

Seasonal Variation in Faunal Distribution within the Sediments of a Canadian Shield Stream, with Emphasis on Responses to Spring Floods

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The vertical distribution of invertebrates within the shallow substrates of a Canadian Shield lake outflow stream was examined to determine the importance of season and spate on distribution pattern. Stream invertebrates were found throughout the year to depths of 25 cm below the sediment surface, only about 5 cm above bedrock. Insect abundance showed a strong seasonal pattern, with highest numbers occurring during early winter (December) in all depth zones. Except for Chironomidae, the majority of the insects found below 5 cm were early instar larvae of those found regularly at the surface. Insect abundance was generally higher at the sediment surface than for all other depth zones combined and consisted mainly of one taxon, *Prosimulium* (Diptera: Simuliidae). Non-insect invertebrates were always more abundant in the hyporheos than at the surface. Total invertebrate abundance (primarily *Prosimulium*) at the sediment surface decreased by about 40% during the spring snowmelt flood, but no significant changes in abundance occurred in the hyporheos during this period. Chemical analysis of surface and interstitial water showed that both pH and alkalinity decreased slightly in surface waters during the flood, but increased within the hyporheos, particularly on the rising limb of the flood hydrograph.

La distribution verticale d'invertébrés dans les substrats peu profonds d'un émissaire d'un lac du Bouclier canadien a été examinée dans le but de déterminer l'importance de la saison et des crues sur l'allure de la distribution. Des invertébrés ont été trouvés tout au long de l'année à des profondeurs de 25 cm en-dessous de la surface des sédiments, à seulement 5 cm au-dessus de la couche rocheuse. L'abondance des insectes présentait une allure saisonnière prononcée, les nombres les plus élevés étant notés au début de l'hiver (décembre), dans toutes les zones de profondeur. À l'exception des chironomidés, la majorité des insectes trouvés à plus de 5 cm de profondeur étaient des larves aux premiers stades de croissance des insectes couramment trouvés à la surface. Les insectes étaient généralement plus abondants à la surface des sédiments que dans toutes les autres zones réunies et ceux-ci étaient généralement représentés par un seul taxon : *Prosimulium* (Diptère : imuliidé). Les invertébrés autres que des insectes étaient toujours plus abondants dans l'hyporhéos qu'à la surface. L'abondance totale des invertébrés (surtout les *Prosimulium*) à la surface des sédiments diminuait de 40 % environ au cours de la crue de printemps due à la fonte des neiges, mais aucune modification appréciable de l'abondance dans l'hyporhéos n'a été notée durant cette période. L'analyse chimique de l'eau de surface et de l'eau interstitielle a montré que le pH et l'alcalinité diminuaient légèrement dans les eaux de surface au cours de la crue, mais que leurs valeurs augmentaient dans l'hyporhéos, surtout pendant la période correspondant à la partie ascendante du graphique de la crue.

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The deeper sediments of streams (known as the hyporheic zone; Williams and Hynes 1974) have been suggested as a possible refuge from short-term physical or chemical stresses for stream invertebrates, since recolonization after flooding or pesticide application is often too rapid to be attributed to downstream drift or upstream migration alone (Williams and Hynes 1976; Williams 1984). Vertical migrations from the hyporheos into the surface layers after a flood have been recorded by Williams and Hynes (1976) and there is some evidence for directed movements deeper into the substrate during

a summer spate (Williams and Hynes 1974). Predictable increases in stream discharge occur regularly in Canadian streams, especially those associated with the rapid melting of snow in spring, but the vertical distribution of the benthos through the stages of a spring flood is not known. The seasonal invertebrate distribution pattern within the sediments of Precambrian (Canadian) Shield streams is also poorly known, largely due to problems in sampling these habitats. In contrast with more conventional streams that possess deep, well-drained gravel substrates, substrates in many shield streams are shallow and consist of large angular materials overlying granitic bedrock, making sampling difficult.

This study is part of a larger study of the distribution of stream invertebrates in acid-impacted streams in central Ontario. The

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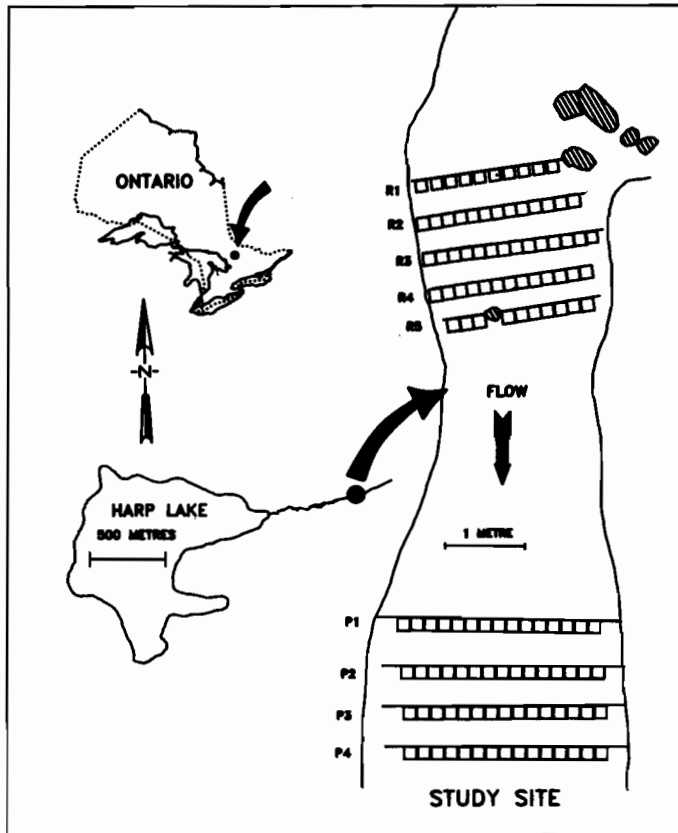


