Reports

Natural Sources of Acid Neutralizing Capacity in Low Alkalinity Lakes of the Precambrian Shield

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A detailed alkalinity budget was constructed for Lake 239 in the Experimental Lakes Area of northwestern Ontario and for three small watersheds in its terrestrial basin. Alkalinity generation in the lake averaged 118 milliequivalents per square meter per year, 4.5 times as high as the areal rate in the terrestrial basin. Although acid deposition in the area is low, only one of the three terrestrial watersheds was a significant source of alkalinity. A second terrestrial watershed yielded very little alkalinity. The third watershed, which contains a wetland, was a sink for, rather than a source of, alkalinity. An analysis of ion budgets for the lake revealed that more than half of the in situ alkalinity production was by biological rather than geochemical processes. The major processes that generated alkalinity were: biological reduction of SO_4^{2-} (53%), exchange of H^+ for Ca^{2+} in sediments (39%), and biological reduction of NO_3^- (26%). Comparison with experimentally acidified Lake 223 revealed that alkalinity production by sulfate reduction increased in response to increased inputs of sulfuric acid.

IN ACID-SENSITIVE LAKES, ALKALINITY (that is, acid neutralizing capacity) is assumed to originate from chemical weathering of geological substrates and ion exchange reactions in the terrestrial portion of a lake's catchment. The acidification of lakes under increased acidic deposition has been assumed to result from such geological processes being exhausted or overwhelmed (*1*). This conclusion may indeed be the case in some lakes of the Adirondacks, where the degree of acidification of three lakes has been shown to be related to the depth of terrestrial soils (*2*). However, we noted that the low-alkalinity lakes of the Experimental Lakes Area (ELA), northwestern Ontario, typically had much higher alkalinities than their inflow streams (*3*), suggesting important aquatic sources of alkalinity. Our long-term data revealed that there was no detectable tendency for lakes or streams draining terrestrial catchments in the area to become more acidic with time (*3*), so that it seemed reasonable to hypothesize that in situ processes in the lakes were a major source of their alkalinity (*4*).

To test this hypothesis, we made detailed alkalinity measurements by Gran titration and budgets for base cations and strong acid anions for 3 years on Lake 239 in the ELA area, on its three tributary streams, on its outflow, and on precipitation (*5*) (Fig. 1). Water budgets for the lake have been measured for 15 years and balance to within a few percent (*6*). All inflow streams and the outflow were gauged with continuous level recorders and flumes or V-notch weirs, which were serviced at least twice a week during the period of flow. Chemical analyses from streams were done weekly, with *p*H, nitrate, ammonium, dissolved inorganic carbon and other perishable analyses performed within a few hours of collection (*7*). Bulk precipitation was collected from a 0.5-m by 0.5-m plexiglass collector on a small rocky island in the lake during the ice-free season and at the meteorological station, 0.5 km west of the lake in winter. Rain samples were filtered and refrigerated within a few hours after each precipitation event and analyzed for perishable ions the same day (*8*). Snow samples were kept frozen and analyzed similarly once a month.

Precipitation supplied negative alkalinity averaging −9.6 milliequivalents per square meter per year directly to the lake and to its catchment (*8*) (Table 1). Alkalinity yield from each terrestrial catchment to the lake was thus the sum of alkalinity production in the catchment plus the alkalinity in precipitation. Of the three terrestrial catchments, one, the Northeast Subbasin, drains a small wetland that consumed alkalinity, so that it supplied negative alkalinity to the lake (*9*). One of the two remaining streams, the Northwest Subbasin, drained a small, rocky upland with shallow overburden. Alkalinity production in this catchment averaged about 10 meq m^{-2} $year^{-1}$, approximately neutralizing rainfall acidity. It supplied a small negative amount of alkalinity to the lake in 1981, and slightly positive amounts in 1982 and 1983 (Table 1). The third stream supplied most of the terrestrially derived alkalinity to the lake (20.7 meq m^{-2} $year^{-1}$). This stream (the East Subbasin) is known to contain small amounts of calcareous material in sediments of the valley bottom; this is unusual for streams in the area (*10*).

