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Paul and Peter Lakes: A Liming Experiment Revisited

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ABSTRACT: From 1951-1976, Peter Lake was limed periodically while neighboring Paul Lake was used as a reference ecosystem. We investigated the persistence and variability of the response of Peter Lake to liming by collecting all available historical data on the lakes and by monitoring the limnological properties of both lakes weekly from June-August, 1984. Physical and chemical changes in limed Peter Lake included increases in pH, alkalinity, dissolved inorganic carbon (DIC) concentration, transparency, oxygen content and summer heat content. These changes occurred rapidly in 1951 and have persisted with little variability until 1984. Several differences in algal and zooplankton community composition and dynamics were associated with the physical and chemical changes. Historical data and our observations indicate that the planktonic community structure of Peter Lake has been more variable than that of unlimed Paul Lake.

INTRODUCTION

In 1951, Arthur D. Hasler began the first whole-lake ecosystem experiment to use a "control" or reference ecosystem (Likens, 1985). Hasler divided the two basins of an hourglass-shaped lake with an earthen dike. He used rotenone to remove the native fish from the lakes and then stocked them with trout. The upstream basin, Paul Lake, was used as a reference ecosystem to determine the effects of lime additions on fish productivity in downstream Peter Lake. Results of the study were summarized in several publications (Johnson and Hasler, 1954; Stross and Hasler, 1960; Stross *et al.*, 1961). Periodic liming of Peter Lake continued until 1976. According to Likens (1985), this pioneering experiment was a model for more recent whole ecosystem experiments at the Hubbard Brook Experimental Forest and the Canadian Experimental Lakes Area.

Liming is one management technique used to mitigate the adverse effects of acid precipitation in lakes (Bengtsson and Dickson, 1980; Driscoll *et al.*, 1982; Fraser and Britt, 1983). Consequently, there have been many recent studies investigating the effects of lime additions on aquatic ecosystems. Most of these studies have lasted only a few years. The experiment in Paul and Peter lakes is the longest liming project known to us and, therefore, provides an interesting opportunity to study the long-term effects of liming.

This paper has two goals. First, we collected and reviewed the historical data on these lakes, much of which was unpublished, to examine them for long-term limnological trends. Second, we analyzed the limnological properties of Paul and Peter lakes in 1984, 8 years after the last liming, to evaluate any persisting differences between the lakes that might be due to the liming of Peter Lake.

METHODS

Peter and Paul lakes are located in section 36, T45N R42W, Gogebic Co., Michigan. They are seepage kettle lakes surrounded on three sides by moraine ridges. A connecting culvert allows water to flow from Paul Lake into Peter Lake when water levels are high. Surface area of Peter Lake is 2.4 ha, and its maximum depth is 19.3 m with an average depth of 8.3 m. Surface area of Paul Lake is 1.2 ha with a maximum depth of 12.2 m and an average depth of 5.0 m. Both lakes have some bog mat development. In 1984, both lakes contained similar densities of largemouth bass (*Micropterus salmoides*) and no other vertebrate planktivores (J. R. Hodgson, D. M. Lodge, J. F. Kitchell, pers. comm.). Invertebrate planktivores include *Chaoborus punctipennis* and *C. flavicans* (von Ende, 1979).

The lakes were sampled weekly from 6 June to 22 August 1984. Permanent sam-

pling stations were established near the deepest point in each lake. Vertical profiles for dissolved oxygen (DO) and temperature were made with a Yellow Springs Instrument Company (YSI) probe and meter. Photosynthetically available radiation (400-700 nm) was measured with a submersible spherical quantum sensor (Li-Cor Model 188B). Water samples were collected from depths corresponding to 100%, 50%, 25%, 15%, 10%, 1% and 0.01% of incident light penetration. Water samples were returned to the laboratory for subsequent analysis.

All water samples were analyzed fluorometrically for chlorophyll *a* using methods described in Strickland and Parsons (1968), substituting methanol for acetone as recommended by Holm-Hansen and Riemann (1978). The fluorometer was calibrated with commercially purchased chlorophyll *a* diluted in 100% methanol. The samples were filtered onto GF/F filters, rinsed with distilled water, frozen, homogenized in 100% methanol and centrifuged to extract chlorophyll *a*.