FIG. 1. Study site and distribution of surface substrate baskets along transects in each of the riffle (R) and pool (P) reaches of Harp Lake Outflow, October 1985 – June 1986.

area in which the study stream is located receives significant inputs of acid precipitation ($\text{pH} \approx 4.2$; Dillon et al. 1978), but the study stream itself is not considered to be acid impacted. The objective of the study was to provide baseline data on the seasonal and spring flood vertical distribution patterns of selected abiotic (pH , alkalinity, and dissolved oxygen) and biotic (invertebrate abundance) parameters in sediments of a non-acid-impacted stream.

Study Site

Harp Lake outflow is located near the town of Huntsville in south-central Ontario ($45^{\circ}23'N$, $79^{\circ}08'W$; Fig. 1). Riparian vegetation is primarily beech-maple (Seip et al. 1985), and the study stream possesses a shallow substrate overlying granitic bedrock (details of catchment geology and soil geochemistry are provided in Jeffries and Snyder 1983). The mean annual pH during 1982–86 was 6.3 (range 5.7–6.8) and the mean alkalinity was 3.3 mg ($65.9 \mu\text{eq}$) CaCO_3/L (range 1.4–4.2 mg/L (28 – $84 \mu\text{eq/L}$) (P. Dillon, Dorset Research Station, Dorset, Ont., unpubl. data).

The study site was 500 m downstream of the lake outlet and consisted of a riffle reach (~ 2 m wide \times 4 m long \times 10–15 cm deep at low water) with a pool (~ 3 m wide \times 5 m long \times 60–75 cm deep) immediately downstream (Fig. 1). Substrate depth averaged about 30 cm in both reaches, although it was more variable in the pool due to deposition and scouring of fine materials associated with variations in stream discharge. The substrate in both zones consisted of large (up to 0.5 m diameter) angular pieces of granite interspersed with smaller

pieces (~ 0.1 m diameter). The large interstitial spaces were filled with gravel and sand. During low water periods the large mineral sediments in the pool zone were overlain by varying amounts of sand and organic debris.

Methods

Invertebrate Sampling

Invertebrates were sampled at 2- to 3-mo intervals from October 1985 to June 1986 to establish the seasonal pattern of vertical distribution within the sediments. Sampling frequency was increased to 2-wk intervals from the beginning of March to assure an adequate pre-flood sample and then at 0, 1, 4, 8, and 24 d after the onset of flooding to obtain flood and post-flood samples. Consequently, many more samples were collected in the spring than at any other time of year. The following sampling periods were designated for the analysis of seasonal distribution: fall, 17 October 1985; early winter, 12 December 1985; late winter, average of samples collected on 11 March and 26 March 1986; flood period, average of samples collected 31 March, 1 April, 4 April, and 8 April 1986; spring, 24 April 1986; and early summer, 12 June 1986.

Hyporheic invertebrate densities were sampled by the standpipe corer of Williams and Hynes (1974) modified for use in the shallow substrates of Harp Outflow. Five 25-mL samples were collected at two depths (10–15 and 20–25 cm) in each reach on each sampling date. The corer did not sample invertebrate densities at the sediment surface (0–5 cm depth), so these were obtained using artificial substrates. Wire baskets ($15 \times 15 \times 5$ cm \times 6 mm mesh) were filled with a standardized volume and size selection of in situ substrate materials and imbedded into the substrate. The basket samples were chosen because they allowed an estimate of density per unit volume (for comparison with hyporheic samples) and because preliminary sampling showed that the baskets compared favourably with kick samples in species composition and relative abundances for the same area of stream (D. J. Giberson, unpubl. data). Sixty baskets were placed into each of the riffle and pool zones prior to leaf fall and autumn rains and left to condition for a minimum of 2 mo. Five were collected randomly from each zone on each sampling day. Benthic insects were identified to genus where possible and to major taxonomic grouping for noninsect invertebrates. Samples were converted to numbers per litre to facilitate comparisons between hyporheic and surface invertebrates.

Water Chemistry and Discharge

Surface water samples for chemical analyses were collected weekly during the study period (October 1985 – June 1986). For the snowmelt study (pre-flood, flood, and post-flood periods; 11 March – 24 April 1986), surface and interstitial water samples (Williams and Hynes 1974) were collected at two locations within each zone on each sample date. Alkalinity was determined by Gran titration, pH by a combination glass electrode standardized against appropriate buffers, and dissolved oxygen (DO) by the Winkler titration at the Dorset Research Laboratory. Water temperature was determined from a maximum-minimum thermometer located just upstream of the study area.

