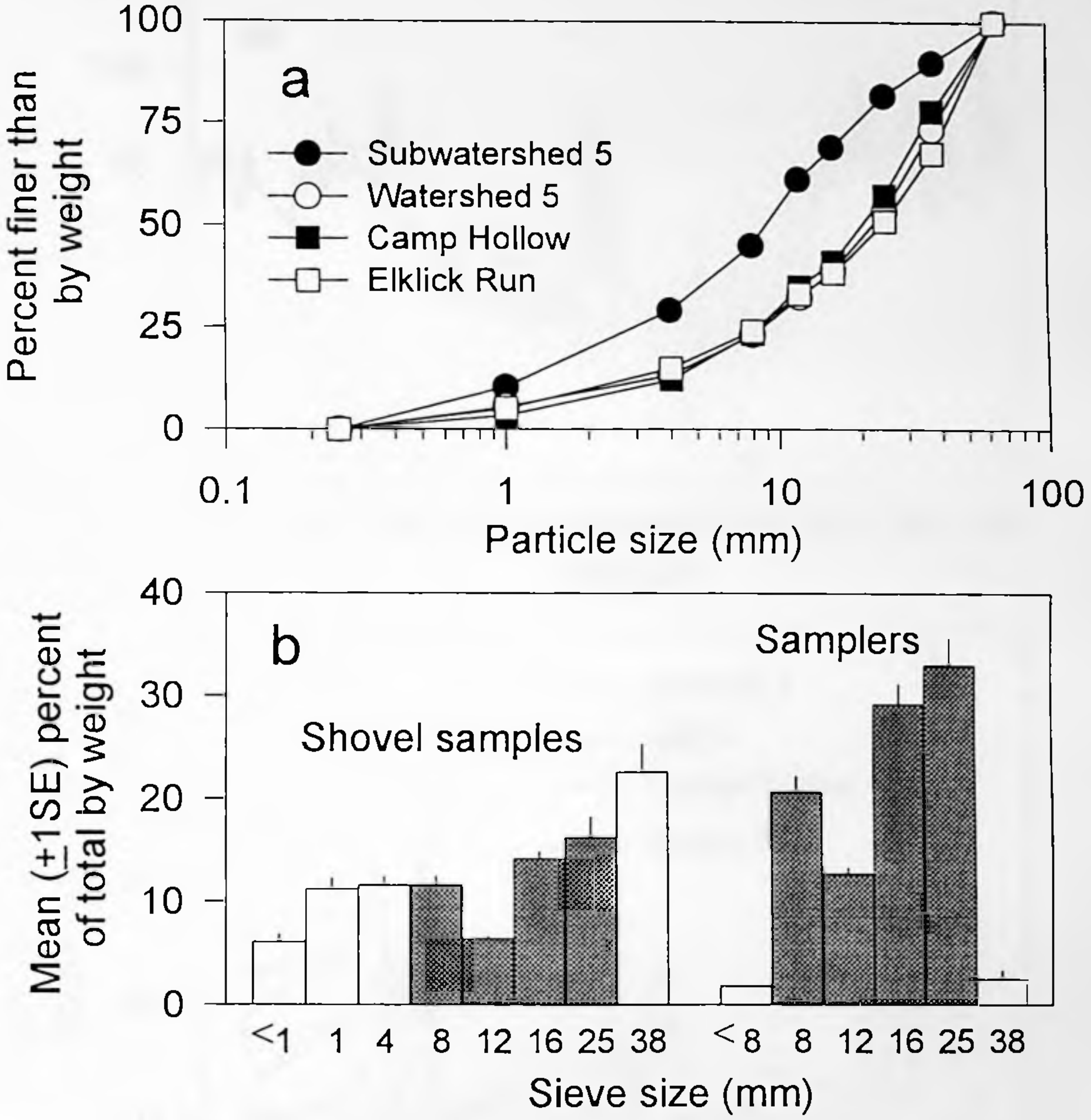
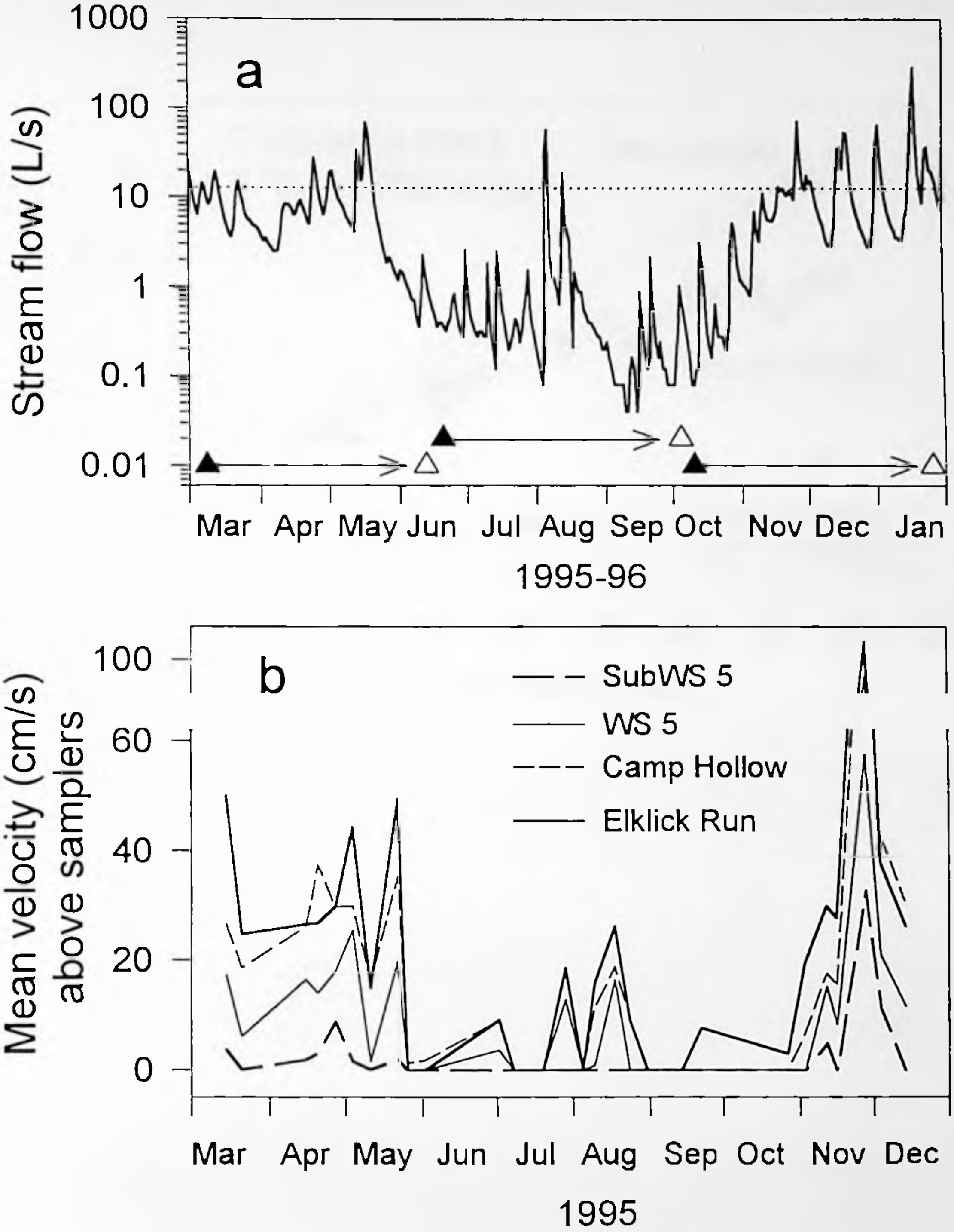
Table 1. Physical, chemical and sedimentological characteristics of study reaches. Water chemistry values are means (±1SE) across dates and levels (n=34). Sediment values are for shovel samples collected at beginning of study

