

## Ionic Mass Balance for a Small High Arctic Wetland Basin During Spring Snowmelt

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### ABSTRACT

Hydrochemical transport within a small high Arctic wetland basin was examined during the 1990 spring snowmelt. Snowcover, lake inflow, hillslope runoff, soil water and basin outflow were monitored for pH, conductivity, and the storage and flux of major ions ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Cl}^-$ ).  $\text{Ca}^{2+}$  was the dominant ion found in the basin's snowpack prior to melt. There was a close association between temporal trends in the conductivity of lake inflow and basin outflow throughout the melt; the latter exhibited higher conductivity levels as a result of inputs of ion-rich water to the fen from the basin hillslopes. Snowcover supplied 51% of the total runoff from the basin, but <3% of the total export of ions. Net retention of  $\text{Na}^+$ ,  $\text{K}^+$  and  $\text{Cl}^-$  was not significantly different from 0, while there was net export of  $\text{Ca}^{2+}$ , and to a lesser extent  $\text{Mg}^{2+}$ , from the basin ( $-42.0 \pm 21.6$  and  $-7.6 \pm 4.1 \text{ kg ha}^{-1}$ , respectively). These ions were probably derived from calcified polar desert soils that mantle the basin's slopes. Spatial variation in net  $\text{Ca}^{2+}$  flux to the fen from the hillslopes was largely attributed to slope aspect and consequent differences in active layer development. The latter appears to have an important control on the contact time between infiltrating meltwater and the soil, and therefore on the release of  $\text{Ca}^{2+}$  to hillslope runoff and the basin outflow.

### INTRODUCTION

Studies of runoff generation in low Arctic and Subarctic wetlands (Roulet and Woo 1986, 1988; Ford and Bedford 1987) indicate that wetland discharge is greatest during snowmelt, due to the limited storage capacity of permafrost or frozen surfaces. This research has also identified the important role played by the active layer (that portion of the soil mantle above perennially frozen material that is subject to seasonal thaw) in the transport of water and associated chemical constituents through Arctic wetland watersheds (Woo 1986). Nevertheless, little is known about the relationship of wetland hydrology to nutrient transport in Arctic regions during snowmelt. It is difficult to infer such behaviour from studies of nutrient yields from

wetland basins in temperate climates, since there appears to be little agreement on the effects of wetlands on nutrient budgets (Devito et al. 1989). For example, Verry and Timmons (1982) found that peatland acted as a nutrient sink during the spring, while Taylor and Pierson (1988) observed a net export of  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$  and  $\text{K}^+$  from a wetland during snowmelt. Many Arctic wetlands are classified as fens, since they receive appreciable hydrochemical inputs from adjacent terrestrial surfaces and water bodies as well as from meteoric water. Thus, the role of wetlands in nutrient uptake, export or transformation during passage of water through them may have important implications on downstream aquatic ecosystems (Devito et al. 1989). This study examines ionic transport within a high Arctic wetland basin during snowmelt. In particular, it assesses the relative importance of three sources of ions to the wetland: the snowpack, lake water and soil water contributed during active layer development.

#### STUDY AREA

Research was undertaken during the 1990 snowmelt period within a small (30.8 ha) high Arctic basin located in the central region of Axel Heiberg Island, N.W.T. ( $79^{\circ} 25' \text{N}$ ,  $90^{\circ} 45' \text{W}$ ). The region experiences a cold, semi-arid climate with a mean annual temperature of  $-19.7^{\circ}\text{C}$  and mean annual precipitation of 441 mm (Adams et al. 1989). The basin's snowpack generally begins to ablate in late May, and the snowmelt period lasts from 1 to 2 weeks (Allan et al. 1986). The basin receives drainage from Colour Lake as well from the surrounding hillslopes. Its central portion is occupied by a fen (1.3 ha) which is vegetated primarily by sedges, cottongrass and sphagnum. Peat accumulation within the fen is at least 0.05 m, and overlies mineral soil. Average depth to the permafrost table within the fen by the end of the summer season is approximately 0.58 m (Allan et al. 1987), and the basin is underlain by continuous permafrost to a depth of more than 600 m (Allan et al. 1986). The basin's soils are classed as cryosols. Block slopes mantle the ridge tops and steep slopes, while gentle slopes and valley bottoms are dominated by static and turbic forms of orthic, brunisolic and gleysolic cryosols (Allan et al. 1986). Cation exchange capacities for static and turbic cryosols range from 7.65 - 11.48 and 4.79 - 9.16 meq/100 g, respectively (Allan et al. 1986). Encrustations of  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  sulphates are often found on the underside of larger material overlying arid soils within the basin.