Stream discharge was measured upstream from the study area by determining the velocity of the water at 0.1- or 0.2-m intervals from stream bank to bank and combining these measurements with the cross-sectional area of the stream (discharge =

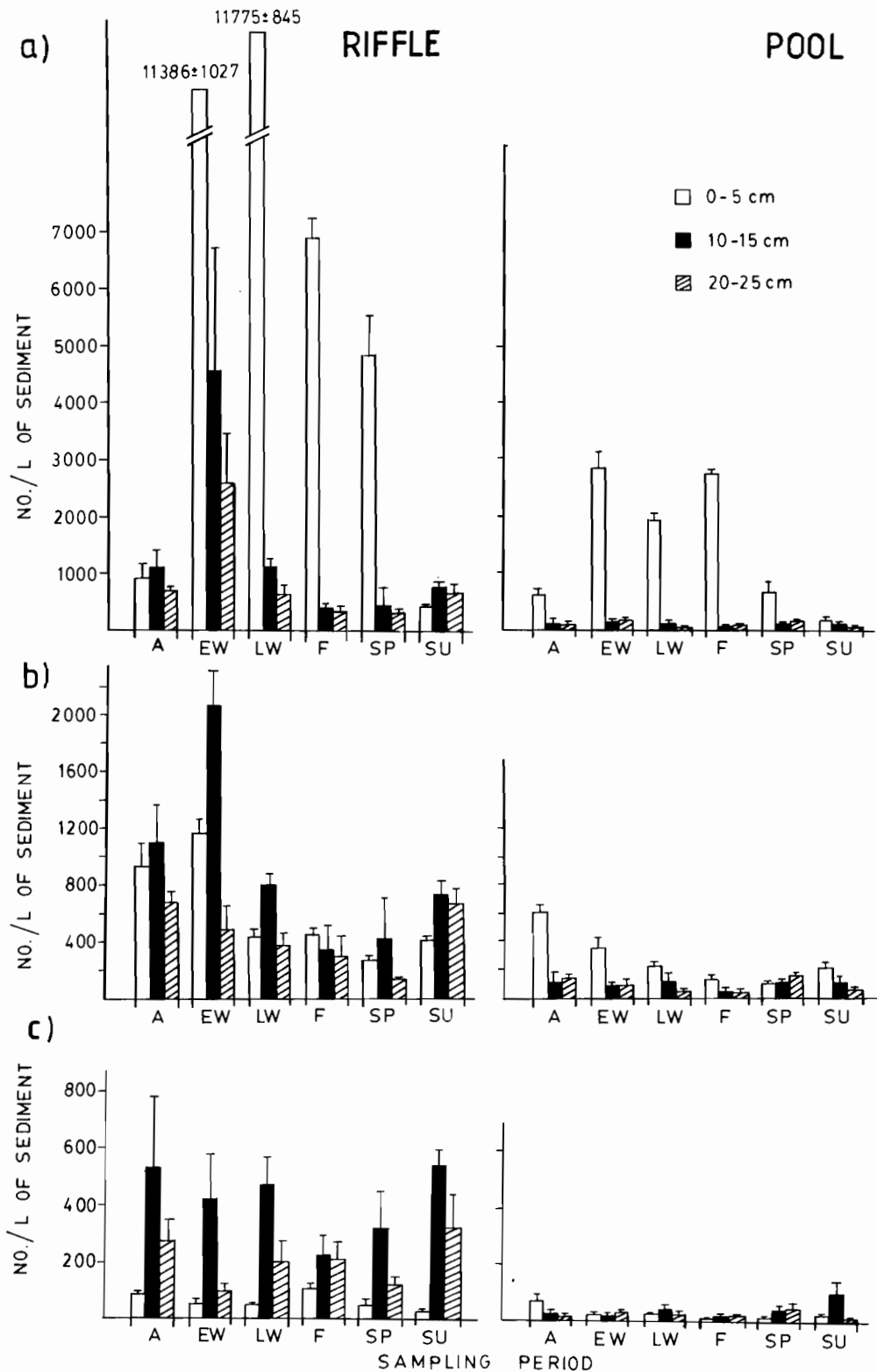


FIG. 2. Seasonal pattern of distribution within the substrates of Harp Lake Outflow, October 1985 – June 1986. (a) Total invertebrate abundance; (b) total invertebrates excluding Simuliidae; (c) Abundance of noninsect invertebrates ($\bar{x} \pm SE$; note difference in scale). A, autumn (17 Oct. 1985); EW, early winter (17 Dec. 1985); LW, late winter (11 Mar. and 26 Mar. 1986 samples averaged); F, flood period (31 Mar. – 8 Apr. 1986 samples averaged); SP, spring (24 Apr. 1986); SU, summer (12 June 1986).