Primary productivity was estimated weekly by the ^{14}C -method. Water samples from depths corresponding to 100%, 50%, 25%, 10% and 1% of incident radiation were collected and placed in 125-ml bottles. Three bottles were filled with water from each depth and inoculated with $5\ \mu\text{Ci NaH}^{14}\text{CO}_3$; one control bottle also received 1 ml saturated DCMU solution (Legendre *et al.*, 1983). The bottles were suspended *in situ* at the depths of sampling from approximately 1000-1600 hr. The contents of the bottles were filtered in the field onto GF/F filters. The filters were rinsed with 0.01N HCl, dried overnight and placed in Bray's solution (Bray, 1960). Radiocarbon activity was determined by liquid scintillation counting with efficiencies determined by using internal standards (Vollenweider, 1974). Total inflection point alkalinity (Gran, 1952) and pH was determined for each depth and DIC was calculated using Table 8-1 in Wetzel and Likens (1979).

Additionally, conductivity profiles were measured on 18 August 1984 with a YSI probe and meter in both lakes. In midsummer, water samples from the euphotic zones in both lakes were filtered and analyzed for absorbance at 440 nm (dissolved color) on a Bausch and Lomb Spectronic 88 with a 10-cm cell (Kirk, 1983).

Solar radiation was monitored continuously using a Belfort pyrhelimeter. These traces were digitized, integrated and converted to estimates of photosynthetically available radiation. Daily volumetric primary productivity was calculated using the measurements of solar radiation, chlorophyll-specific photosynthesis from the weekly samples and light extinction from weekly light profiles (Carpenter *et al.*, 1986).

Zooplankton was collected by vertical hauls of a 80- μm mesh Nitex net. The efficiency of the net was determined by comparing number of organisms per liter collected from vertical hauls with those collected from 6-7 depths with a 24-l Schindler-Patalas trap. The zooplankton were preserved in 5% formalin and later identified, counted and measured with a binocular dissecting scope. Crustacean lengths (exclusive of setae and spines) were converted to dry masses using equations in Table 7.2 in Downing and Rigler (1984). We calculated the dry mass of *Holopedium gibberum* from a general zooplankton equation in Peters and Downing (1984) in order to exclude its sheath. Rotifer masses were calculated from formulae in Table 7.5 in Downing and Rigler (1984). We assumed dry mass/wet mass = 0.1 for rotifers (Pace and Orcutt, 1981).

Water samples collected from three depths in the epilimnion were pooled to obtain phytoplankton samples. These samples were preserved with Lugol's iodine solution. Samples were concentrated by settling and the phytoplankton identified, enumerated and measured on an inverted microscope. Species-specific cell volumes were estimated by approximating algal cell shapes to geometric figures, excluding the loricae and the gelatinous sheaths.

RESULTS

Manipulations and historical observation to 1980.—Most of the hydrated lime inputs to Peter Lake occurred in the 1950s with application continuing until 1976 (Table 1). The

composition of the hydrated lime was 30.5% calcium and 17.0% magnesium, with a hydroxide equivalent of 96.5% (Stross and Hasler, 1960). After the initial liming, alkalinity and pH values of Peter Lake increased (Tables 2 and 3). Although different methods of determining alkalinities were used through the years, alkalinities in Peter Lake have consistently remained 2 to 5 times higher than those of Paul Lake. The pH in Peter Lake has remained higher as well.

TABLE 1. — Amounts of hydrated lime added to Peter Lake

Year	Application (kg)	Source
1951	2495	Stross, 1958
1952	2677	Stross, 1958
1953	726	Stross, 1958
1955	23	Stross, 1958
1956	102	Stross, 1958
1959	1179	Gammon and Hasler, 1959
1962	277	Malueg, 1963
1969	4537	Schmitz, 1977
1976	907	Schmitz, 1977

TABLE 2. — Reported alkalinity or DIC values from Paul and Peter lakes. In liming years, both preliming and postliming data appear for Peter Lake. The units reported from fixed end point alkalinity methods are mg L⁻¹ CaCO₃, mg L⁻¹ HCO₃⁻ and methyl orange alkalinity (M.O. Alk.), while $\mu\text{eq L}^{-1}$ are reported for total inflection point alkalinity