#### METHODS

Stratified random snow surveys of the hillslope (20 points), fen (18 points) and lake (32 points) snowpacks were conducted weekly from 25 May 1990 to the

end of melt. Depth-integrated samples were retrieved with a M.S.C. snow sampler. Samples were analyzed in the field for pH and conductivity, using an Orion Mk.111 digital pH meter and a Barnstead conductivity bridge (model PM7CCB). Conductivities were corrected to 25°C. Spot measurements of inputs to the basin from Colour Lake and basin outputs were obtained using the

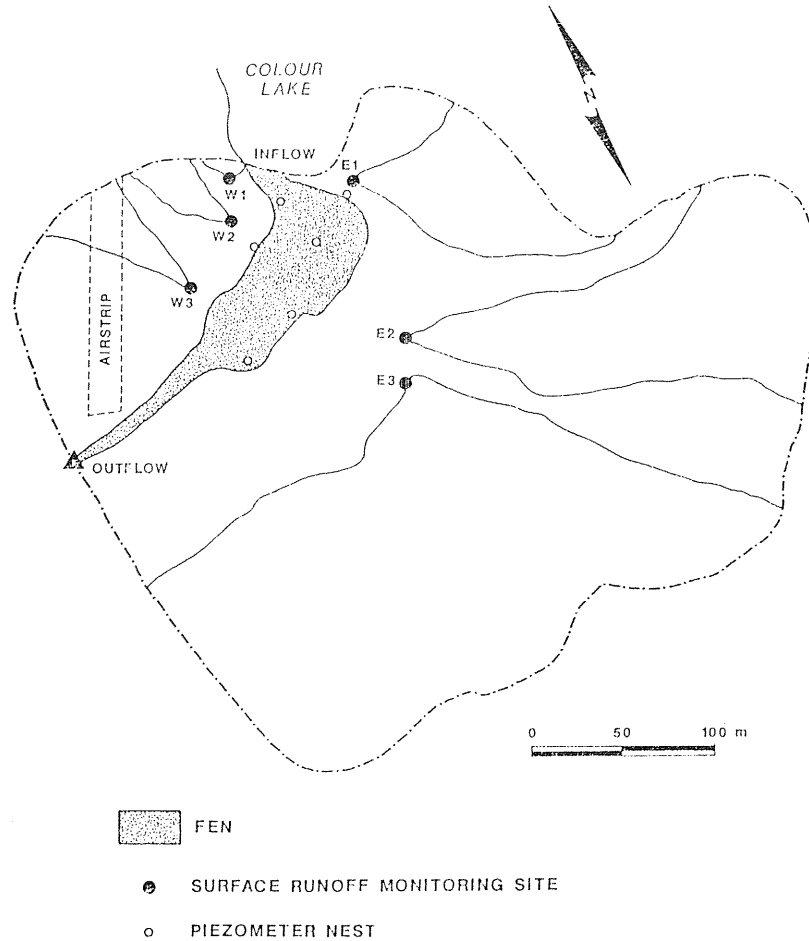


Figure 1 - Colour Lake wetland basin.

velocity-area method (Fig. 1). Flow velocity was determined using a pygmy current meter. Runoff from 6 streams draining the surrounding hillslopes was monitored following the initiation of melt (Table 1, Fig. 1). Spot measurements of discharge were obtained using either the velocity-area method or by pressing a plastic bag into the stream channel for a known time period and then determining the volume of water retrieved (Allan et al. 1986). Discharge measurements of lake inflow, basin outflow and surface runoff were made at 0700 h, 1300 h, 1630 h and 2300 h daily throughout the study period. Daily water samples were obtained at all discharge monitoring sites for field measurement of pH and conductivity. In addition, selected snowpack, inflow,

outflow and hillslope runoff samples were stored in acid-washed nalgene bottles for subsequent analysis. Six piezometer nests were installed within the fen and in footslope areas of the basin prior to spring melt (Fig. 1) Each nest contained four piezometers, the depths of the first three being

TABLE 1 - SUBCATCHMENT CHARACTERISTICS, COLOUR LAKE WETLAND BASIN.

Subcatchment	Area (m <sup>2</sup> )	Ave. Slope	Aspect (azimuth bearing)
E1	1.5 X 10 <sup>4</sup>	0.253	292°
E2	4.1 X 10 <sup>4</sup>	0.210	286°
E3	1.2 X 10 <sup>5</sup>	0.156	12°
W1	7.3 X 10 <sup>2</sup>	0.038	180°
W2	2.4 X 10 <sup>3</sup>	0.020	155°
W3	3.9 X 10 <sup>3</sup>	0.019	154°