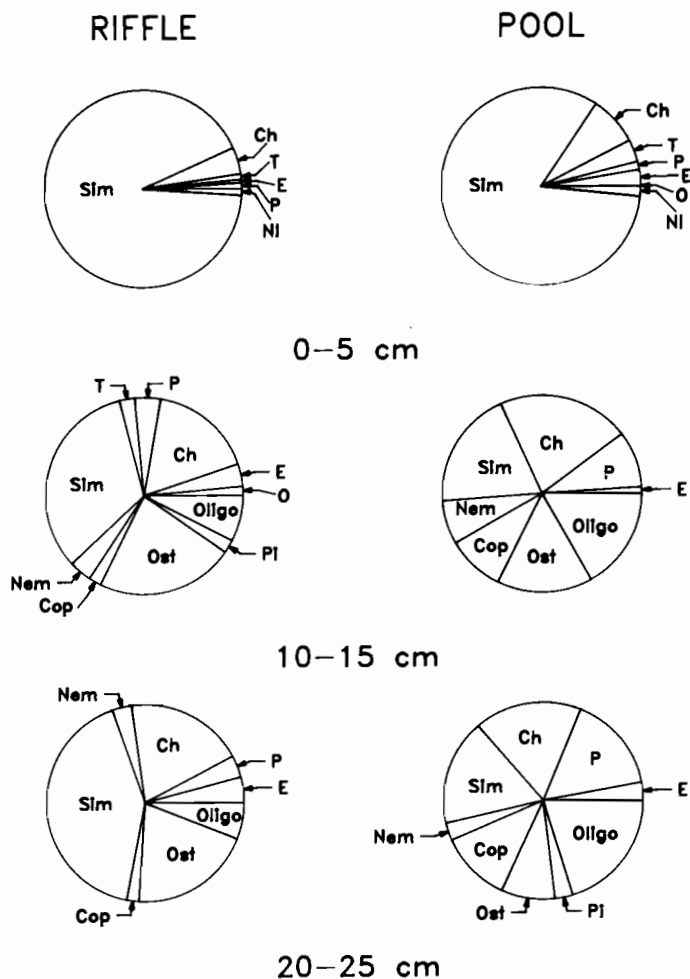


FIG. 3. Proportion of invertebrate groups inhabiting different depth zones in two reaches of Harp Outflow, October 1985 – June 1986. E, Ephemeroptera; P, Plecoptera; T, Trichoptera; Ch, Chironomidae; Sim, Simuliidae; O, other insects; NI, noninsect invertebrates; Ost, Ostracoda; Oligo, oligochaetes; Nem, nematodes; Pi, Pisidiidae; Cop, Copepoda.

cross-sectional area \times velocity). Water velocity was measured with either an Ott or a Teledyne Gurley Pygmy meter.

Results

Seasonal Distribution

Invertebrates

Total invertebrate abundance varied seasonally in all depth zones (0–5, 10–15, and 20–25 cm) and both reaches. Invertebrates were most abundant at the surface (0–5 cm) during the winter months in the riffle reach and during the winter and the spring flood period in the pool (Fig. 2). Total numbers in the hyporheos (10–15 and 20–25 cm depths) reached peak values in the riffle in early winter and were generally low throughout the year in the more unstable pool reach (Fig. 2). Densities within the hyporheos were not related to those at the surface on any given sampling date. However, most insects in the hyporheos at this time were early instar larvae of those found at the sediment surface later in the year (instar analysis was based on wingpad development in hemimetabolous insects and size in holometabolous ones; D. J. Giberson, unpubl. data).

Faunal composition, particularly of the insect taxa, also varied seasonally in all depth zones. Insects were generally

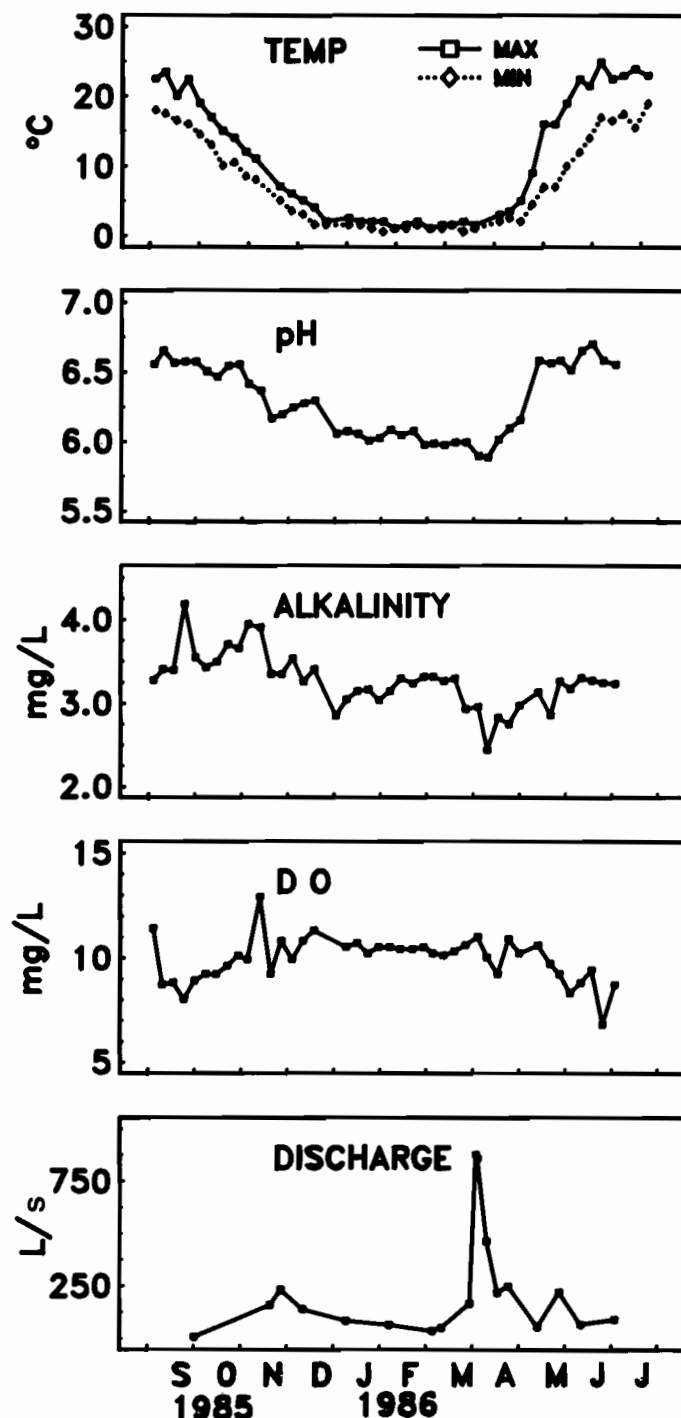


FIG. 4. Physical (temperature and discharge) and chemical (DO, pH, and alkalinity) patterns in Harp Lake Outflow, September 1985 – July 1986.

common in the surface sediments throughout the year, but were only important in the substrate during the fall–winter and early summer recruitment periods (Fig. 2). Noninsect invertebrates, on the other hand, varied little seasonally, but were more common in the hyporheic zone than at the surface (Fig. 2c).