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Table 1. An annual alkalinity budget for Lake 239 based on Gran titrations. Averages are given with standard error of the mean.

Budget	Alkalinity yields to Lake 239 (keq $year^{-1}$)					Average alkalinity yield* (meq m^{-2} $year^{-1}$)	Average alkalinity production (+) or consumption (−)† (meq m^{-2} $year^{-1}$)
	Basin area (ha)	1981	1982	1983	Average 1981–1983		
NW inflow	56.4	−0.1	0.4	0.5	0.3 ± 0.2	0.5	10.1
NE inflow	10.6	−1.4	−1.6	−0.7	−1.2 ± 0.3	−11.8	−2.2
E inflow	170.3	36.3	40.2	29.2	35.2 ± 3.2	20.7	30.3
Direct runoff‡	100.0	21.4	23.6	17.2	20.7 ± 1.9	20.7	30.3
Total terrestrial input	337.2	56.2	62.6	46.2	55.0 ± 4.8	16.3	25.9
Precipitation to surface	54.3	−1.3	−8.3	−6.0	−5.2 ± 2.1	−9.6	
Precipitation and terrestrial input	54.3	54.9	54.3	40.2	49.8 ± 4.8	91.7§	
Outflow	54.3	93.9	136.3	55.4	95.2 ± 23.4	175.3§	
Annual change in mass (ΔM_a)	54.3	39.6	−11.2	26.6	18.4 ± 15.2	33.8§	
Alkalinity produced (P_a)‖	54.3	78.6	70.8	41.9	63.8 ± 11.2		117.5 ± 20.6

*Alkalinity yield is measured. Alkalinity production is calculated as production = yield − precipitation. †The difference between precipitation input and outflow losses to the basin divided by basin area. ‡Based on the assumption that outputs per square meter are similar to the E subbasin. §Average alkalinity input and output per square meter of lake surface. ‖Calculated according to Eq. 1. Values are annual averages and standard errors of the mean.

Table 2. Mass balance budgets for nonproteolytic ions of potential significance to the alkalinity of Lake 239 for 1981–1983. Data are annual means for 1981–1983, in kiloequivalents per year. Numbers in parentheses are standard errors of the means of total input (*I*) and outflow (*O*) for the three annual values.

	Ca^{2+}	Mg^{2+}	Na^+	K^+	NH_4^+	SO_4^{2-}	Cl^-	NO_3^-	Base cations (Σ)	Strong acid anions (Σ)	Alk*
I	102.0(16.2)	55.0(9.7)	46.4(8.3)	17.5(3.9)	9.4(1.3)	99.1(22.8)	13.7(3.0)	11.7(1.4)	230	124	106
O	101.6(26.4)	52.2(13.8)	43.2(12.9)	14.8(4.0)	0.9(0.2)	75.7(19.4)	12.1(4.3)	2.1(0.8)	213	90	123
ΔM	16.7§	−2.7	1.7	3.8§	1.3§	2.5§	−4.3	−0.6	21	−2	23
P_a†	16.3§	−5.5	−1.5	1.1§	−7.2§	20.9§	5.9	10.2§	3‡	37‡	40‡

*Alkalinity = Σ base cations − Σ strong acid anions. †P_a = alkalinity produced from sediments = $O + \Delta M - I$ for cations and $I - (O + \Delta M)$ for anions, where ΔM is the change in mass of an element in the lake. ‡Alkalinity generated by addition of base cations and removal of strong acid anions, respectively. §Statistical significance of the annual change in mass in the lake (ΔM) and $I - O$ are based on paired *t* tests (*14*); P_a is considered to be significant if either ΔM or $I - O$ is significantly different.

In addition to the streams, 30% of the terrestrial area drained directly to the lake. Much of this area is rocky with shallow overburden. However, the area near the ELA campsite on the west side of the lake (Fig. 1), about 7% of the terrestrial drainage area, has an overburden of up to 20 m in depth. Twenty piezometers in this area yielded chemical concentrations slightly less than the East Subbasin stream (*11*). In order to make our calculations as conservative as possible (that is, we would underestimate alkalinity production in the lake), we assumed that all direct flows to the lake had chemistry similar to the East Subbasin.