0.05, 0.10 and 0.15 m below ground surface. The installation depth of the fourth piezometer depended on the variability of permafrost depth at each site. Water samples were extracted every second day using a hand pump following development of the active layer. Samples were analyzed in the field for pH and conductivity. Active layer thickness was measured bi-weekly at the surface runoff monitoring sites and the basin outflow. Measurements were obtained by driving a stake into the ground until the permafrost table was encountered. Air temperature was recorded twice daily at a Stevenson screen located just outside the basin. Total hours bright sunshine was monitored for 12 h consecutive periods using a dual Stokes-Campbell bright sunshine recorder. Precipitation was recorded using a Nipher snow gauge, while ionic inputs to the basin were monitored using a bulk sampler lined with a plastic bag. Snowpack, lake inflow, hillslope runoff, and basin outflow water samples were preserved with 1N HNO<sub>3</sub> and stored at 4°C prior to analysis at Trent University. Ca<sup>2+</sup> and Mg<sup>2+</sup> were determined using atomic absorption, while Na<sup>+</sup> and K<sup>+</sup> were determined using atomic flame emission. Lanthanum was added to samples and standards to reduce spectral interference from other species in solution. Cl<sup>-</sup> was determined using an Orion Cl<sup>-</sup> electrode (Model 94-17B).

The ionic load held in the basin snowcover was estimated using:

$$SP_{ij} = (WE_j \cdot C_{ij} \cdot A_j) \quad (1)$$

- where  $SP_{ij}$  = load of ion  $i$  in surface type  $j$ 's snowcover  
 $WE_j$  = mean water equivalent (w.e.) of surface type  $j$ 's snowcover  
 $C_{ij}$  = mean concentration of ion  $i$  in surface type  $j$ 's snowcover  
 $A_j$  = area of surface type  $j$

Ion export in lake inflow, hillslope runoff and basin outflow was calculated

over discrete time intervals determined by the frequency of sampling. Export was estimated as the product of the water export between two consecutive sampling times and the mean concentration of the two water samples. These interval exports were then summed over the entire monitoring period to yield an overall export for the spring melt. The results for the water and ionic budgets are expressed as retention (RT) where:

$$RT = (\text{total inputs} - \text{total outputs}) / \text{basin area} \quad (2)$$

The magnitude of the total error associated with the water and ionic budget calculations was approximated as follows (Winter 1981):

$$S_T = [S_{SP}^2 + S_{LI}^2 + S_{BO}^2]^{0.5} \quad (3)$$

where  $S_T$  = 1 SD of the total error

$S_{SP}$  = 1 SD of the error associated with the estimated ionic load held in the snowpack

$S_{LI}$  = 1 SD of the error associated with the ionic input to the basin in lake inflow

$S_{BO}$  = 1 SD of the error associated with the ionic output from the basin

The variance of the ionic load in the snowpack and in discharge (i.e. a product) was approximated by:

$$\text{var}(X, Y) = \bar{X}^2 \cdot S_Y^2 + \bar{Y}^2 \cdot S_X^2 + S_Y^2 \cdot S_X^2 \quad (4)$$

where X is a hydrological variable (w.e. or water volume) and Y is ionic concentration. As Devito et al. (1989) note, this is equivalent to adding the square of the percent errors for both the hydrological and chemical measurements. The relative error in estimated snowpack ionic loads was calculated from observed w.e. and concentration data. The relative error associated with total water volume estimates was assumed to be  $\pm 35\%$  (Winter 1981), while the analytical and sampling error associated with snowpack and stream chemistry was assumed to be  $\pm 10\%$  (Devito et al. 1989).

## RESULTS AND DISCUSSION

### Snowcover

Hydrochemical characteristics of the basin snowcover at peak w.e. (8 June 1990) are presented in Table 2. Comparison of ion loads held in the snowpack on 1 June and 8 June showed no consistent differences; therefore there do not appear to have been significant losses of ions from the basin's snowcover prior to melt. The total water volume contained in the snowpack on 8 June was estimated at  $4.8 \times 10^4 \text{ m}^3$ . Water equivalent depths were higher than peak w.e. recorded in 1984 and 1985 for hillslopes draining to Colour Lake (Allan et al. 1987). Average snowpack w.e. of the eastern portion of the basin was slightly larger than that of either the western slopes or the wetland. This may reflect drifting of snow from the relatively level western part of the basin to the lower fen surface and the eastern footslopes as a result of

south-westerly winds that are common in this area (Allan et al. 1987). Differences in average water equivalent of snowpack within the basin were reflected in the higher ionic loads held by the eastern snowpacks. Cation content of the snowpack was dominated by Ca<sup>2+</sup>, and this has been noted in previous snow surveys in the Colour Lake basin (Allan et al. 1987) as well as

TABLE 2 - WATER EQUIVALENT AND SNOWPACK CHEMISTRY, 8 JUNE 1990, COLOUR LAKE WETLAND BASIN.