	Subwatershed 5	Watershed 5	Camp Hollow	Elklick Run
Stream order	1	2	3	4
Watershed area (ha)	10	36	178	575
Mean annual discharge (L/s)[1]	2	10	43	139
Reach gradient (%)	6.7	4.6	2.7	1.2
Reach elevation (m)	756	720	677	647
Depth to bedrock (cm)[2]	27,37,38	15, >53, >56	82, 100,110	76, 100, >100
pH	6.3 (0.03)	6.3 (0.02)	6.8 (0.03)	7.3 (0.04)
Conductivity (μS/cm)	32.5 (0.51)	32.4(0.61)	47.9 (1.82)	99.5 (6.45)
Alkalinity (mg/L as $CaCO_3$)	5.2 (0.40)	5.6 (0.34)	12.2 (0.99)	41.1 (3.72)
Calcium (mg/L)	2.7 (0.09)	2.6 (0.09)	5.1 (0.34)	15.5 (0.11)
Magnesium (mg/L)	1.1 (0.03)	1.1 (0.03)	1.6 (0.07)	2.1 (0.04)
Potassium (mg/L)	0.9 (0.04)	0.9 (0.04)	1.0 (0.04)	0.9 (0.04)
Sodium (mg/L)	0.8 (0.03)	0.8 (0.04)	0.8 (0.03)	0.9 0.04)
Chloride (mg/L)	0.6 (0.02)	0.6 (0.02)	0.6 (0.01)	0.7 (0.02)
Sulfate (mg/L)	7.1 (0.21)	6.7 (0.14)	6.8 (0.06)	7.0 (0.12)
Nitrate (mg/L)	0.2 (0.01)	0.2 (0.01)	0.6 (0.02)	0.6 (0.02)
D_g[3] (mm)	6.4	15.3	14.8	15.0
Fredle index of substrate permeability[4]	2.5	7.1	7.3	6.7

1. Values determined from regression. See text for details.
2. Values determined from three pits excavated in each reach. Value for Subwatershed 5 is depth to a clay layer.
3. Geometric mean diameter excluding particles >64 mm, after Platts, Shirazi and Lewis (1979).
4. After Lotspeich and Everest (1981).



Angradi and Hood: Fig. 1



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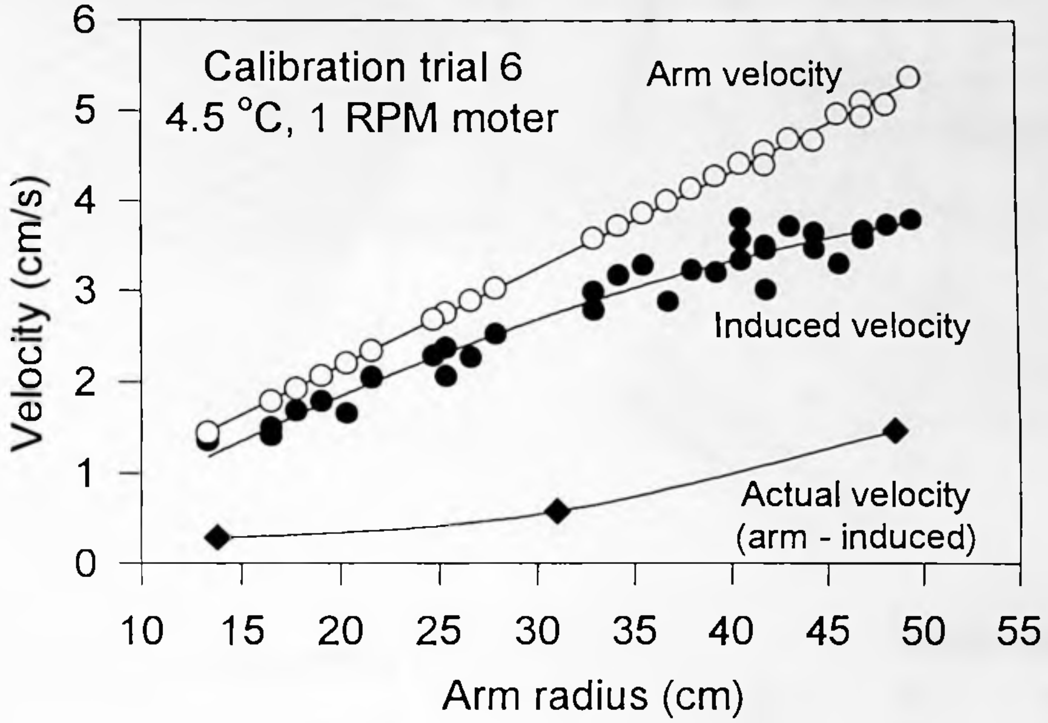