Calculated average terrestrial alkalinity production in the entire catchment of the lake was only 26 meq m^{-2} $year^{-1}$. Since about 10 meq m^{-2} $year^{-1}$ of the alkalinity produced was used to neutralize incoming precipitation, the average yield to lake by streamflow from the entire terrestrial basin was only 16 meq m^{-2} $year^{-1}$ (Table 1).

If precipitation and terrestrial yield were the only sources of alkalinity for Lake 239 and 1981–1983 inputs were typical, the lake's alkalinity would be less than 70 μeq $liter^{-1}$ (*12*). However, the measured alkalinity concentration of the lake averaged 151 μeq $liter^{-1}$. In addition, there was a substantial alkalinity loss from the outflow of the lake. Annual alkalinity production (P_a) in the lake was calculated as

$$P_a = \Delta M_a + O_a - I_a \qquad (1)$$

where ΔM_a is the annual change in mass of alkalinity in the water column, O_a is the annual loss of alkalinity by outflow, and I_a is the annual alkalinity input, all measured by Gran titration. Water level in the lake differed by only 0.021 m on the first and last dates used for calculation of ΔM_a and is thus ignored in the calculation. The years 1981, 1982, and 1983 were the 4th, 6th and 9th driest years in a 14-year record and are assumed to represent long-term values. Average alkalinity generation in the lake was 118 ± 21 meq m^{-2} $year^{-1}$ or about 4.5 times the average production for terrestrial areas and about 7.4 times the average yield (Table 1). Moreover, although the terrestrial area was more than six times that of the lake, total alkalinity production in the lake (64 ± 11 keq $year^{-1}$) exceeded the total supply of alkalinity to the lake from terrestrial drainage (55 ± 5 keq $year^{-1}$).

By assuming electroneutrality, the relative contributions of various ions to alkalinity (Alk) can be calculated from the balance between input, output, and change in mass in the lake of nonprotolytic cations and anions, where

$$\begin{aligned} \text{Alk} &= (Ca^{2+} + Mg^{2+} + Na^+ + K^+ + NH_4^+) \\ &\quad - (SO_4^{2-} + NO_3^- + Cl^-) \\ &= HCO_3^- + OH^- + CO_3^{2-} + A^- - H^+ \end{aligned} \qquad (2)$$

and A^- represents organic anions. For simplicity, we ignore organic anions here (*13*). The ions CO_3^{2-} and OH^- were negligible in all samples analyzed. No other ions contributed significantly to the alkalinity budget of Lake 239. Alkalinity as calculated by both Eqs. 1 and 2 can assume negative values.

There was no significant difference between average alkalinity produced in the lake as measured by Gran titration (Table 1 and Eq. 1) and that calculated from ionic balance (Eqs. 1 and 2; Table 2) for the 3 years when both were measured (*14*). The latter contains more uncertainty, because it represents the summation of eight separate ionic budgets, some of which cannot be measured as precisely as Gran alkalinity. The agreement between Gran alkalinity measurements and those calculated by ion balance on individual samples is shown in Fig. 2. The average P_a and standard deviation for 1981–1983 (n = 3) by Gran titration was 64 ± 11 keq $year^{-1}$ for the whole lake, whereas that calculated by ion balance was 40 ± 37 keq $year^{-1}$ (mean and standard error, respectively). The difference between these values was not statistically significant (*14*).