Simuliids, especially *Prosimulium*, comprised about 90% of the total annual surface (0–5 cm) population in both reaches (Fig. 3). The extremely high numbers of blackflies (>600 000/m² at the sediment surface during the winter months) obscured the distribution pattern for the other taxa, so vertical distribution was plotted both including (Fig. 2a) and excluding (Fig. 2b)

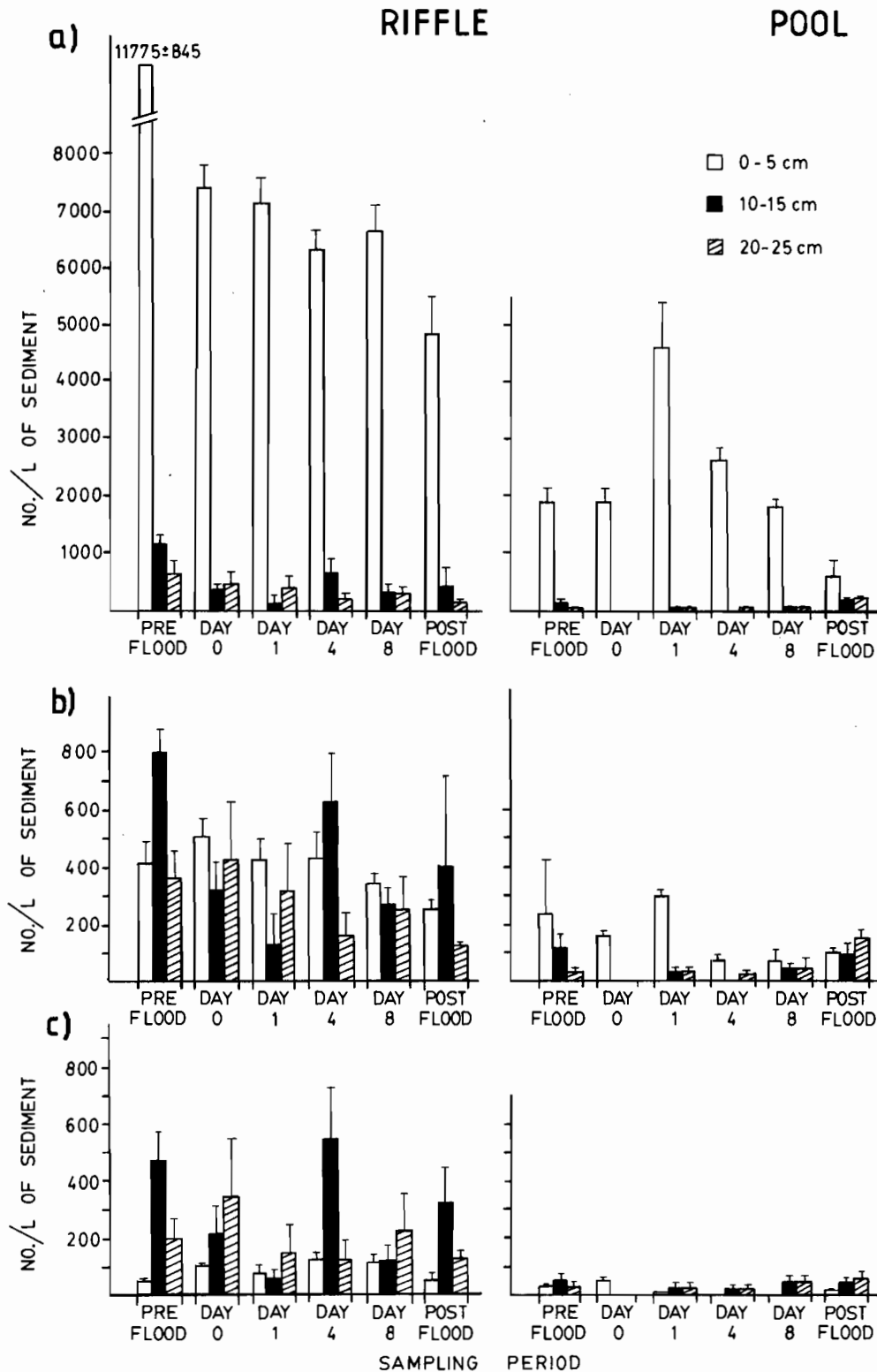


FIG. 5. Depth distribution of invertebrates in Harp Lake Outflow during the spring snowmelt flood, 31 Mar. – 8 Apr. 1986. (a) Total invertebrates; (b) total invertebrates excluding Simuliidae; (c) noninsect invertebrates ($\bar{x} \pm SE$; note difference in scale). Preflood and postflood periods correspond to late winter and spring periods, respectively, from Fig. 2.

the Simuliidae. The peak in surface densities, for example, occurred later (late winter, Fig. 2a) for blackflies than for the remaining invertebrates (early winter, Fig. 2b). The hyporheic zone, on the other hand, showed the same general pattern whether or not blackflies were excluded from the analysis, with

a density peak in early winter in the riffle, and no pattern in the pool.