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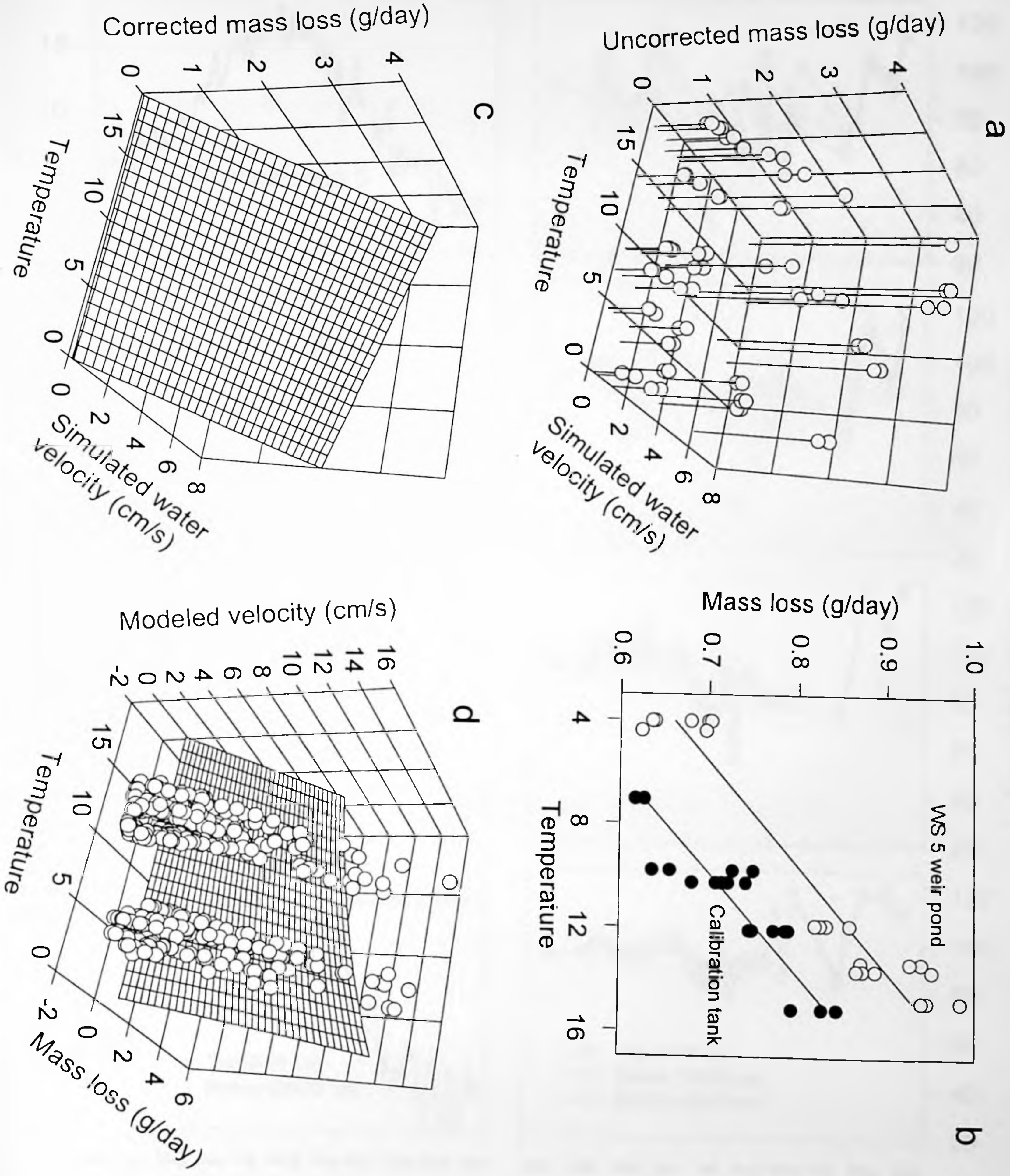

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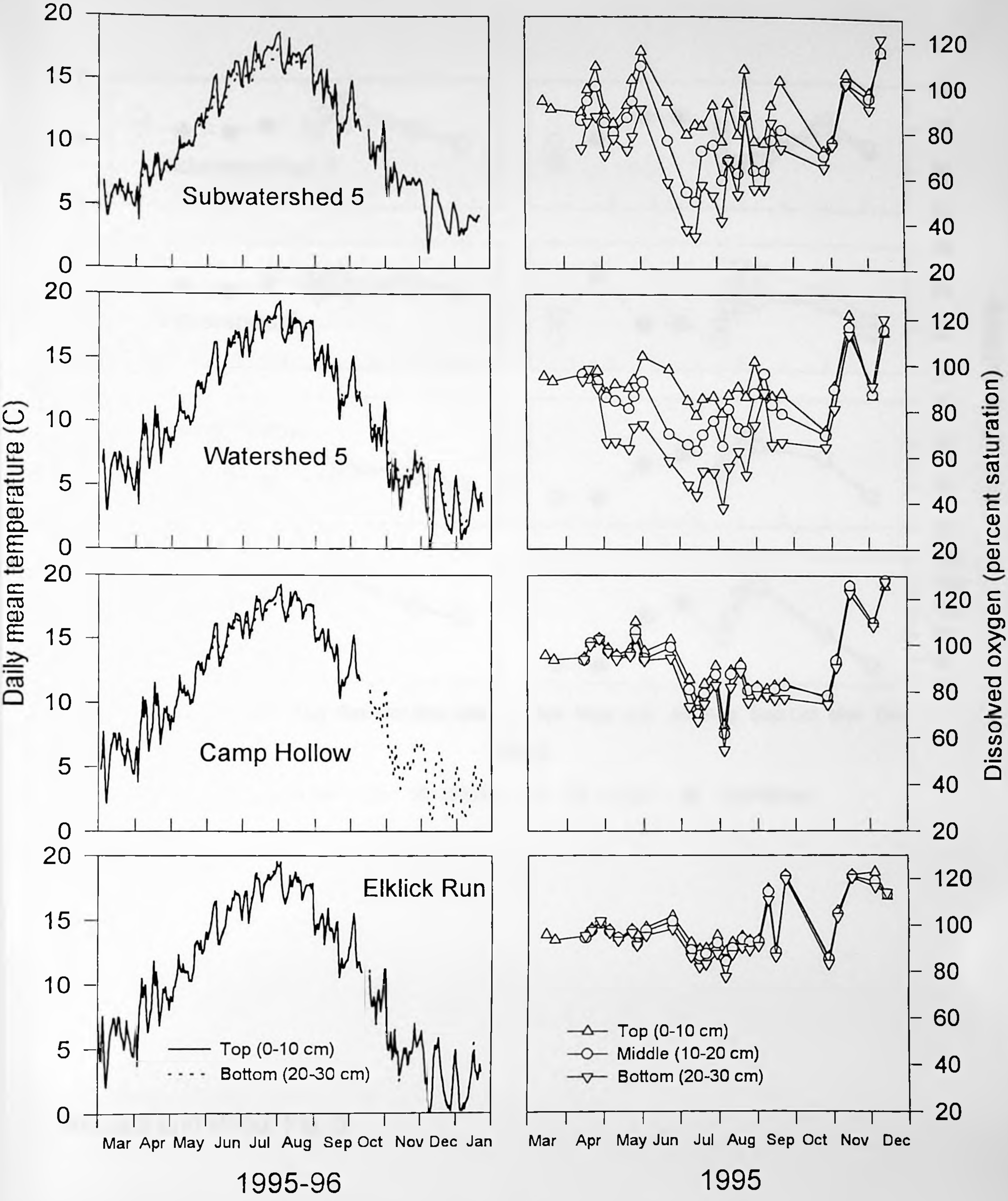