Alkalinity in lakes caused by increasing concentrations of cations results largely from diffusion of calcium and potassium from sediments. While ammonium, iron, and manganese are also released from sediments of Lake 239, organisms in the water column consume all of the ammonium that diffuses from sediments, and high redox potentials in the water column reprecipitate iron and manganese so that they contribute little alkalinity to the water column (*15*). Alkalinity can also be produced by processes removing anions. Common anion-removing processes in lakes are sulfate removal—for

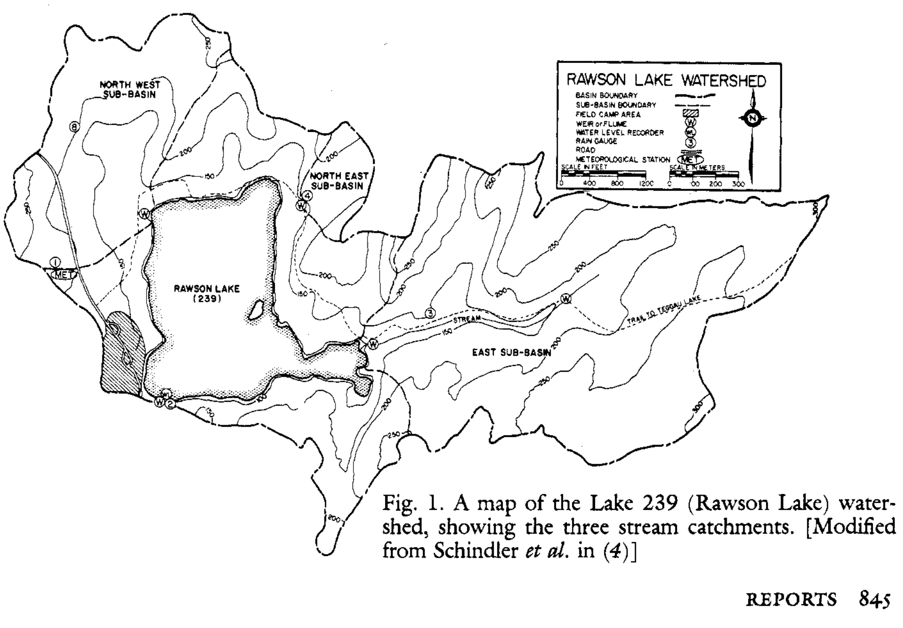

Fig. 1. A map of the Lake 239 (Rawson Lake) watershed, showing the three stream catchments. [Modified from Schindler *et al.* in (*4*)]

example, by sulfate reduction followed by precipitation of iron sulfides or binding as organic sulfur, denitrification, and biological removal of nitrate (*16*). Many of the ionic changes that can affect alkalinity are difficult to detect, because they involve relatively small changes in concentration of the ion in the lake (*14*).

Most of the alkalinity generated in the lake could be accounted for by sulfate removal (39 meq m^{-2} $year^{-1}$), exchange of H^+ for calcium in the sediments (29 meq m^{-2} $year^{-1}$), and reduction of nitrate (19 meq m^{-2} $year^{-1}$) (Tables 2 and 3). While statistically significant, exchange of H^+ for potassium was only 2 meq m^{-2} $year^{-1}$. The removal of NH_4^+ from the lake consumed 13 meq m^{-2} $year^{-1}$ of alkalinity. The contributions of sodium, magnesium, and chloride to the alkalinity budget were not statistically significant.

Table 3. Within-lake ionic processes affecting the alkalinity budgets of Lake 239 (natural) and Lake 223 (acidified to *p*H 5 with H_2SO_4). Values are 1981–1983 averages of total alkalinity production. Negative numbers represent alkalinity consumption.

Ion	Lake 239 (meq m^{-2} $year^{-1}$)	Alkalinity generated (+) or consumed (−) (%)	Lake 223 (meq m^{-2} $year^{-1}$)	Alkalinity generated (+) or consumed (−) (%)
Ca^{2+}	29	39*	76	19*
Mg^{2+}	−10	−14	−37	−9*
Na^+	−3	−4	−10	−2
K^+	2	3	−12	−3
NH_4^+	−13	−18*	−20	−5
Mn^{2+}			7	2*
SO_4^{2-}	39	53*	368	92*
Cl^-	11	15	11	3
NO_3^-	19	26*	19	5*
Total	74	100	402	100

*Statistically significant contributions to the alkalinity budget, based on paired *t* tests of ΔM and $I - O$.