	East slopes	West slopes	Fen
water equivalent (m)	0.163±0.041	0.102±0.022	0.149±0.044
pH - mean	5.0	4.7	4.9
- range	4.8 - 5.4	4.5 - 4.9	4.6 - 5.0
conductivity (µS cm <sup>-1</sup> )	8.89 ± 4.55	4.60 ± 0.42	8.29 ± 6.16
Concentration (mg L <sup>-1</sup> )			
Ca <sup>2+</sup>	0.64 ± 0.21	0.37 ± 0.09	0.65 ± 0.19
Mg <sup>2+</sup>	0.09 ± 0.02	0.09 ± 0.05	0.10 ± 0.03
Na <sup>+</sup>	0.03 ± 0.01	0.02 ± 0.01	0.03 ± 0.01
K <sup>+</sup>	0.11 ± 0.03	0.04 ± 0.01	0.12 ± 0.07
Cl <sup>-</sup>	0.20 ± 0.04	0.12 ± 0.02	0.16 ± 0.04
Load (g m <sup>-2</sup> )			
Ca <sup>2+</sup>	0.105±0.044	0.037±0.012	0.097±0.041
Mg <sup>2+</sup>	0.015±0.005	0.009±0.006	0.015±0.006
Na <sup>+</sup>	0.006±0.002	0.002±0.001	0.005±0.003
K <sup>+</sup>	0.018±0.007	0.004±0.002	0.018±0.013
Cl <sup>-</sup>	0.033±0.011	0.012±0.003	0.024±0.009

in studies of temperate snowcovers (e.g. Barica and Armstrong 1971). However, whereas Na<sup>+</sup> has been found to be an important component of the cation content of mid-latitude (Barica and Armstrong 1971) and coastal alpine snowcovers (Zeman and Slaymaker 1975), it made only a small contribution here. This suggests reduced inputs from industrial and marine sources to snowcover in the Colour Lake area. Minor contributions to the basin's snow chemistry from the latter source are indicated by the low Na<sup>+</sup>/Cl<sup>-</sup> ratios in snow (0.15 - 0.19) relative to that observed in seawater, which has values in the order of 1.8 (Drever 1988).

#### Ion Transport During Snowmelt

Snowmelt runoff began on 8 June and continued over a 14 day period, during which there was no measurable precipitation. Hydrographs for the basin outflow, lake inflow and stream channels are presented in Fig. 2, while temporal trends in conductivity are shown in Fig. 3. We have selected

conductivity to summarize the general trends in ionic concentrations, since it was strongly correlated with  $[Ca^{2+}]$  and  $[Mg^{2+}]$  ( $r$  values ranging from 0.74 to 0.99 and from 0.65 to 0.95, respectively), which were the dominant ions found in streamflow.