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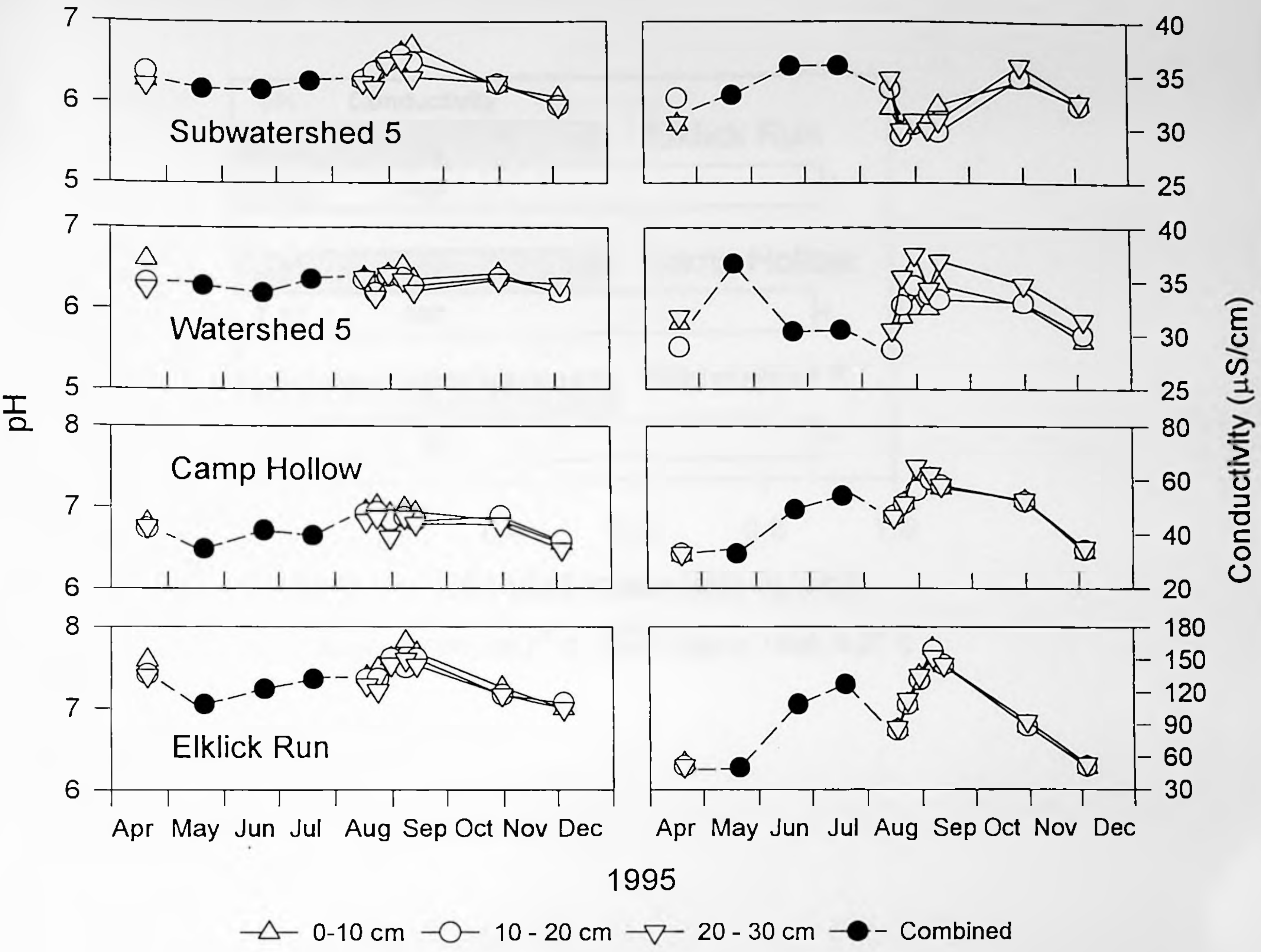

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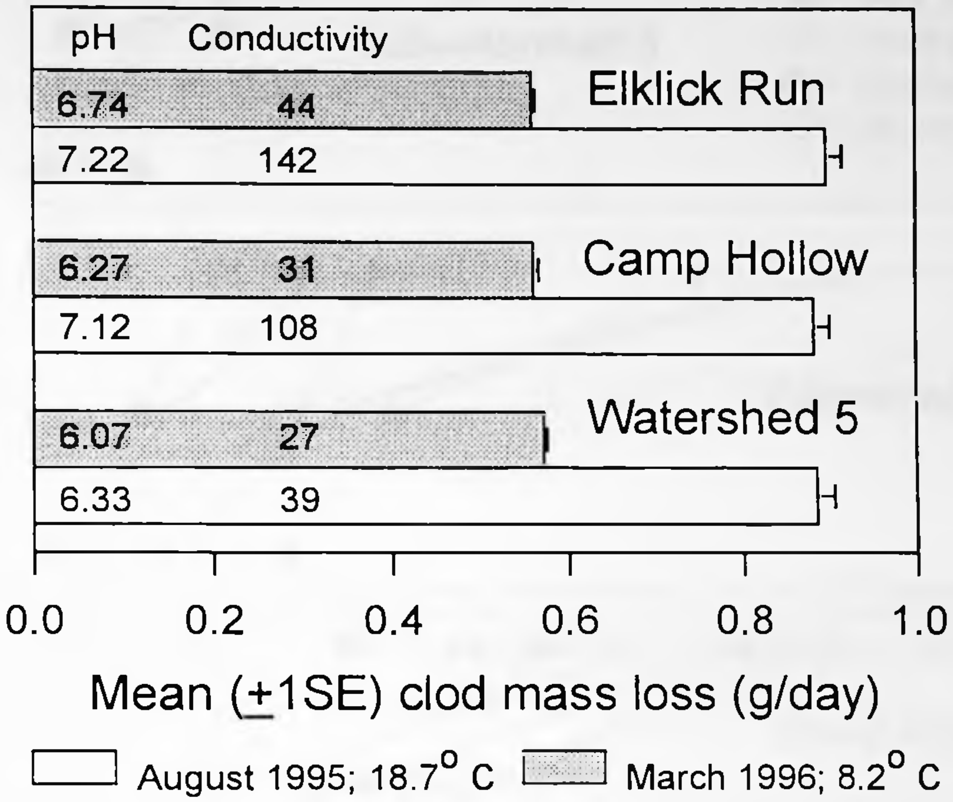