It is of interest to compare the "natural" alkalinity budget with that of an acidified lake. Lake 223, in the ELA, has been purposely acidified with sulfuric acid. Most of the lake's watershed has only 0 to 1 m of overburden, so that it was assumed to be similar to the Northwest Subbasin, contributing little alkalinity to the lake. An upstream lake also contributed little alkalinity to Lake 223 (*17*). Acid added was a large source of negative alkalinity. Within-lake processes affecting the alkalinity of Lake 223 are compared with those in Lake 239 in Table 3. Addition of sulfuric acid to Lake 223 caused greatly increased alkalinity generation by sulfate removal (*18*). The rate of removal of SO_4^{2-} in Lake 223 was almost 10 times that in Lake 239, contributing about 92% of the total within-lake alkalinity generation. Calcium exchange in Lake 223 was also 2.5 times as high as in Lake 239. The increased acidity of Lake 223 also caused manganese to become a small, but significant, contributor to the alkalinity budget. Whereas in Lake 239 manganese was assumed to enter in complexed form—that is, not contributing significantly to charge balance—the acidification of Lake 223 caused a substantial flux of Mn^{2+} from sediments to overlying water in the anoxic hypolimnion. Iron was a net "sink" for alkalinity in both lakes, even though it appeared seasonally in large quantities in the anoxic hypolimnion of Lake 223. Inexplicably, the acidification of Lake 223 also caused increased movement of magnesium to sediments, which would consume alkalinity (*17*).

The rates of exchange of all other ions of importance to the alkalinity budget were remarkably similar in the two lakes. The similar fluxes of nitrate and ammonium in the two systems make it seem unlikely that acidification with sulfuric acid disrupts the nitrogen cycle, as has been suggested (*19*). Calcium exchange of sediments in Lake 223 was only 2.5 times as high as in Lake 239, indicating that calcium exchange has much less effect on the alkalinity budget of acidified lakes than biologically mediated reactions.

Our lakes are chemically similar to acid-vulnerable freshwaters throughout much of the Precambrian Shield in North America (*20*). Our results suggest that the terrestrial watersheds of such lakes are not necessarily the predominant sources of alkalinity, even when the acidity of precipitation has not been increased by man under natural conditions. Although anthropogenic inputs are clearly capable of overwhelming the combined in situ and watershed-based alkalinity sources in lakes, biological alkalinity-generating processes in lakes are actually stimulated by sulfate and nitrate to increased rates in acidified environments (*21*). As a result, we predict that the recovery of alkalinity to normal values in lakes should be relatively rapid once the acidity of atmospheric deposition is reduced.