Year	Paul	Peter Prelime	Peter Postlime	Unit	Source
1951	5.8	5.8	19.5	mg L ⁻¹ CaCO ₃	Johnson and Hasler, 1954
1955	9.0	27.5	—	mg L ⁻¹ HCO ₃ ⁻	Stross, 1958
1959	6.0 – 6.5	24.0 – 26.0	31.0 – 38.0	M.O. Alk.	Gammon and Hasler, 1959
1962	8.0 – 10.0	20.0	25.0	mg L ⁻¹ CaCO ₃	Malueg, 1963
1975-1980	12.5*	20.0*	—	mg L ⁻¹ CaCO ₃	Greene, 1980
1984	45.7	173.6	—	$\mu\text{eq L}^{-1}$	This study

*Average values from data collected over this 5-year period

TABLE 3. — Reported pH values from Paul Lake and Peter Lake

Year	Paul	Peter Prelime	Peter Postlime	Source
1951	5.9	5.9	7.3	Johnson and Hasler, 1954
1955	6.4	7.1	—	Stross, 1958
1959	6.5	6.7	8.3	Gammon and Hasler, 1959
1962	6.7	7.3	8.3	Malueg, 1963
1975-80	6.2*	7.2*	—	Greene, 1980
1984	6.18	6.73	—	This study

*Average value from data collected over this period

Precipitation of humic colloids, presumably associated with the increased alkalinity, increased the depth of the euphotic zone by as much as 160% (Stross and Hasler, 1960). In 1951, the depth of 1% light penetration (defined as the euphotic zone depth or Z_e) was 2.7 m in Paul Lake and 4.3 m in Peter Lake (Johnson and Hasler, 1954). After further lime additions, the euphotic zone depth in Peter Lake increased to 7.0 m (Stross and Hasler, 1960). Malueg (1963) recorded Z_e at 7.5 m in Peter Lake and 4.4 m in Paul Lake. Average Z_e from 1975-1980 was 2.9 m in Paul Lake and 5.1 m in Peter Lake (Greene, 1980). In 1984, Z_e ranged from 5-6 m in Paul Lake and 6-8 m in Peter Lake. This enhanced light penetration also increased the annual heat content of Peter Lake as compared to Paul Lake (Stross, 1958).

Johnson and Hasler (1954) attributed high fish survivorship in Peter Lake in 1952, as compared to the high fish mortality in Paul Lake, in part to a reduced rate of oxygen consumption associated with the precipitation of humic colloids. The increased euphotic zone depth may have also contributed to the increased oxygen available at the lower depths by allowing photosynthesis to occur at greater depths.

The planktonic community changed with the liming. Malueg (1963) found more phytoplankton species in Peter Lake than in Paul Lake. Originally, both lakes contained large numbers of *Daphnia pulex* and *Holopedium gibberum* (Stross *et al.*, 1961). Following liming, these species were replaced in dominance in Peter Lake by *Daphnia rosea* (identified as *D. longispina* in earlier studies according to Kitchell and Kitchell, 1980) and *Diaptomus* (Stross *et al.*, 1961). Paul Lake continued to support populations dominated by *Daphnia pulex* and *Holopedium gibberum*.

All the fish in both lakes were removed by rotenone and replaced with trout during the initial experiment in 1951. Trout were restocked into both lakes for several years (Johnson and Hasler, 1954; Stross *et al.*, 1961), but the population declined and eventually disappeared. After the mid-1960s, minnows (Cyprinidae) dominated the fish community, but their numbers declined after largemouth bass were introduced into Peter Lake in 1975 and Paul Lake in 1978 (J. F. Kitchell, pers. comm.).

1984 observations.—Major differences remain between Paul and Peter lakes. Alkalinity values in unlimed Paul Lake were ca. 40-50 $\mu\text{eq L}^{-1}$ in the epilimnion and increased in ca. 70 $\mu\text{eq L}^{-1}$ in the hypolimnion (Fig. 1). DIC values in Paul Lake were between 1.0-1.5 mg L^{-1} in the epilimnion and 2.0-3.0 mg L^{-1} in the hypolimnion. In limed Peter Lake, alkalinity and DIC values were ca. 170 $\mu\text{eq L}^{-1}$ and 3.0 mg L^{-1} , respectively, in the mixed layer and around 200-230 $\mu\text{eq L}^{-1}$ and 4.0-5.0 mg L^{-1} , respectively, in the hypolimnion (Fig. 1). Average pH values for Paul Lake were 6.18 (Table 3) in the mixed layer and 6.08 in the hypolimnion (range 5.45-6.59). The average pH values for Peter Lake were 6.73 (Table 3) in the epilimnion and 6.65 in the hypolimnion (range 6.17-6.91).

