

tion of relatively fresh en echelon cracks along the fault during the month before the last Parkfield mainshock¹⁷, and by the rupture of a water main only hours before it¹⁸. The relationship between intermediate-term precursors (months to years) and short-term precursors (hours to weeks) is unknown.

It is important that independent precursors are observed in order to gain confidence during the process of refining an earthquake prediction. The observations of seismic quiescence and deformation deficiency are independent and are affected by different sources of error. Thus their nearly synchronous onset strongly suggests that these lasting changes are real. The two types of changes are probably not physically independent, however, because a common underlying process may cause both phenomena.

It is also important to attempt the identification of precursors before the mainshock has occurred in order to learn what misinterpretations are made when one is faced with data which may contain potential precursors. This attempted earthquake prediction is notable in being based on four lines of evidence: regular recurrence, seismicity rate decrease of 45%, deformation rate decrease of 20% and a *b*-value increase of 25%. □

Received 15 March; accepted 18 April 1990.

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ACKNOWLEDGMENTS. We thank W. D. Stuart for discussions and comments, and R. Bilham, E. Roeloffs and C. Morte for comments on the manuscript. This work was supported in part by the U.S. Geological Survey external grants program.

Biological recovery of an acid lake after reductions in industrial emissions of sulphur

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THERE is now considerable evidence from Canada¹⁻⁴, Norway⁵, Sweden⁶ and Scotland⁷ that lake and stream acidification is chemically reversible. Water quality improvements have been shown to occur rapidly when inputs of sulphur are reduced⁸. However, there is little evidence that biological systems recover after emission reductions⁹. We report here on changes in the biological community of an acid-stressed lake near the metal smelters at Sudbury, Canada, during a 10-year period (1978-1988) after smelter emissions of sulphur were reduced by more than 50%. Our studies of the fish, benthic invertebrates, and zooplankton in this lake show that rapid recovery and reinvasion occurs among some acid-sensitive species.

The study was conducted on Whitepine Lake (47°17'N, 80°50'W), a clear, dilute (conductivity around 30 μmho cm⁻¹)

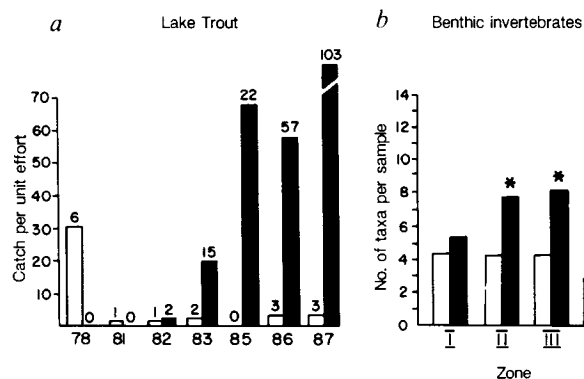


FIG. 1 a, Catch per unit of effort. Number of lake trout caught in experimental gillnets (1.8-7.6-cm mesh) in Whitepine Lake. Data standardized to 100 h of netting effort. Only naturally produced fish are included in the figure. The total number of adults (open columns) and juveniles (solid columns) captured in each year is indicated. b, Changes in the number of taxa of benthic invertebrates in Whitepine Lake. Three replicate samples were collected at each of three stations in each offshore zone (I, 8-21 m; II, 4-8 m; III, 1.5-4 m) using an 15 × 15 cm Ekman dredge on May 20, in both 1982 (open columns) and 1988 (solid columns). Samples were sieved through a 600-μm mesh screen before counting. Sampling was repeated in October of both years with similar results. The nearshore rocky areas (IV, <1 m) were sampled with artificial substrates (23 × 23 × 15 cm cages filled with 5-10-cm diameter clean stones) placed in triplicate at five sites. The placement and retrieval dates were 25 May and 19 July, respectively, in both 1983 (open columns) and 1988 (solid columns). Autumn samples were also collected using artificial samplers; again with similar results. * Depth zones showing significant increases (*t*-test, *P* ≤ 0.05) in number of taxa between sampling periods.

headwater lake (surface area 67 ha, maximum depth 22 m), located in a forested area 90 km north of Sudbury. The lake receives both wet and dry inputs of sulphur, but is outside the zone of high deposition of metal particulates from the Sudbury smelters¹ (water concentrations of Cu and Ni <2 μg l⁻¹). In 1980 the lake was acidic (pH <5.5) and its fish population showed classical signs of acid stress: acid-tolerant yellow perch (*Perca flavescens*) were very abundant, while acid-sensitive species such as lake trout (*Salvelinus namaycush*), burbot (*Lota lota*), and white suckers (*Catostomus commersoni*) were extremely rare and were not reproducing¹⁰.