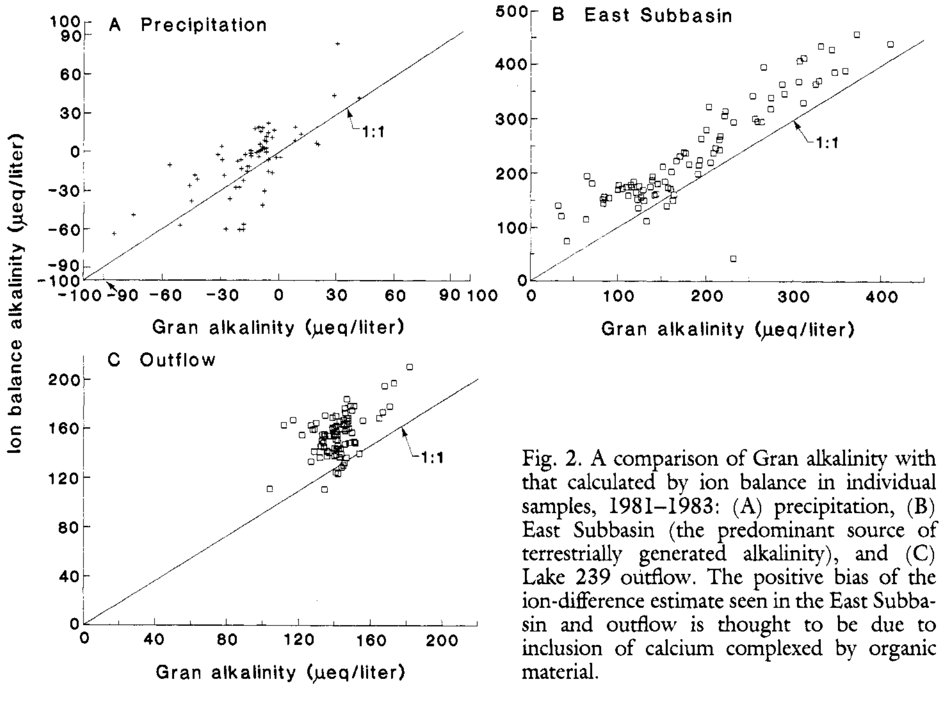

Fig. 2. A comparison of Gran alkalinity with that calculated by ion balance in individual samples, 1981–1983: (A) precipitation, (B) East Subbasin (the predominant source of terrestrially generated alkalinity), and (C) Lake 239 outflow. The positive bias of the ion-difference estimate seen in the East Subbasin and outflow is thought to be due to inclusion of calcium complexed by organic material.

REFERENCES AND NOTES

1. National Research Council of Canada, *Acidification in the Canadian Aquatic Environment* (NRCC 18475, Ottawa, 1981); Swedish Ministry of Agriculture, *Environment '82 Committee, Acidification Today and Tomorrow* (Stockholm, 1982).
2. R. April and R. Newton, *Water Air Soil Pollut.* **26**, 373 (1986); C. S. Cronan, *ibid.*, p. 355.
3. ELA lakes range in alkalinity from 0 to 224 μeq $liter^{-1}$ with a mean near 60 μeq $liter^{-1}$ [D. W. Schindler and T. Ruszczynski, *Can. Fish. Mar. Serv. Tech. Rep. 1147* (1983)]. Of seven streams draining terrestrial watersheds in the area, only two had positive alkalinity [S. E. Bayley and D. W. Schindler, in *Effects of Acid Deposition on Forests, Wetlands and Agricultural Ecosystems*, T. Hutchinson and K. Meema, Eds. (Springer-Verlag, New York, in press)].