The transparency of Peter Lake differed from that of Paul Lake (Fig. 2). The euphotic zone depth in unlimed Paul Lake was around 5.75 m for most of the summer, although it occasionally decreased to 5.0 m. In limed Peter Lake, Z_e was ca. 7.0 m in the early summer, then decreased to 6.0 m for a short time, and by the end of August was around 8.0 m. Dissolved color was negligible in Peter Lake (no absorbance at 440 nm), while color was detected in Paul Lake (0.02 absorbance units at 440 nm).

Isotherms (Fig. 3) indicated that limed Peter Lake maintained slightly higher temperatures than Paul Lake throughout the sampling period. The thermocline generally began around 3.0-3.5 m in Paul Lake and 4 m in Peter Lake. Highest mixed-layer dissolved oxygen content in Paul Lake occurred in early June ranging from 8.0-10.0 mg L^{-1} ; these values declined for the rest of the summer to ca. 6.0 mg L^{-1} (Fig. 4). Below 6 m, the oxygen content was less than 1.0 mg L^{-1} for most of the summer. Highest mixed-layer dissolved oxygen content in Peter Lake also occurred in early June with values around 8.0-10.0 mg L^{-1} ; these values declined to ca 7.0 to 8.0 mg L^{-1} for the rest of the summer (Fig. 4). The deoxygenated zone (< 1.0 mg L^{-1}) began at 7.0 m.

Chlorophyll *a* concentrations were similar in both lakes (Fig. 5). Mean mixed-layer

chlorophyll *a* concentration in Paul Lake was $3.42 \mu\text{g L}^{-1}$ with maxima of $6.0\text{--}7.0 \mu\text{g L}^{-1}$ in early July and mid-August. Mean mixed-layer chlorophyll *a* in Peter Lake was $2.54 \mu\text{g L}^{-1}$ with the highest values occurring in early June. Both lakes also had chlorophyll maxima at depths corresponding to 0.01% incident radiation; these maxima probably correspond to a layer of photosynthetic bacteria (Parkin and Brock, 1980). This chlorophyll maximum persisted in Paul Lake for the entire summer. Conductivity profiles taken in midsummer indicated that Paul Lake was meromictic, with conductivity ranging from $45\text{--}60 \mu\text{mhos cm}^{-1}$ in the monimolimnion, compared to $20 \mu\text{mhos cm}^{-1}$ in the overlying water. The pigment maximum was associated with the chemocline. In contrast, conductivity in Peter Lake ranged from $28\text{--}36 \mu\text{mhos cm}^{-1}$ with no apparent chemocline.