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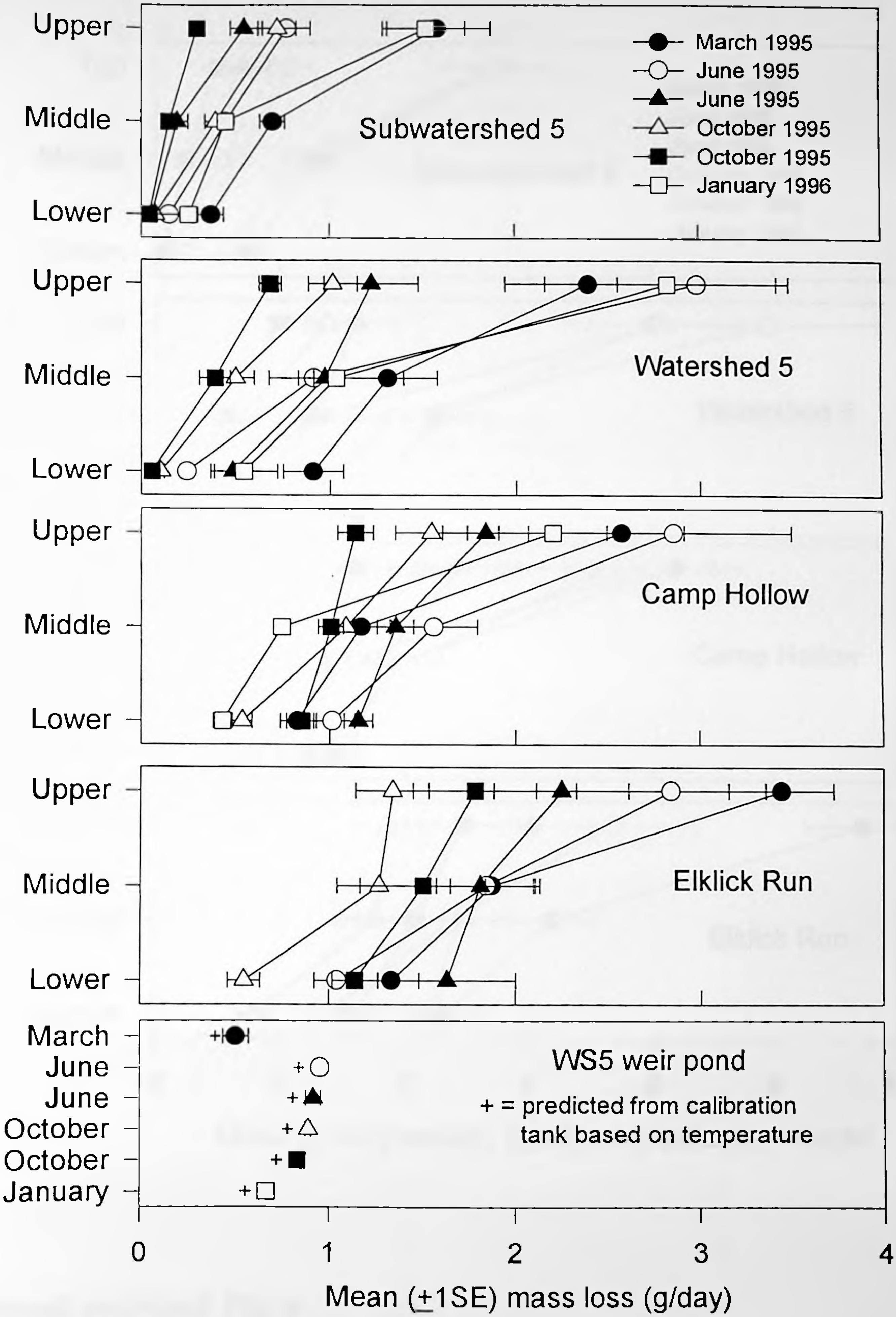