4. Elsewhere we have documented the in situ production of alkalinity in lakes. See D. W. Schindler, R. Wagemann, R. B. Cook, T. Ruszczynski, J. Prokopowich, *Can. J. Fish. Aquat. Sci.* **37**, 343 (1980); C. A. Kelly, J. W. M. Rudd, R. B. Cook, D. W. Schindler, *Limnol. Oceanogr.* **27**, 891 (1982); R. B. Cook and D. W. Schindler, *Ecol. Bull.*, R. B. Cook, C. A. Kelly, D. W. Schindler, M. A. Turner, *Limnol. Oceanogr.* **31**, 134 (1986).
5. Acidometric Gran titrations were performed as described in W. Stumm and J. J. Morgan, *Aquatic Chemistry* (Wiley-Interscience, New York, 1970). The equivalence point occurred at *p*H values between 4.5 and 5.0, depending on the inorganic carbon concentration of the sample [D. S. Jeffries, *Can. J. Fish. Aquat. Sci.* **37**, 901 (1980)]. Detailed ionic budgets for terrestrial catchments are given by S. E. Bayley *et al.*, Newbury (in preparation) and S. E. Bayley and D. W. Schindler in (*3*).
6. K. G. Beaty, *Can. Data Rep. Fish. Aquat. Sci. 285* (1981); *ibid. 480* (1984); unpublished data. The long-term residual in the water budget of the lake is approximately 3%.
7. Methods used were described by M. P. Stainton, M. J. Capel, and F. A. J. Armstrong [*Fish. Mar. Serv. Misc. Spec. Publ. 25* (1977)], except that ion chromatography was used for sulfate measurements. Chemical samples were taken weekly from all streams during the ice-free season, which ranged from 25 to 30 weeks. Because streamflows were measured continuously and the records digitized to yield daily values, estimates of stream chemistry for days between weekly sampling were derived by linear interpolation with time. For the elements of concern here, there is little relation between concentration and flow. Combined sampling and analytical errors as a percentage of the mean concentration were as follows: Ca, 0.9; Mg, 2.0; Na, 0.9; K, 3.2; NH_4, 6.4; SO_4, 2.0; NO_3, 4.7; and Cl, 16.0.
8. G. A. Linsey, M. P. Stainton, D. W. Schindler, *Can. J. Fish. Aquat. Sci.* (in press).
9. The average alkalinity of precipitation at ELA is slightly negative. The Northeast Subbasin contains a small *Sphagnum* bog of *p*H 4, which constitutes about one-third of the drainage basin [S. E. Bayley *et al.*, *Can. J. Fish. Aquat. Sci.* (in press)].
10. The East Subbasin contains small amounts of calcareous lacustrine sediments deep in the overburden, apparently originating from glacial Lake Agassiz, which covered part of the area about 10,000 years ago. Such deposits are rare in the drainages of small lakes in the area. Four other streams in the ELA area have been sampled periodically. Only one yielded positive alkalinity [S. E. Bayley and D. W. Schindler, in (*3*)].
11. K. Kennedy, thesis, University of Waterloo, Ontario (1974).
12. If there were no in-lake sources, alkalinity should equal average annual input of alkalinity from precipitation plus terrestrial yield (49.75×10^9 μeq) divided by the average outflow (738×10^6 liters).
13. Organic acids in Lake 239 are about equally split between weak acids (pKa values >7) and strong acids (pKa's <4), [A. Herczeg, thesis, Columbia University, New York, (1985)]. Although removal of organic anions generates a small amount of alkalinity, their omission does not affect our conclusions.
14. For individual ions, the statistical significance of ΔM was based on paired t tests of two depth profiles of seven samples each, taken at identical depths in the first and last samplings in the study. The significance of $I - O$ was judged by paired t tests of annual I versus annual O ($n = 3$). The significance level used was $P = 0.05$. Because Gran alkalinity was not measured before 1981, and ion exchange rather than dionex methods were used for sulfate, budgets given here are for 1981–1983 only. Analysis of other ions for the period of record (9 to 13 years) were similar to 1981–1983 values. The significance of the difference between annual alkalinity calculated by Gran titration and ion balance was similarly tested.
15. S. L. Schiff and R. F. Anderson, *Water Air Soil Pollut.*, in press.
16. Although redox conditions are high at the sediment surface, low redox values occur a few millimeters below the sediment-water interface. As a result, sulfate is reduced as it diffuses into sediments, as shown by low porewater sulfate concentrations. High concentrations of iron and manganese also occur in sediment porewaters, but they are reoxidized as they diffuse to the sediment-water interface. On processes affecting alkalinity, see C. A. Kelly, J. W. M. Rudd, R. B. Cook, D. W. Schindler, *Limnol. Oceanogr.* **27**, 868 (1982); C. T. van Breeman, C. Driscoll, J. Mulder, *Nature (London)* **307**, 599 (1984); J. L. Schnoor and W. Stumm, in *Chemical Processes in Lakes*, W. Stumm, Ed. (Wiley, New York, 1985), pp. 322–338.
17. The alkalinity budget of Lake 223 is described by R. B. Cook, C. A. Kelly, D. W. Schindler, M. A. Turner, *Limnol. Oceanogr.* **31**, 134 (1986).
18. Sulfate reduction in ELA lakes is normally limited by the concentration of sulfate and increased as a linear function of sulfate concentration [R. B. Cook and D. W. Schindler, *Ecol. Bull.* (*Stockholm*) **35**, 115 (1983); D. W. Schindler, in *Chemical Processes in Lakes*, W. Stumm, Ed. (Wiley, New York, 1985).
19. O. Grahn, H. Hultberg, L. Landner, *Ambio* **3**, 8 (1974).
20. F. A. J. Armstrong and D. W. Schindler, *J. Fish. Res. Board Can.* **28**, 171 (1971); D. W. Schindler and T. Ruszczynski in (*3*); C. Langlois, A. Lemay, J. Ouzillean, Y. Vigneault, *Can. Fish. Mar. Serv. Data Rep. 1972* (1985); R. A. Lillie and J. W. Mason, *Wis. Dept. Nat. Resour. Tech. Bull. 138* (1983); Ontario Ministry of Environment, *Acidic Precipitation Ont. Study Rep. AP1002/81* (1981); R. B. Davis, *LSA Exp. Tech. Bull. 88* (1978).
21. Sulfate and nitrate reduction in acidified lakes of eastern Ontario and the Adirondacks have been shown to occur at rates similar to those in Lake 223 [J. W. M. Rudd and C. A. Kelly, *Limnol. Oceanogr.* (in press)]. Both processes also occur in *Sphagnum* bogs at *p*H values of 4 or less [H. F. Hemond, *Ecol. Monogr.* **50**, 507 (1980); S. E. Bayley, *et al.*, (in press)]. Work in mesocosms (1 m in diameter) by S. Schiff and R. F. Anderson [*Water Air Soil Pollut.* (in press)] confirms that calcium exchange, nitrate reduction, and sulfate reduction are the most important alkalinity generating processes in ELA lakes. D. W. Schindler [*Water Air Soil Pollut.* (in press)] shows that these processes are important in all acid-sensitive lakes for which input-output balances are available.