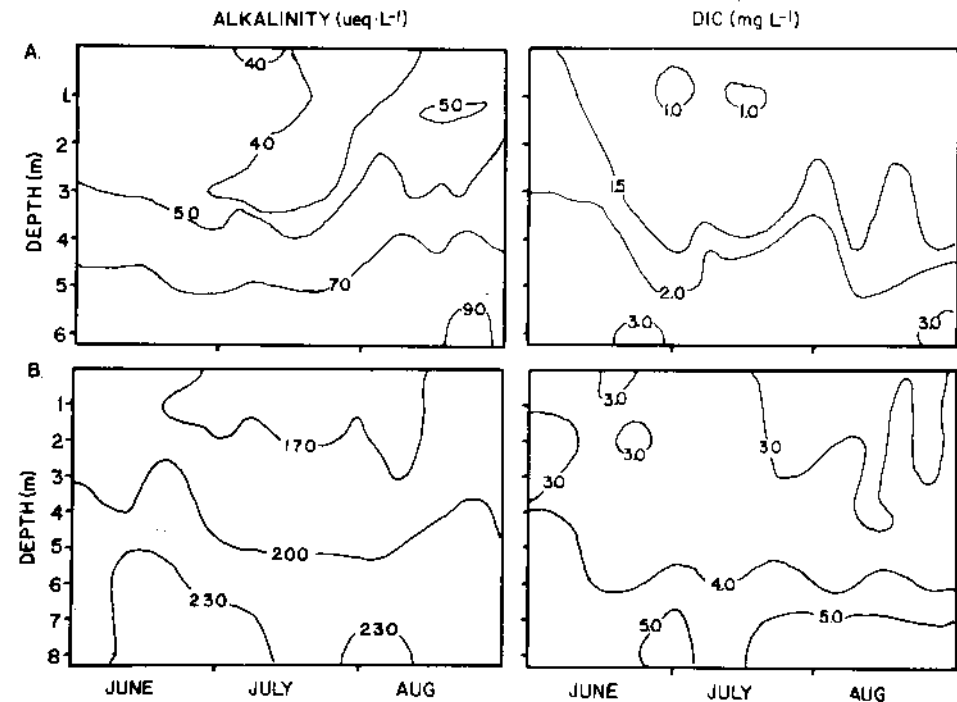


Fig. 1. — Alkalinity ($\mu\text{eq L}^{-1}$) and dissolved inorganic carbon (mg L^{-1}) isopleths for Paul (A) and Peter (B) lakes

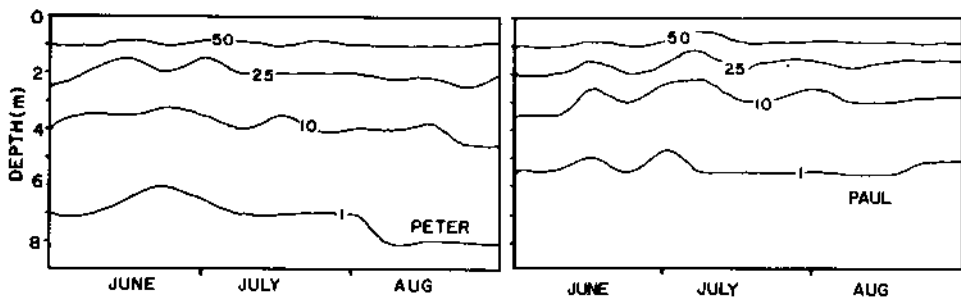


Fig. 2. — Isopleths of light extinction expressed as a percentage of surface irradiance for Paul and Peter lakes

Primary productivity, expressed on a volumetric basis, was similar for both lakes (Fig. 6). Primary productivity in Peter Lake fluctuated between 50-100 $\text{mmol C m}^{-3} \text{d}^{-1}$ in the early part of the summer and decreased to between 30-70 $\text{mmol C m}^{-3} \text{d}^{-1}$ for the rest of the summer. Primary productivity in Paul Lake peaked early in the summer with a peak at 230 $\text{mmol C m}^{-3} \text{d}^{-1}$, but by the middle of July productivity was fluctuat-