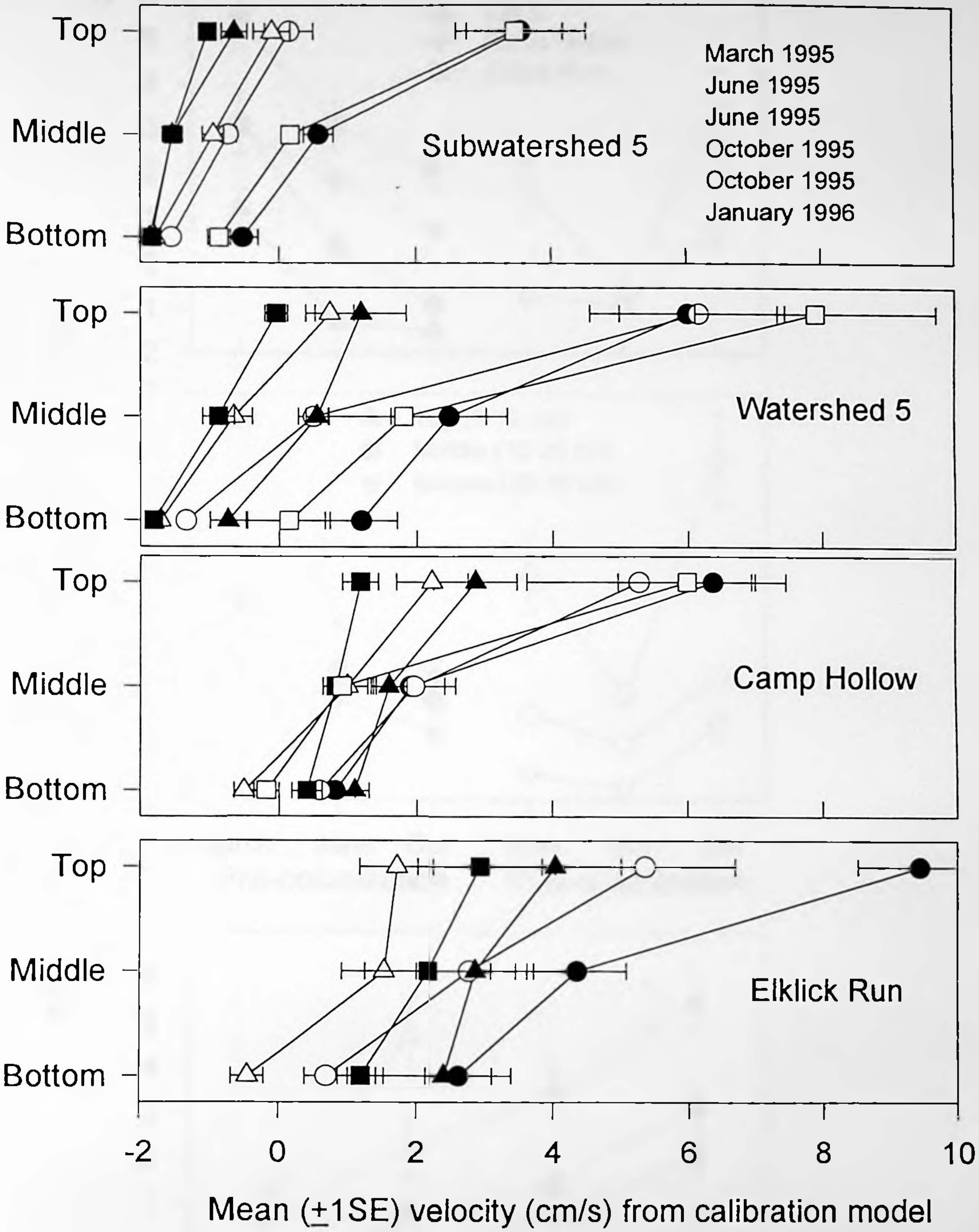
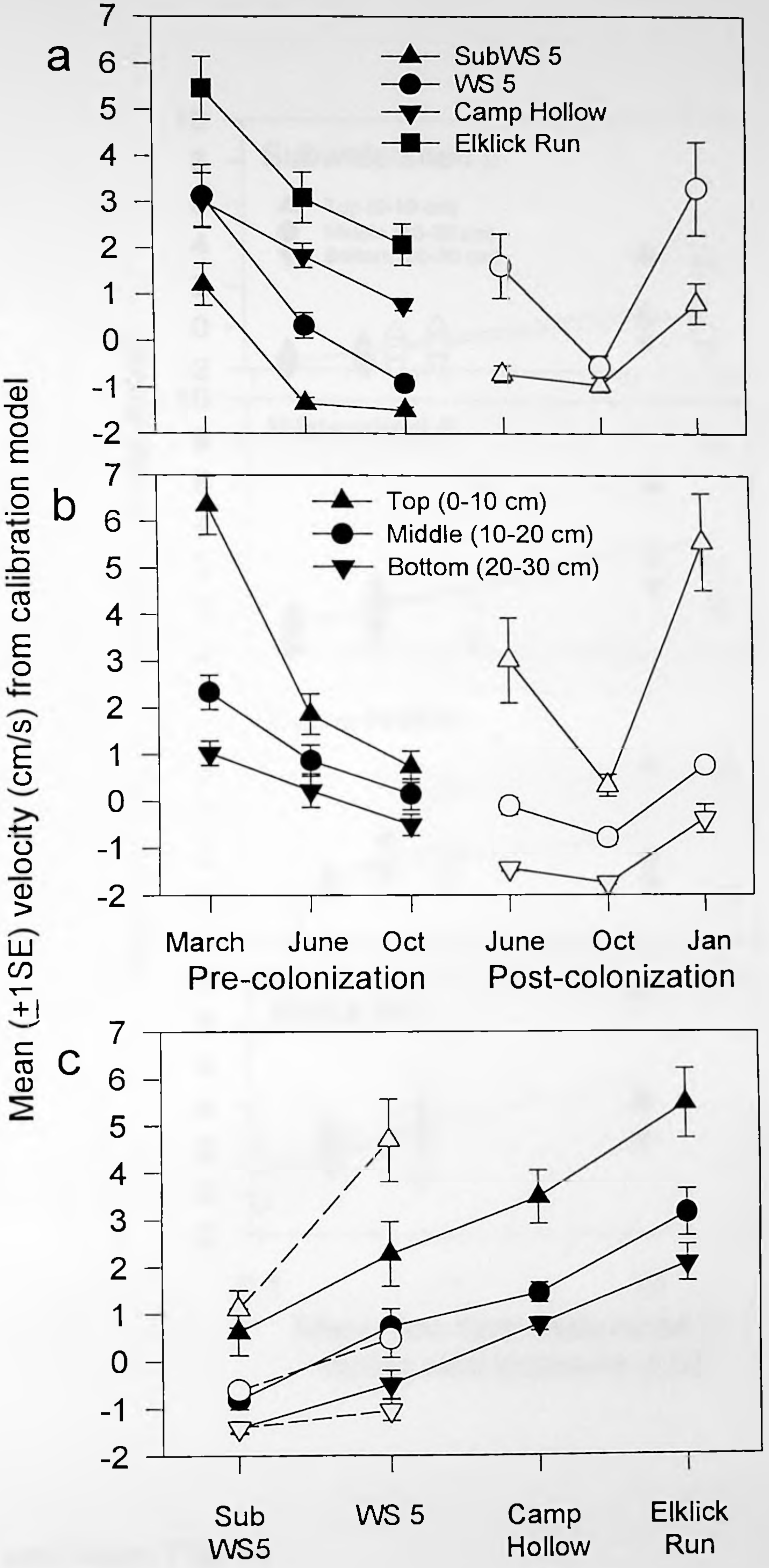