The pattern of vertical distribution varied among the insect orders (Fig. 3), although generally, Diptera (Chironomidae and small Simuliidae) were the most abundant in the hyporheic

TABLE 1. Chemical data for surface and interstitial waters of Harp Lake Outflow, 11 March – 12 June 1986. N/A = no sample collected for that date; ranges given where >1 sample taken. Alk, mg CaCO₃/L; DO, mg O₂/L.

Date	Parameter	Riffle						Pool					
		Water column		10 – 15 cm		20 – 25 cm		Water column		10 – 15 cm		20 – 25 cm	
		\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}	Range
11 March	pH	6.04	6.03–6.06	N/A		5.93	5.88–5.96	6.03	6.00–6.06	N/A		6.17	6.13–6.21
	Alk	3.3	3.19–3.49			5.66	4.91–6.41	3.30	3.19–3.49	N/A		9.96	8.86–16.5
	DO	N/A		N/A		N/A		N/A		N/A		N/A	
26 March	pH	5.99	5.97–6.00	6.02	6.00–6.04	6.23	6.22–6.25	5.95	5.94–5.96	5.90	5.80–6.00		
	Alk	3.00	2.97–3.03	4.26	3.36–5.16	12.2		2.81	2.79–2.82	5.62	4.91–6.41	29.0	27.6–30.4
	DO	N/A		N/A		N/A		N/A		N/A		N/A	
31 March	pH	5.93	5.93–5.94	5.94	5.90–5.97	6.18	6.15–6.21	5.93	5.91–5.94	6.00	5.95–6.05	6.21	6.16–6.29
	Alk	2.60	2.55–2.64	4.45	4.23–4.67	9.43	6.61–12.3	2.47	2.47–2.47	4.59	3.23–4.59	17.3	14.2–20.5
	DO	N/A		N/A		N/A		N/A		N/A		N/A	
1 April	pH	5.89	5.89–5.89	6.0	6.07–6.10	6.25	6.14–6.36	5.90	5.89–5.90	6.49	6.49–6.49	6.53	6.51–6.55
	Alk	2.53	2.52–2.53	9.59	7.71–11.5	12.9	9.31–16.4	2.64	2.55–2.72	22.4	22.1–22.8	25.9	25.1–26.7
	DO	5.50		1.60		4.40		11.2		1.20		1.20	
4 April	pH	5.85	5.84–5.86	6.32	6.31–6.32	6.26	6.26–6.26	5.87	5.86–5.88	6.15	6.04–6.24	6.31	6.12–6.15
	Alk	2.29	2.26–2.32	9.09	7.01–11.2	13.8	12.7–14.9	2.35	2.33–2.38	8.07	4.47–11.9	12.4	6.04–18.7
	DO	11.5	11.4–11.6	5.80	5.60–6.00	4.10	1.00–7.20	10.4	9.60–11.2	4.10	0.80–7.60	4.60	4.00–5.20
8 April	pH	5.96	5.96–5.96	6.19	6.16–6.21	5.93	5.90–5.96	5.94	5.94–5.94	6.18	6.18–6.19	6.44	6.42–6.47
	Alk	2.35	2.33–2.36	9.85	8.03–11.7	4.32	4.11–4.53	2.33	2.32–2.34	9.28	9.06–9.49	20.7	20.0–21.4
	DO	10.5	9.60–11.4	8.10	5.60–10.6	1.10	0.60–1.60	10.4	10.0–10.8	6.90	3.20–10.8	1.70	0.80–2.60
24 April	pH	6.14	6.13–6.14	5.90	5.85–5.94	6.26	6.16–6.36	6.10	6.09–6.11	6.35	6.10–6.59	6.36	6.29–6.49
	Alk	2.85	2.80–2.90	6.39	3.95–8.83	15.8	15.3–16.3	2.88	2.90–2.86	18.7	10.6–26.8	20.3	15.7–24.9
	DO	10.9	10.6–11.2	8.70	6.20–11.2	3.30	3.20–3.40	11.2	11.0–11.4	1.60	1.20–2.00	1.40	1.20–1.60
12 June	pH	6.39	6.39–6.40	6.20	6.15–6.25	6.05	6.00–6.0	6.48	6.48–6.49	6.38	6.29–6.46	6.51	6.45–6.58
	Alk	3.46	3.26–3.66	7.72	4.46–11.0	8.35	8.55–9.14	3.65	3.58–3.72	24.0	20.2–27.8	27.7	26.0–29.3
	DO	10.6		4.2		3.6		8.8		8.6		1.4	

zone. The mayflies most commonly encountered at the lower depth zones were leptophlebiids (*Leptophlebia cupida* Say, *Paraleptophlebia adoptiva* McD., and *Habrophlebia vibrans* Needham), although small ephemereids (*Eurylophella verisimilis* McD. and *E. funeralis* McD.) were also found. All stonefly genera were found in the hyporheos at some point during the study period, but *Leuctra* was found most frequently and in the highest numbers. Trichoptera were not common in the hyporheic zone, although they were well represented at the surface. However, small net-spinning larvae (*Hydropsyche*, *Cheumatopsyche*, and *Chimarra*) were found in October and December to depths of 10–15 cm. Coleoptera, Megaloptera, and Odonata were rarely found in any depth zone.