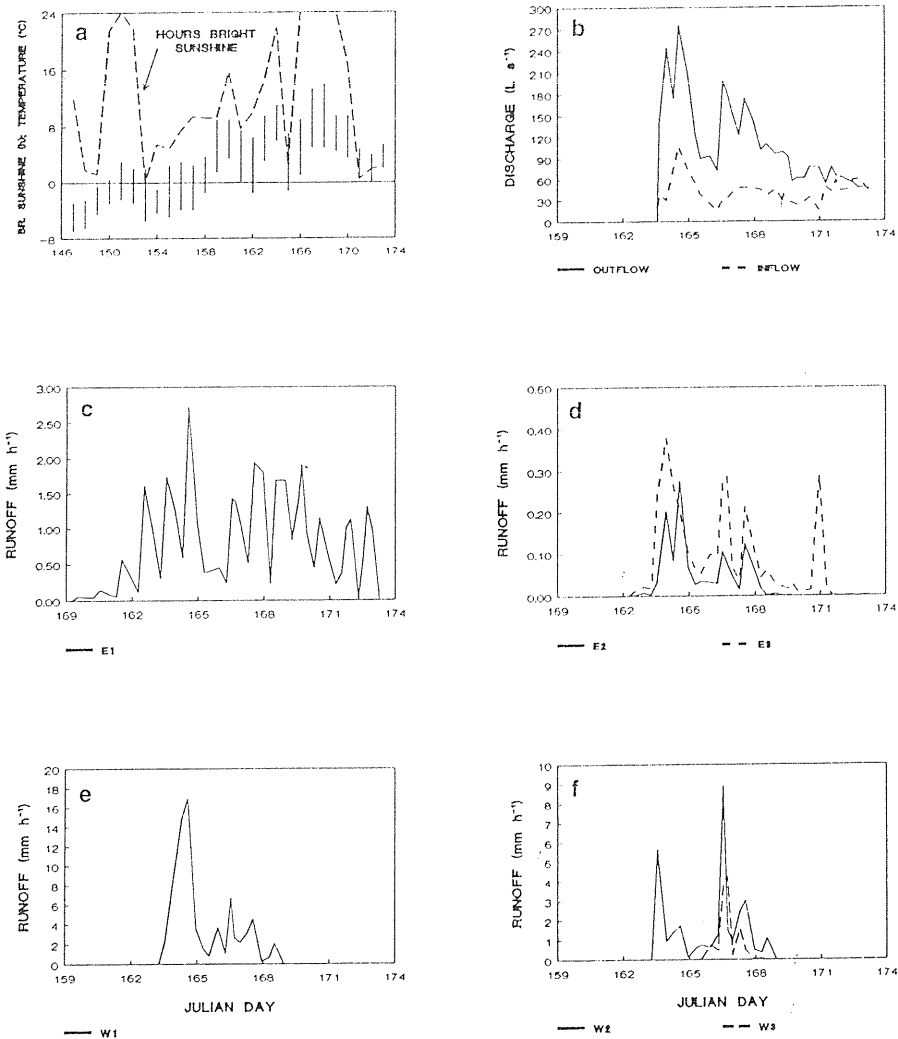


Figure 2 - (a) Air temperature and number of hours of bright sunshine; (b) inflow from Colour Lake and basin outflow; (c-f) hillslope runoff.

Streamflow began on eastern slopes between 8 - 11 June. Runoff from the west streams began on 12 June due to shading by mountainous terrain, and lake inflow and basin outflow began the same day. Lake inflow, hillslope runoff and basin outflow all exhibited diurnal variations in discharge. The magnitude of these variations tended to decrease over time, due to increased active layer development, less snowcover, and relatively steady daily inputs of solar radiation towards the end of ablation (Fig. 2).

Inflow from Colour Lake exhibited a large initial peak discharge on 13 June that was comparable to the 1985 peak of  $106 \text{ L s}^{-1}$  (Allan et al. 1987). Conductivity data suggest that this rapid response may be attributed to the movement of meltwater over the lake's ice cover, rather than to the displacement of lake water by meltwater entering the lake through the ice cover, as hypothesized by Allan et al. (1987). Despite the development of a clearly defined moat of water ringing Colour Lake's ice cover on 12 June, the lake ice remained attached to the shore. Thus, the initial discharge pulse from the lake was associated with a peak conductivity in the order of  $200 \mu\text{S cm}^{-1}$ . This is similar to the conductivity of surface runoff observed in 1984, 1985 (Allan et al. 1987) and 1990 (Fig. 3), whereas lake water may have conductivities ranging from 600 to  $800 \mu\text{S cm}^{-1}$  (Adams and Allan 1987). The subsequent gradual decline in the conductivity of the lake outflow may be the result of discharge of more dilute meltwater (snowmelt and lake ice) that