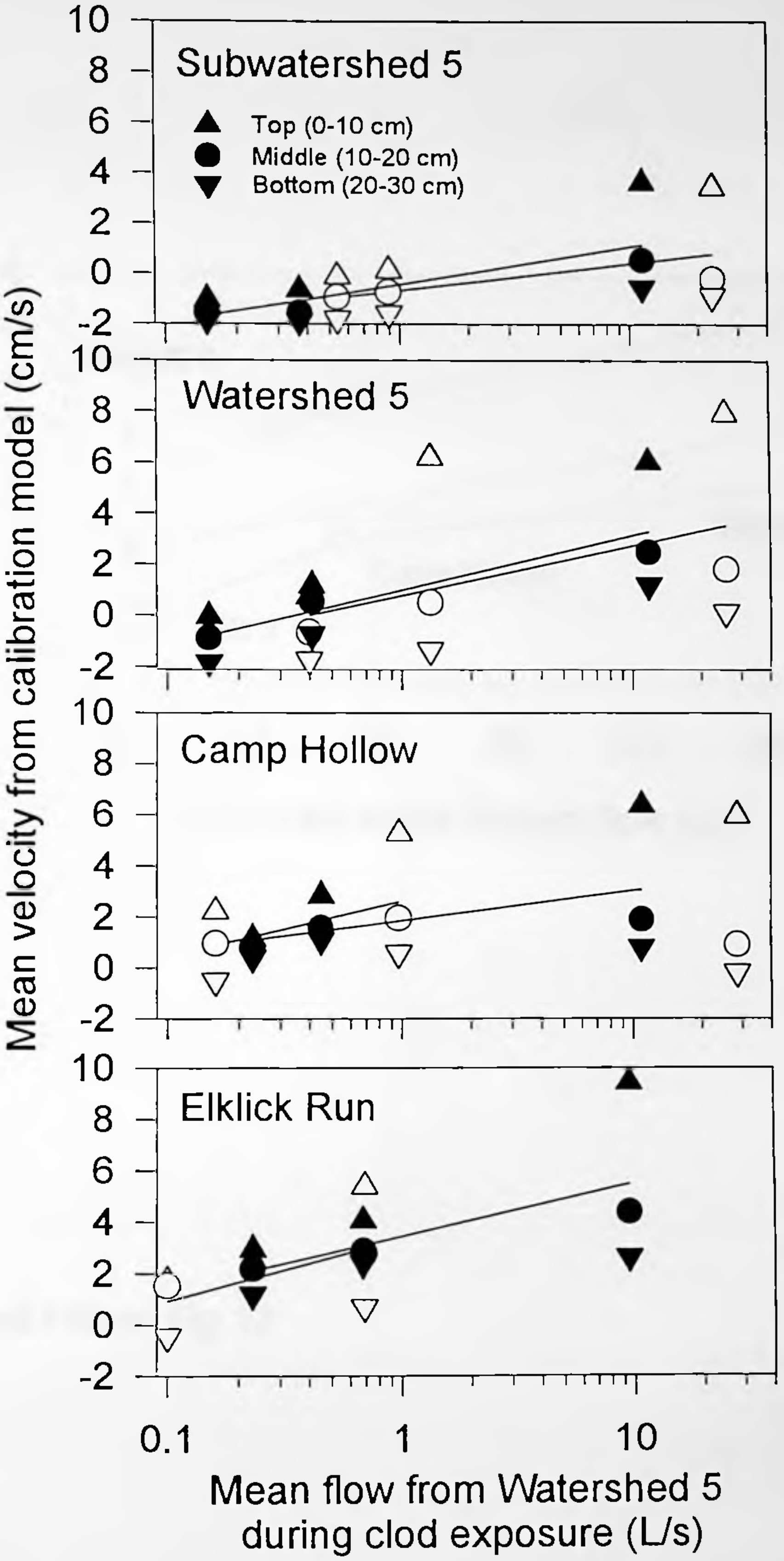
Angradi and Hood: Fig. 8



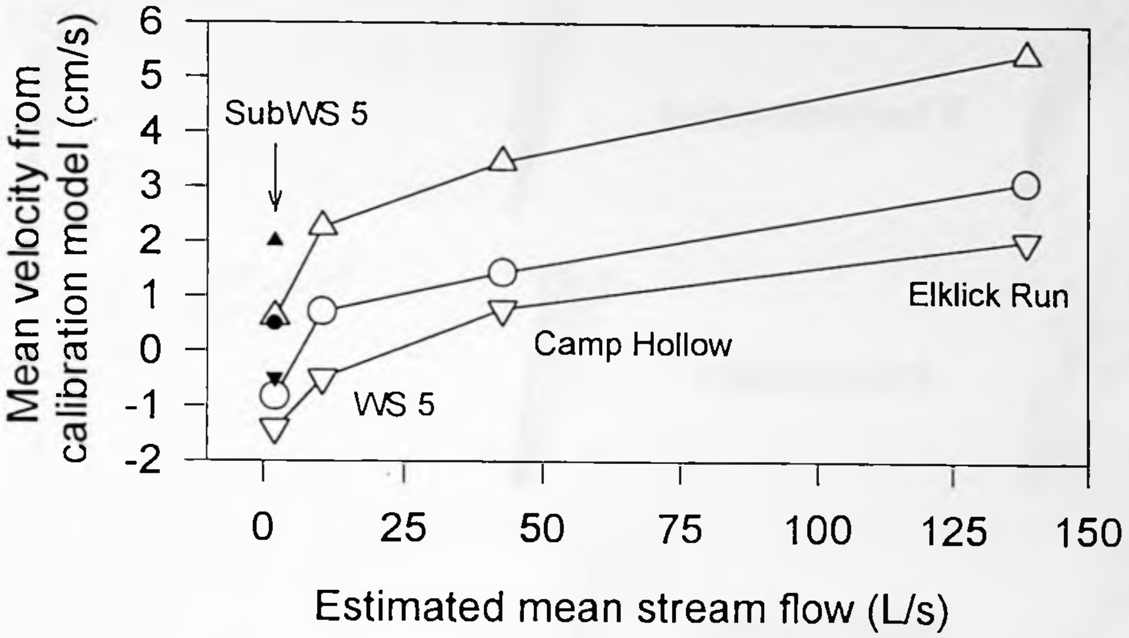
Angradi and Hood: Fig. 9



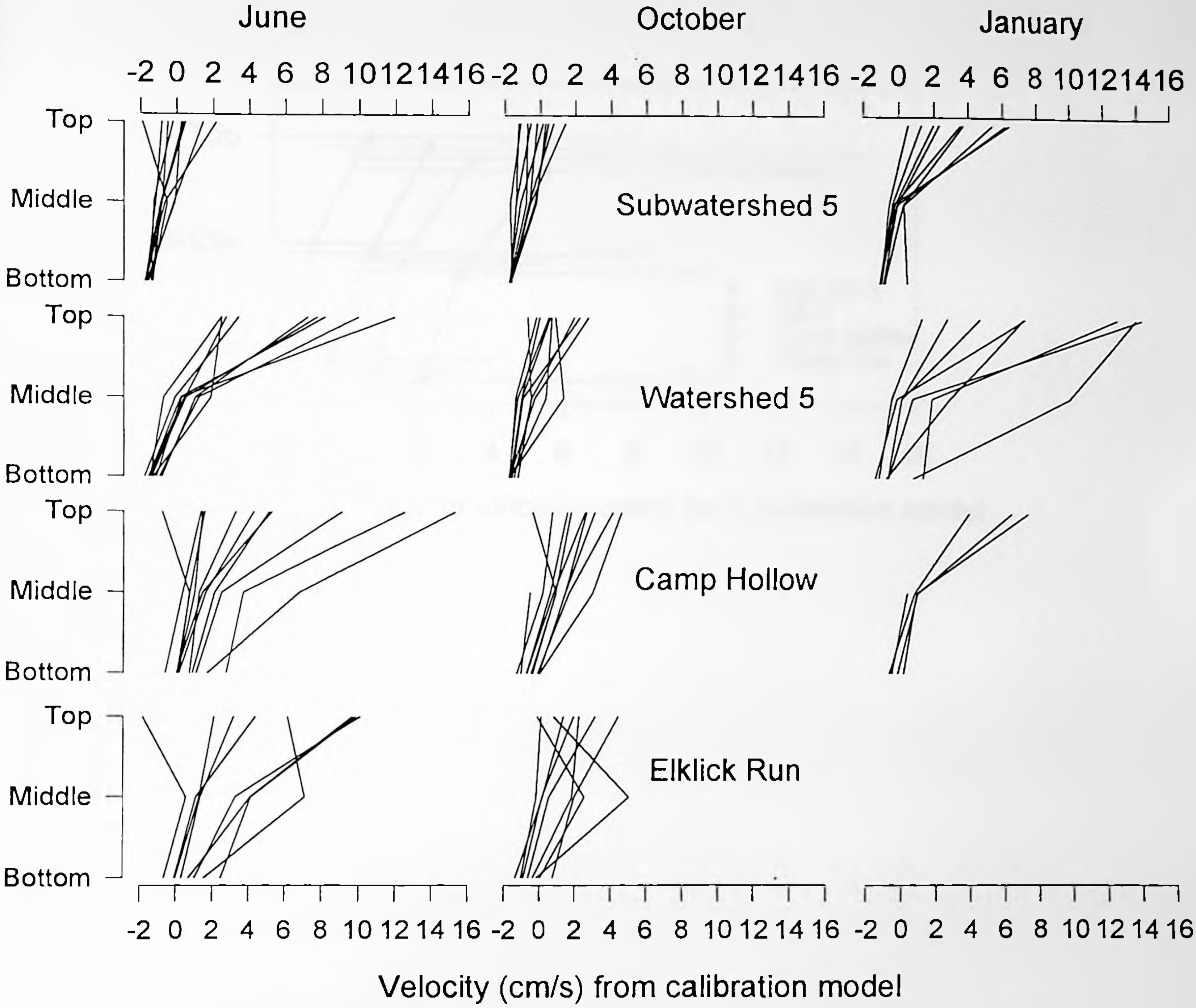