Monitoring of lake water quality began in 1980. Fish populations were assessed during 1978, 1981, 1982, 1983, 1984, 1986, and 1987 using similar sampling sites and capture gear (variable mesh gillnets, trapnets, plexiglas minnow traps)¹¹. Benthic invertebrates inhabiting soft sediments were sampled in 1982 and 1988, with a depth-stratified sampling design and an Ekman dredge collector. Artificial substrate collectors were used in 1983 and 1988 to sample invertebrates that occupied rocky nearshore areas. Zooplankton were collected at least monthly during the open water periods of 1980-1988. Zooplankton samples were collected with a 12.5-cm diameter 80-μm mesh plankton net drawn vertically through the water column at a mid-lake site.

Water quality improved significantly (*P* < 0.01) from 1980 (pH 5.4, acid-neutralizing capacity (ANC) 1 μequivalent l⁻¹) to 1988 (pH 5.9, ANC 11 μequivalent l⁻¹) (Table 1). Specific conductance and concentrations of SO₄, Ca and Al all declined with reductions in industrial emissions of SO₂ (Table 1).

The first evidence of biological recovery was the appearance of naturally produced young lake trout from the remnant adult population. Young lake trout first appeared in 1982 and became increasingly abundant throughout the rest of the study (Fig. 1). Production of young trout by the remnant adult population was discovered during routine monitoring of hatchery fish added to this lake in 1980 and 1981¹¹. Each hatchery fish was marked before addition by removing the adipose fin. During monitoring of these individuals an increasing number of unmarked fish

TABLE 1 Water quality data for Whitepine Lake, 1980-1988

	Sudbury emissions of SO ₂ (×10 ³ tonnes)*	pH	Acid-neutralizing capacity (μequivalent l ⁻¹)	Conductivity (μmho cm ⁻¹)	Ca (μequivalent l ⁻¹)	SO ₄ (μequivalent l ⁻¹)	Total Al (μg l ⁻¹)
1980	935	5.4 (5.3-5.8)	1±5	37±2	156±18	237±20	69±20
1981	837	5.7 (5.6-5.8)	4±2	35±1	145±31	235±12	59±21
1982	389	5.8 (5.8-5.9)	10±4	36±3	138±17	218±20	44±15
1983	538	5.8 (5.7-5.8)	8±3	32±1	123±5	198±22	36±12
1984	767	5.8 (5.7-5.8)	8±2	32±2	125±10	198±24	40±15
1985	769	5.8 (5.7-5.9)	12±4	31±1	119±13	195±4	50±11
1986	725	5.9 (5.8-5.9)	12±4	29±1	120±9	177±17	34±10
1987	730	6.0 (5.9-6.1)	15±1	30±4	115±13	196±23	26±11
1988	718	5.9 (5.9-6.0)	11±3	30±4	115±6	195±10	40±14

Annual means (±1 s.d., range given for pH) are calculated from monthly data ($n=4-11$) for samples collected through the epilimnion and metalimnion. Changes through time were determined to be significant ($P < 0.01$) for all of the above chemical parameters using linear correlation analysis of log-transformed (except pH) data against time in months.

* Annual averages for SO₂ emissions (×10³ tonnes) before the study were: 1960-64, 2,241 tonnes; 1965-69, 2,202 tonnes; 1970-74, 1,867 tonnes; 1975-79, 1,064 tonnes.

occurred in yearly catches. By 1987, the naturally produced fish were far more abundant than the stocked fish, and dominated (87%) the gillnet catches. These young fish began to appear at least two years before the stocked fish had reached sexual maturity (age 5, Autumn 1984).

Other researchers have shown that lake trout do not reproduce when pH drops below 5.5-5.6 (refs 12-13). Our study showed that this effect is reversible; successful reproduction occurred when pH increased above 5.5.

Successful reproduction did not occur in the white sucker and burbot populations, and these species were not observed after 1984. Very few adults (less than five fish observed) were present for each species, a fact that presumably contributed to their extinction. In a lake where adult white suckers were abundant and were not reproducing under low pH conditions, successful reproduction has been shown to occur with an increase in pH (ref. 14).

The rapid increase in abundance of lake trout, an omnivorous predator, caused marked changes in prey populations. Trapnet catches of perch, a common prey species of lake trout¹⁵, declined

from 145 per night in 1982 to approximately 2 per night in 1987. Densities of benthic invertebrates in the deep zones of the lake (8-21 m) that are occupied by lake trout declined from 1140 m⁻² in 1982 to 650 m⁻² in 1988. In contrast, the density of invertebrates in the shallow areas (0-8 m), the principal foraging area of perch, increased with the decline in abundance of perch. Soft sediment areas provided 550 invertebrates m⁻² in 1982, 1,320 m⁻² in 1988; rocky areas, 6 invertebrates per sample in 1983, 164 per sample in 1988.