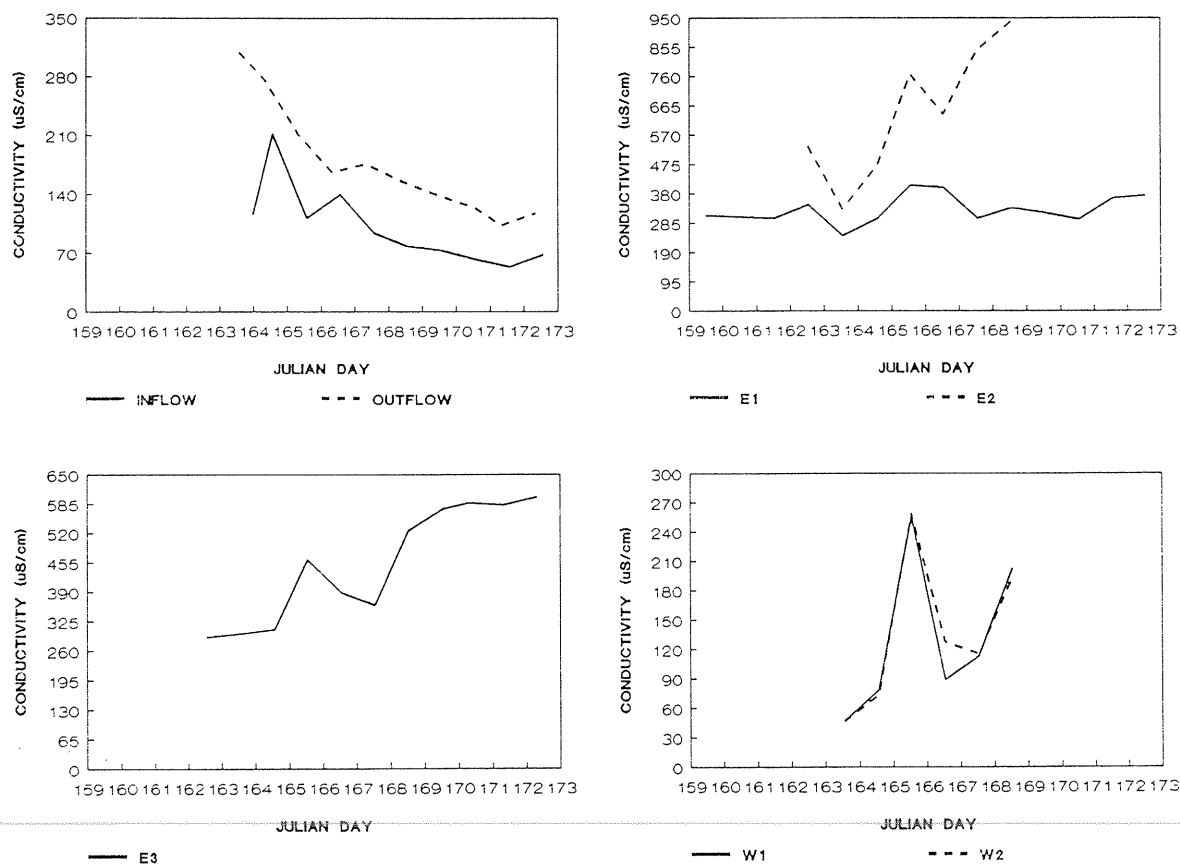


Figure 3 - Conductivity in lake inflow, basin outflow and hillslope runoff, spring 1990.



moves beneath the ice cover without mixing with the resident lake water.

Conversely, the conductivity of hillslope runoff was generally higher than either the lake inflow or basin outflow (Fig. 3). Conductivity of runoff from several of the subcatchments tended to increase over time, which reflects the interaction of flow rate, contact time between runoff and soil, and active layer development. Thus, the large initial discharge pulse from E2, E3, W1 and W2 (Fig. 2) was concomitant with limited active layer thicknesses (Fig. 4), leading to reduced soil-water interactions and relatively low conductivities in surface runoff. Increased active layer development later in the monitoring period allowed enhanced infiltration, reduced surface runoff, increased contact time between meltwater and soil, and higher conductivities. However, this association between active layer growth and conductivity in surface runoff was absent in E1, which had an almost constant conductivity combined with the greatest active layer development of any subcatchment. The cause of this behaviour is not known.

Despite the contribution of hillslope runoff of high conductivity to the fen, the conductivity of the basin outflow tended to mirror levels in lake inflow, leading to an overall decrease in ionic concentration in basin output during the melt period. This may be due to the integration of spatial and temporal variations in runoff inputs by the basin (Fig. 2), leading to a relatively constant "background" input of ions that was superimposed upon the lake inflow to the wetland. In this way, the temporal pattern of conductivity in the lake inflow was preserved in the basin outflow.

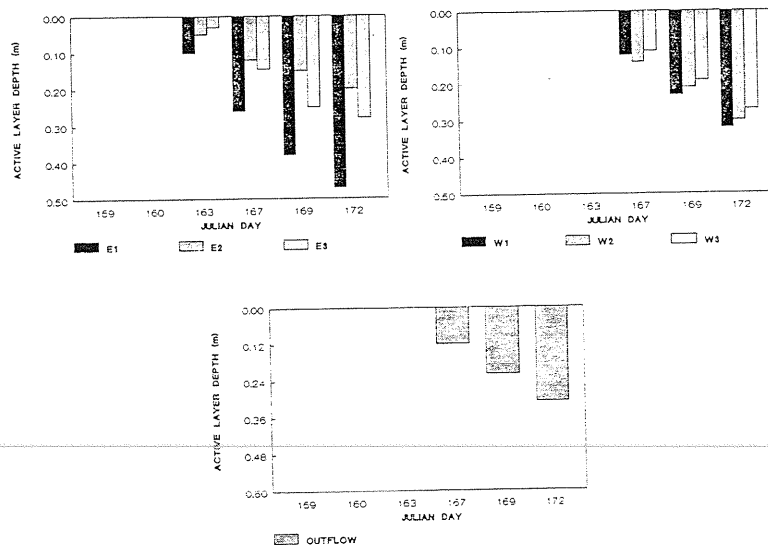


Figure 4 - Active layer development within the monitored subcatchments and at the fen outflow, spring 1990.

### Water and Ion Budgets for the Basin

Water and ion budgets are summarized in Table 3. The error associated with these budgets must be considered in their interpretation. Thus although the output of water from the basin slightly exceeded inputs, suggesting that soil water contributed to basin outflow during active layer development, the net export was not statistically significant. Table 3 indicates that the snowpack supplied 51% of the total input of water to the basin, but < 3% of the total ionic output from the basin. In all cases, inflow from Colour Lake was the dominant input of ions to the basin. Lake inflow also supplied approximately 36% of the total runoff from the basin.

Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup> did not experience net retention or export. However, the results indicate substantial net export of Ca<sup>2+</sup>, and to a lesser extent Mg<sup>2+</sup>, from the basin. Losses of these ions are similar in magnitude to those observed by Taylor and Pierson (1988) for a temperate wetland basin during spring melt. However, our results contrast with those of Verry and Timmons (1982), who found that peatland acted as a pronounced nutrient trap during spring melt.

TABLE 3 - WATER AND IONIC BUDGETS ( $\pm 1$  SD), COLOUR LAKE WETLAND BASIN.  
NEGATIVE VALUES FOR NET RT REPRESENT INPUT < OUTPUT; POSITIVE VALUES  
REPRESENT INPUT > OUTPUT.

	Input		Output	Net RT
	Snowpack	Lake		
Water (m <sup>3</sup> X 10 <sup>4</sup> )	4.82 $\pm$ 1.56	3.41 $\pm$ 1.19	9.49 $\pm$ 3.32	-1.25 $\pm$ 3.86
Ions (kg ha <sup>-1</sup> )				
Ca <sup>2+</sup>	0.98 $\pm$ 0.52	14.44 $\pm$ 5.28	57.37 $\pm$ 20.98	-41.95 $\pm$ 21.64*
Mg <sup>2+</sup>	0.14 $\pm$ 0.07	2.93 $\pm$ 1.07	10.70 $\pm$ 3.91	-7.63 $\pm$ 4.06*
Na <sup>+</sup>	0.06 $\pm$ 0.03	0.62 $\pm$ 0.23	1.65 $\pm$ 0.60	-0.97 $\pm$ 0.65
K <sup>+</sup>	0.17 $\pm$ 0.09	0.69 $\pm$ 0.25	2.27 $\pm$ 0.83	-1.41 $\pm$ 0.87
Cl <sup>-</sup>	0.31 $\pm$ 0.16	0.31 $\pm$ 0.11	1.16 $\pm$ 0.42	-0.54 $\pm$ 0.47

\* - Net RT significantly different from 0 at p = 0.05.

A portion of the net Ca<sup>2+</sup> and Mg<sup>2+</sup> export would have been supplied by soil water released during active layer development, although water balance estimates (Table 3) indicate that the active layer supplied only a small fraction of total discharge from the basin. Nevertheless, this water may have been in contact with soil, regolith and vegetation for sufficient time to permit the attainment of chemical equilibrium. In addition, Ca<sup>2+</sup> and Mg<sup>2+</sup>

may have been taken into solution as surface runoff and lake inflow interacted with soil and vegetation on the hillslopes and in the fen during passage through the basin. Thus Fig. 5 demonstrates the similarity between the conductivity of interstitial water sampled from the piezometers and that of hillslope runoff, both of which exceeded conductivities measured in lake inflow and the basin's snowcover. The polar desert soils covering the basin's slopes are usually alkaline, due to base saturation and the presence of free carbonates (Tedrow 1977).  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  held in these soils may have been released to water moving on and within the basin's slopes as a result of cation exchange with  $\text{H}^+$  carried in meltwater. Pronounced differences between the pH of the premelt snowpack (pH of 4.5 - 5.4) and that of hillslope runoff (pH of 6.5 - 7.0) and soil water (pH of 5.5 - 7.0) are consistent with this process. The importance of hillslope runoff to the overall export of  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  from the basin suggests that further examination of the nature of ion export from these slopes is required.

#### Role of Active Layer Development in Ion Export from Basin Hillslopes

The similarity between the conductivity of interstitial water and of hillslope runoff throughout the snowmelt (Fig. 5) suggests that the active layer plays an important role in ion export from the basin's slopes. Variations in both the timing and maximum extent of active layer development were observed within the basin (Fig. 4), and could largely be attributed to differences in aspect of the various subcatchments (Table 1). Spatial variations in active layer development in turn assist in explaining differences in net  $\text{Ca}^{2+}$  export from the subcatchments to the fen (Fig. 6),