Angradi and Hood: Fig. 10



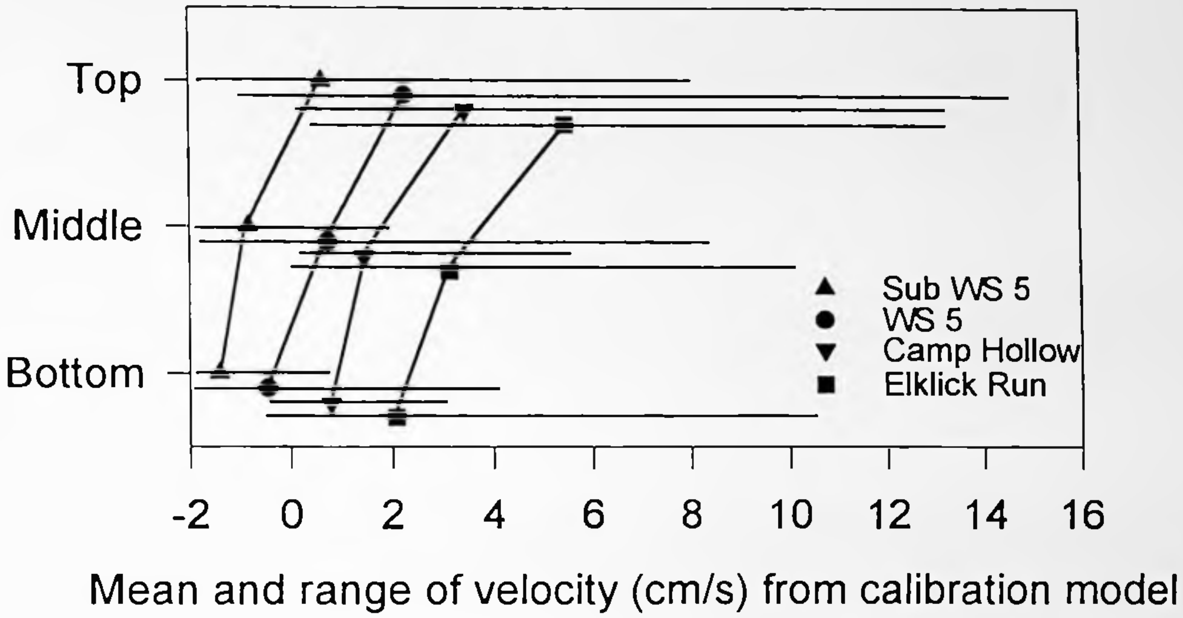
Angradi and Hood: Fig. 11



Angradi and Hood: Fig 12



Angradi and Hood: Fig. 13



Angradi and Hood: Fig. 14