Chemistry and hydrology

Discharge during the study period ranged from 5.6 to 878.5 L/s (Fig. 4). The peak flows in autumn (November) and late spring (May) were the result of rain storms, while the maximum flows in early spring (late March and April) were due to the combination of the melting of the surrounding snowpack and the ice from the lake. The pH of surface water ranged from a maximum of 6.7 in the summer to a minimum of 5.9 recorded during peak flows in spring ($\bar{x} \pm SE = 6.25 \pm 0.04$; $N = 42$). Alkalinity ranged from 2.43 to 4.18 mg CaCO₃/L ($\bar{x} = 3.26$) and dissolved oxygen varied from 6.8 to 12.9 mg/L ($\bar{x} = 9.9 \pm 0.17$, $N = 41$) during the study.

Spring Flood Patterns

Invertebrates

The pattern of invertebrate distribution varied between

reaches during the flood. Total invertebrate abundance decreased sharply in surface samples in the riffle at the beginning of the flood and then remained relatively constant for the rest of the study period (Fig. 5a). The greatest reduction within this total was for blackfly larvae, while densities for other invertebrates were largely unchanged (Fig. 5b). In contrast, there was little change in surface density in the pool with the initial increase in discharge (Fig. 5a). However, by day 2 of the flood (24 h after onset of flooding), numbers in the pool reach (again primarily Simuliidae) increased in surface samples before gradually dropping to pre-flood levels by day 8 (Fig. 5a, 5b).

Hyporheic densities were extremely variable at all depths in the riffle and very low in the pool during this period (Fig. 5). Numbers decreased for all groups within the hyporheos in the riffle reach following the onset of flooding, but this trend was not significant (Student's t ; $p > 0.05$). An increase in numbers at 10–15 cm depth on day 4 of the flood (Fig. 5) was primarily due to an increase in noninsect invertebrates at that depth (Fig. 5c). Ostracods, oligochaetes, and nematodes represented the majority of the invertebrates found in the substrate at this time. Few insects were found in the hyporheos during the flood in either reach, and most of those present were chironomids.

Chemistry and hydrology

The surface water chemistry differed markedly from that of interstitial water in Harp Outflow during the spring snowmelt flood (Table 1). Both pH and alkalinity decreased slightly in surface water but increased in the substrate, especially on the rising limb of the snowmelt hydrograph (see Fig. 4); fluctua-

tions in both parameters were noted on the falling limb. Alkalinity was always higher in the substrate than at the surface regardless of hydrologic regime. Dissolved oxygen followed no consistent pattern within the substrate, ranging from 1.0–10.0 mg/L, and was near saturation at the surface.

Discussion

Seasonal Pattern

We found stream invertebrates in the shallow substrates of Harp Outflow throughout the year, supporting Williams' (1984) contention that the hyporheic zone is an important universal habitat for benthos. However, the pattern of abundance in the different depth zones varied seasonally and was related to the timing of recruitment of the dominant insect taxa. Invertebrates found in the hyporheos were generally small in size, and most of the insects found below 5 cm depth were in early developmental stages (developmental stage was determined by wingpad development in hemimetabolous insects and size in holometabolous ones; D. J. Giberson, unpubl. data). Most of the insects had their major recruitment period in the fall or early summer (mayflies: D. J. Giberson, unpubl. data; all other insects: R. J. Hall, unpubl. data), and the highest numbers in all depth zones corresponded to these periods. Small insects have been previously reported to use the substrate as a "nursery" (Coleman and Hynes 1970; Williams and Hynes 1974; Godbout and Hynes 1982), although strong seasonal patterns were not noted (Hynes 1974; Bishop 1973). Williams (1984) suggested that eggs may fall into interstitial spaces after oviposition, then the larvae hatch and eventually move from the deep sediments to the surface as a result of increased demands for space and/or food. In Harp Outflow, we found small-stage larvae of many taxa in the substrate before encountering them in surface samples.

Harp Outflow showed a unique pattern of depth distribution, however, when compared with other studies of the hyporheos of streams. The majority of the total stream invertebrate fauna was generally reported at >5-cm sediment depths, even where substrates were as shallow as those in Harp Outflow (Coleman and Hynes 1970; Bishop 1973; Williams and Hynes 1974; Hynes 1974, Morris and Brooker 1979; Hynes et al. 1976). However, most of the invertebrates in Harp Outflow were found from 0 to 5 cm into the sediments. This pattern was largely due to one taxon, *Prosimulium*, a surface-dwelling filter-feeder commonly reported in great numbers in riffles below lakes (Cushing 1963; Wotton 1979; Bronmark and Malmqvist 1984). When *Prosimulium* was excluded from the analysis, the pattern of depth distribution was similar to that found in other studies, and the hyporheic fauna dominated the total fauna.