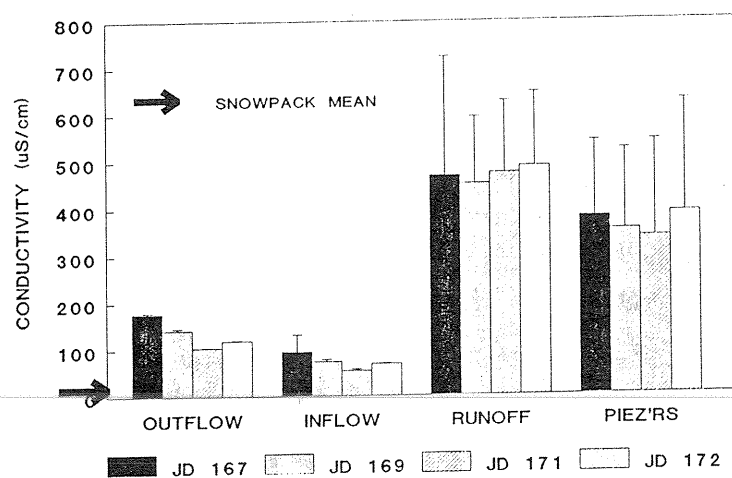


Figure 5 - Conductivity of lake inflow, basin outflow, hillslope runoff and soil water sampled from piezometers, spring 1990.

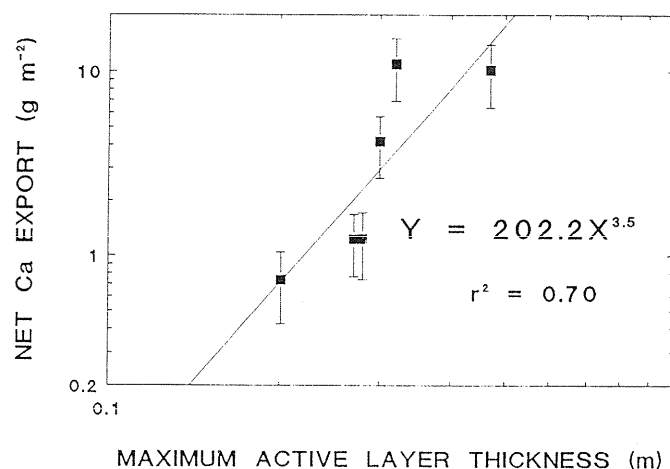


Figure 6 - Net  $\text{Ca}^{2+}$  export from the subcatchments during the monitoring period vs active layer thickness at the end of spring snowmelt.

such that thicker active layers at the end of the snowmelt period were associated with a larger net export of  $\text{Ca}^{2+}$ . Increased active layer thickness would promote contact between infiltrating meltwater and the soil and regolith, leading to enhanced cation exchange and release of  $\text{Ca}^{2+}$  to hillslope runoff. However, the pronounced scatter about the best-fit line suggests that other factors, such as spatial variations in soil properties and vegetation cover, may also influence net export of  $\text{Ca}^{2+}$  from the hillslopes.

This mechanism contrasts with the findings of Allan et al. (1986), who attempted to explain spatial variations in streamflow chemistry in Colour Lake basin. They found that differences in active layer development could not explain spatial variations in ionic inputs to Colour Lake from the surrounding hillslopes. Instead, these variations were attributed to the effects of localized gelifluction, which exposed underlying regolith and led to increased concentration of particular ions in surface runoff. Such a mechanism does not appear to operate in the wetland basin, since the hillslopes draining to the wetland were not subject to pronounced gelifluction.

#### CONCLUSIONS

1.  $\text{Ca}^{2+}$  was the dominant ion found in the basin's snowpack.  $\text{Na}^+$  made only a minor contribution to the total ionic load of the snowcover.
2. Spatial and temporal variations in the contribution of hillslope runoff to the fen were integrated by the basin in such a way that ionic and

runoff contributions were superimposed on the temporal trend of lake inputs to the basin. Thus, outflow conductivity levels were consistently higher than those of the incoming lake water due to hillslope inputs, but closely followed the temporal trend exhibited by the lake inflow.

3. There was appreciable error associated with the water and ionic budgets determined for the basin. The snowpack supplied 51% of basin runoff, but <3% of ions transported from the basin during spring melt. The majority of ions were supplied to the basin by hillslope runoff, as result of interactions with the soil surface and vegetation, and the release of ion-rich interstitial water during active layer development. There was a net export of  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  from the basin, while  $\text{RT} = 0$  for all other ions. Excess  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  were likely derived from the calcified polar desert soils that mantle the basin's hillslopes
4. Spatial variations in net  $\text{Ca}^{2+}$  export from hillslopes to the fen can be partially accounted for by slope aspect and consequent variations in active layer development during the snowmelt period, although differences in vegetation cover and soil properties are probably also important. Nevertheless, the initial stages of active layer development may have important implications for nutrient transport in high Arctic wetland ecosystems.

#### ACKNOWLEDGEMENTS

We acknowledge the support and assistance of: NSERC, Canada; RCGS, Canada; NRTG, DIANA, Canada; PCSP, Canada; the McGill Axel Heiberg Station; P. Doran (Trent) and M. Myers (DRI, Nevada).

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