Although changes in fish predation may explain many of the changes in invertebrate populations, direct effects of water quality improvements were also detected. The number of taxa of benthic invertebrates increased from 39 in 1982/83 to 72 in 1988 (Fig. 1) and the relative abundance of many of the original species changed dramatically. Three new species of mayfly (*Hexagenia* sp., *Ephemera* sp., *Caenis* sp.) and two species of oligochaetes (*Vejdovskyella comata*, *Slavina appendiculata*) appeared in the most recent survey. A single specimen of gastropoda (*Ferrissia* sp.) was also captured for the first time in 1988. Taxa scarce in the early survey, including leeches and crayfish (*Orconectes propinguis*), increased in numbers coincident with improvements in water quality. The benthic survey also indicated an increase in Iowa darters (*Etheostoma exile*), a bottom-dwelling fish. One new zooplankton species (*Epischura lacustris*) also appeared in the collections after 1981. On the basis of previous studies all the above species can be considered acid-sensitive¹⁶⁻²².

Whitepine Lake is only one of many lakes in the Sudbury area where water quality has improved following reduced emissions of sulphur (Fig. 2). In January 1980 and January 1987, we sampled 66.6% ($n=104$) of all known lake trout lakes (ranging from extinct to healthy populations) within a 1.4×10^3 km² area around Sudbury. The sample set was slightly biased towards larger lakes (surface area 38-13,130 ha) to permit sampling by fixed-wing aircraft. Increases in pH ($\bar{x}\Delta\text{pH}=0.37$) and ANC ($\bar{x}\Delta\text{ANC}=23$ μequivalent l⁻¹) occurred in 98.1 and 97.3% of the lakes, respectively. The number of lakes with pH below the threshold for reproduction of lake trout (pH < 5.5) declined from 45 (43.3%) to 20 (19.2%) (Fig. 2).

In summary, our data show that rapid chemical and biological recovery of industrially-acidified lakes can be accomplished simply by reducing the emission to the atmosphere of acidifying substances. Conditions suitable for the survival and reproduction of lake trout and other acid-sensitive organisms can return without liming or other ameliorative treatments. □

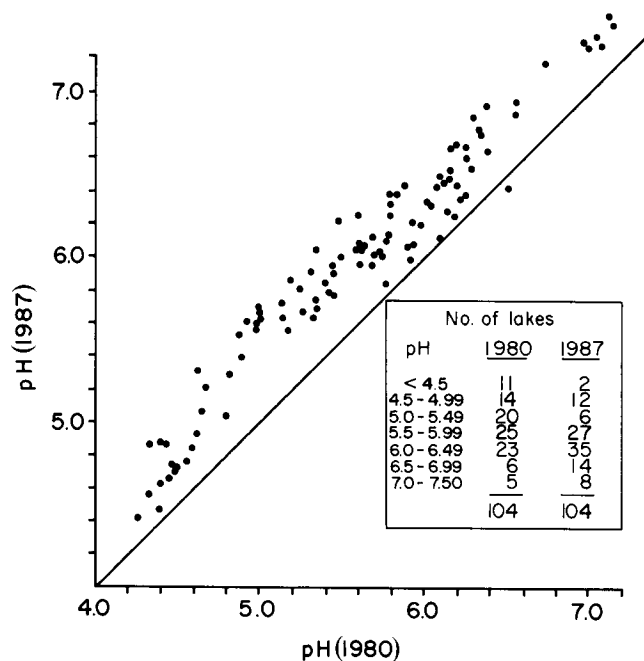


FIG. 2 Change in pH of 104 lake-trout lakes near Sudbury, Canada between 1980 and 1987. Water samples were collected with a 5-m tube composite sampler through the ice. The pH distribution of the sampled lakes is presented in the inset table. For further evidence of regional scale recovery of water quality see refs 1 and 2.

Received 2 October 1989; accepted 14 March 1990.

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ACKNOWLEDGEMENTS. We thank D. Farara, P. Gale and V. Liimatainen for assistance and P. Dillon, D. Schindler, K. Mills and D. Wales for constructive criticism. Funding was provided by Ontario Ministry of Natural Resources and Ontario Ministry of the Environment through the APIOS program.

Tritrophic effects of a simple architectural mutation in pea plants

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WHEN studying interactions between trophic levels, ecologists often restrict their attention to two levels as a means of simplifying the analysis; unfortunately, this simplification can be misleading if tritrophic interactions (such as plant-herbivore-predator) cannot be understood by simply adding together pairwise interactions (plant-herbivore plus herbivore-predator, for example)^{1,2}. We examined the significance of tritrophic interactions by asking how the morphology of the common pea (*Pisum sativum*) influences the population growth of pea aphids (*Acyrtosiphon pisum*) in the presence and in the absence of a third trophic level. We found significant interactions between the first trophic level (peas) and the third trophic level (ladybird beetles) in determining aphid population growth. Our results point out how simple genetic changes can yield morphological variants in plants that differ dramatically in their resistance to herbivores due to the effects of plant architecture on enemies of the herbivore.