22. Supported by the Department of Fisheries and Ocean, Canada. S. E. Bayley and K. G. Beaty assisted in the calculation of terrestrial basin outputs. R. F. Anderson, S. E. Bayley, G. J. Brunskill, P. Campbell, R. E. Hecky, R. Hesslein, and S. Schiff provided helpful discussions or reviewed the manuscript.

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Antarctic Mesopelagic Micronekton: Evidence from Seabirds That Pack Ice Affects Community Structure

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Through a multidisciplinary project (AMERIEZ), with an unusual complement of components, previously unknown temporal and spatial dimensions to the structure of Antarctic epipelagic and mesopelagic communities were revealed. In late spring, an abundance of crustacean species thought to occur only below 300 meters was detected in ice-covered surface waters. Evident in ice-free waters were the expected occurrence patterns of these normally nonmigratory mesopelagic organisms. Where the pack was consolidated and little light penetrated to depth, primary and secondary production was confined to ice floes, and the physical environment immediately beneath the ice was reminiscent of a mesopelagic one. This suite of characteristics possibly explains why the crustaceans resided at the surface.

ANTARCTIC PACK ICE COVERS 10 PERcent of the world ocean at its maximal extent during early spring (*1*). Associated with the ice is a distinct biological community, including in-ice living algae and bacteria, epipelagic micro- and macrozooplankton, fishes, birds, and pinnipeds (*2*, *3*). As the pack recedes, ultimately to be confined to seven major refugia by early summer (*4*), open-water species, particularly those of upper trophic levels, move southward with the retreating ice edge (*2*, *3*). The open-water community takes advantage of its major phytoplankton bloom, which occurs when waters previously shielded by ice are exposed to the long hours of summer sunlight and low density meltwater imparts significant vertical stability to the water column (*5*).

In contrast to epipelagic species, the influence of seasonal ice cover and changing day length is poorly known for the deeper-living (100 to 1000 m) mesopelagic component of the Antarctic marine community. In other areas of the world's oceans, a substantial fraction of the mesopelagic fauna migrates from 200- to 500-m daytime depths to or near the surface at dusk, and returns to depth at dawn. These organisms orient to a constant light level or isolume, which moves up and down in the water column with the setting and rising sun (*6*). At night, vertical migrators can make up greater than 70 percent of the micronektonic biomass in the top 100 m (*7*). In the Antarctic, species exhibiting light-oriented movement could have radically different vertical distributions through the austral seasons if light-mediated behavior is maintained throughout the year-

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