The composition of the hyporheic fauna was similar to other studies, even for studies outside of Ontario or Canada (Coleman and Hynes 1970; Bishop 1973; Williams and Hynes 1974; Hynes et al. 1976). For example, the taxa most common in the substrates in Harp Outflow (chironomids (Diptera), leptophlebiids and small ephemeroptera (Ephemeroptera), and detritivorous stoneflies (Plecoptera)) were also the most abundant in substrates in the Speed River, Ontario (Coleman and Hynes 1970; Williams and Hynes 1974) and in streams in Wales (Hynes et al. 1976) and Malaysia (Bishop 1973). Williams (1984) has suggested that invertebrates that inhabit the hyporheic zone must possess certain characteristics, such as small size, tubular-shaped bodies, and/or hard protective

shells that withstand crushing, which allow them to colonize the interstitial habitat. These characteristics are all shared by the taxa listed above and probably contribute to the worldwide pattern.

The presence of large numbers of early instar *Prosimulium* in the substrate in the late fall – early winter was unexpected. Blackflies are usually considered to be restricted to the surface because they feed by filtering food particles from the current (Hynes 1970). However, first instar *Prosimulium* are very small, possess no fans (for filtering), and feed primarily on very fine organic material (D. A. Craig, University of Alberta, pers. comm.) which is common in interstitial spaces (Williams 1984). A recent study of the hyporheos in northwestern Ontario also recorded *Prosimulium* larvae to considerable depths (>30 cm; Jeffrey et al. 1986).

Noninsect arthropods were more common within the substrate than at the surface throughout the year in Harp Outflow. These are often found in riffle benthos or drift samples and are usually considered to be accidental imports from lentic areas, although it has been suggested that some may inhabit the hyporheic zone (Shiozawa 1986; Williams 1984). Our study indicates that they are an important component of the hyporheic community.

Conclusions

Short-term pH depressions of as much as two units, with major effects of biota, occur regularly in the poorly buffered Canadian Shield streams of south-central Ontario (Jeffries et al. 1979; Hall et al. 1980; Hall et al. 1982; Hall and Likens 1984; Hall et al. 1988). These depressions are often associated with the rapid increases in stream discharge that accompany snowmelt and the spring rains or the fall rains and concomitant reduction in evapotranspiration. The present study was intended to characterize organism response to the physical effects of flooding in the stable substrates of a Canadian Shield outflow stream which is not acidified. Our intention was to provide baseline data that would be helpful in separating the responses of the invertebrate fauna to physical as opposed to chemical effects in more acidified systems.

No statistically significant discharge-related vertical movements were noted in Harp Outflow and invertebrate densities (excluding blackflies) remained relatively constant in surface samples in the riffle throughout the flood period. This constancy is in contrast with other studies, where spates have been reported to drastically reduce benthic fauna in streams (McClay 1968; Scullion and Sinton 1983; Reice 1984). Subsequent rapid recolonization after spates, probably via vertical migrations (Williams and Hynes 1974; Williams and Hynes 1976; Poole and Stewart 1976), have lead many workers to suggest that invertebrates actively move into the substrate during a flood. The lack of evidence for such movements during the spring flood in the present study probably relates to the stability of the Harp Outflow substrates. Surface substrate materials in Harp Outflow were large and underwent little movement during the flood. They probably provided sufficient refugia to keep large numbers of organisms from being dislodged or forced into the hyporheos.

No movement patterns were related to changes in the chemistry of the system. Harp Outflow is not considered to be affected by acidic precipitation and no effects were anticipated. However, flood conditions were related to some interesting patterns in the pH and alkalinity of the interstitial water. pH showed

no consistent trend with depth in the substrate at low flow, but was always higher in the substrate during the spring flood. Alkalinity was also higher in the substrate.

These results contrast with those reported from hardwater streams in which pH has been shown to decrease with depth in the substrate (Burbanck and Burbank 1967; Williams and Hynes 1974; Williams 1984). The contrast in patterns is probably related to differences in groundwater chemistry (Bottomly et al. 1984; Reuss and Johnson 1985; Reynolds et al. 1986). During a flood, groundwater makes up the major portion of streamwater on the rising limb of the hydrograph (Hynes 1983; Bottomly et al. 1984). In hardwater, high-alkalinity systems characterized by thick soil overburdens, soil decomposition processes and concomitant production of CO₂ are expected to exert the major influence on shallow groundwater chemistry, decreasing the pH and alkalinity of water moving through the streambed. In softwater, lower-alkalinity systems with thin to nonexistent soil cover, generation of base cations dominates groundwater chemistry, leading to increases in pH and alkalinity. Our study shows the importance of taking pH and/or associated chemical measurements from the habitat actually occupied by stream invertebrates, since the pH of water even a few centimetres into the substrate can differ markedly from that of the water column.

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Appendix: List of Taxa

Insecta

- Ephemeroptera
 - Leptophlebia*
 - Paraleptophlebia*
 - Habrophlebia*
 - Baetis*
 - Eurylophella*
 - Stenonema*
 - Isonychia*
- Plecoptera
 - Isoperla*
 - Malenka*

Podmosta gp.
Taeniopteryx
Leuctra
Odonata
 Calopterygidae
 Gomphidae
Megaloptera
 Nigronia
Trichoptera
 Cheumatopsyche
 Hydropsyche
 Chimarra
 Rhyacophila
 Ptilostomis
Diptera
 Prosimulium
 Simulium
 Orthoclaadiinae
 Tanypodinae
 Chironomini
 Tanytarsini
 Tipulidae

Ceratopogonidae
Empididae
Coleoptera
 Elmidae
 Ectopria
Crustacea
 Copepoda
 Ostracoda
 Cladocera
Mollusca
 Pisidiidae
Nematoda
Annelida
 Oligochaeta
Arachnida
 Acarina