Numerous studies suggest that plant morphology may indirectly influence herbivores by affecting predators or parasites³⁻⁶. To show that such phenomena represent tritrophic interactions, however, one needs to factor out the direct effects of plant morphology on herbivores from the indirect effects mediated by the third trophic level. We distinguished these direct and indirect effects by using a factorial design in which two different treatments of plant architecture (normal versus leafless peas) were crossed with two predator treatments (with and without ladybirds), and rates of aphid population growth were used as the response variable. A significant interaction between the predation and the plant architecture treatments would be evidence for a tritrophic interaction. Because we were also interested in the extent to which within-species variation in plant morphology shapes plant-herbivore-predator interactions, we sought architectural variants that were known to differ genetically at a limited number of loci. Previous investigations of the interplay between plant morphology and herbivore enemies have involved different species of plants^{3,7,8}, or different artificial substrates⁹, or varieties of the same species that differ at an unknown number of unspecified genetic loci^{4,5}. In contrast, we used highly backcrossed strains of peas that differed at only two loci: a normal variety and a leafless variety that is distinguished

by homozygous recessive mutations at the *afla* and the reduced stipule loci¹⁰.

For each experiment, individual pea plants were grown in pots 21 cm in diameter and 21 cm deep, and were enclosed in cages 32 cm tall. An excess of late instar (IV) or adult apterous aphids were first placed on each plant, and then aphids were removed until we achieved the desired initial density, which was the same for all plants within any experiment. Although we were not able to produce perfectly identical age distributions of aphids on all plants, we did not introduce any consistent biases. After the aphid populations were established, the desired number of predators (either *Coccinella septempunctata*, *Hippodamia variegata*, or *Propylea quatuordecimpunctata*) were added to plants in the 'with predator' treatment and all of the plants were caged.

Experiments were initiated with identically aged pea plants (3-5 weeks old, depending on the experiment) and were allowed to run for 2-4 days. Although 2-4 days might seem a short time over which to observe population change, it proved to be an interval over which aphid numbers changed by as much as $\pm 100\%$ (this is because our final census included newborn aphids).

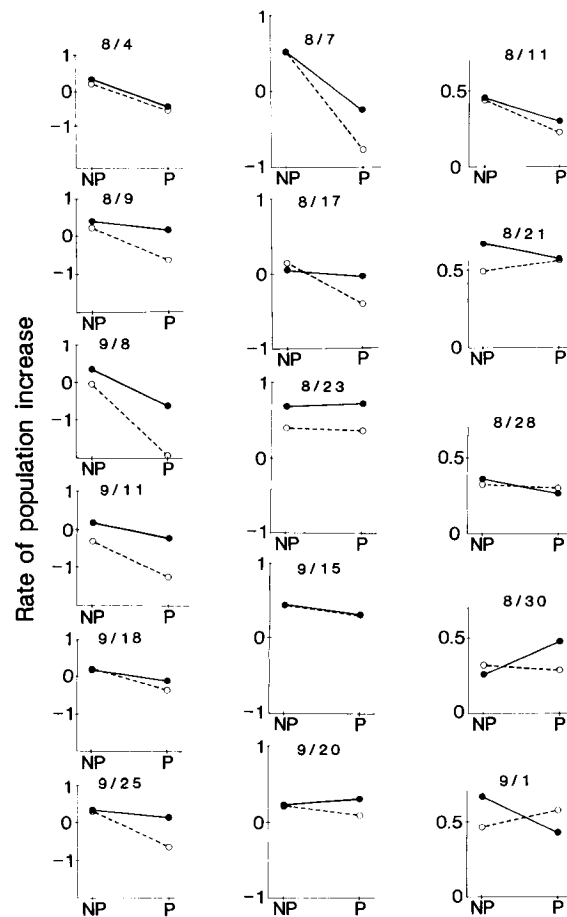


FIG. 1 Instantaneous rate of aphid population growth (per day) in factorial experiments that manipulated presence of ladybird predators (NP, no predators; P, with predators) and the architectural variety of pea. ---○---, Leafless mutant; —●—, normal leafy genotype. Left column of graphs, experiments with *Coccinella septempunctata*; middle column, *Hippodamia variegata*; right column, *Propylea quatuordecimpunctata*. Each set of axes is also labelled with the date on which the experiment terminated. The decline in aphid population growth from NP to P is a measure of predator impact; the differences in slope of dashed and solid lines reflect possible interaction effects (see Table 1 for statistical significance) or 'three-trophic-level effects'. The scale is expanded fourfold for *Propylea* versus *Coccinella* and *Hippodamia* columns; thus the effects of *Propylea* are negligible in comparison with *Coccinella* or *Hippodamia*.