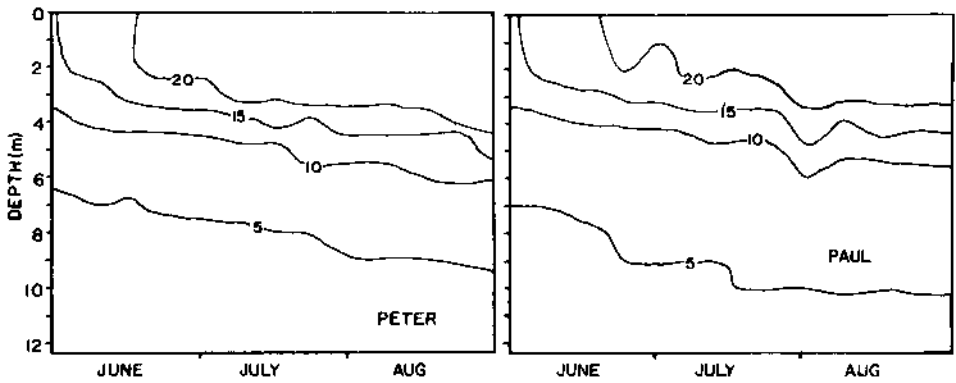


Fig. 3. — Isotherms ($^{\circ}\text{C}$) for Paul and Peter lakes

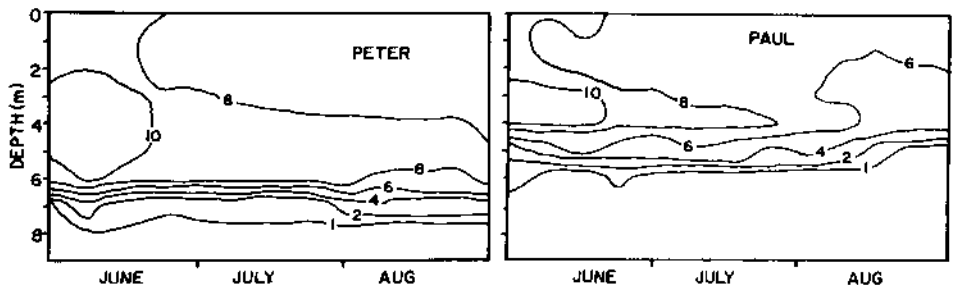


Fig. 4. — Dissolved oxygen (mg L^{-1}) isopleths for Paul and Peter lakes

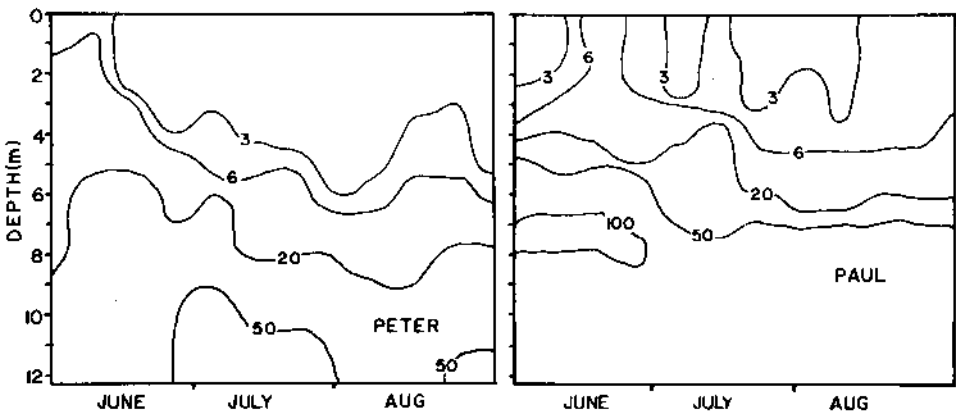


Fig. 5. — Chlorophyll *a* ($\mu\text{g L}^{-1}$) isopleths for Paul and Peter lakes

TABLE 4.—Abundance of phytoplankton species in Paul and Peter lakes expressed as percentage of total population for June-August 1984

Taxon	Paul	Peter
Cyanophyta		
<i>Anabaena circinalis</i>	3.2	3.3
<i>A. planctonica</i>	0	5.1
<i>Chroococcus dispersus</i>	<1	<1
<i>C. limneticus</i>	0	2.2
<i>Dactylococcopsis smithii</i>	<1	<1
<i>Gomphosphaeria lacustris</i>	<1	1.5
<i>Merismopedia tenuissima</i>	2.3	0
Chlorophyta		
<i>Ankistrodesmus</i> sp.	<1	0
<i>Ankya judayi</i> sp.	<1	<1
<i>Arthrodesmus</i> sp.	<1	1.5
<i>Asterionella</i> sp.	<1	0
<i>Cerasterias</i> sp.	0	<1
<i>Glosteriopsis longissima</i>	<1	<1
<i>Cosmarium</i> sp.	0	6.0
<i>Crucigenia</i> sp.	<1	<1
<i>Gloeoecystis</i> sp.	8.8	1.9
<i>Oocystis</i> sp.	21.1	13.1
<i>Quadrigula lacustris</i>	<1	<1
<i>Schroederia</i> sp.	<1	<1
<i>Sphaerocystis schroeteri</i>	3.6	5.4
<i>Selenastrum minutum</i>	<1	<1
<i>Staurastrum</i> sp.	<1	<1
Misc. microflagellates	7.6	<1
Chrysophyta		
<i>Asterionella</i> sp.	<1	0
<i>Chryso-sphaerella longispina</i>	6.6	7.8
<i>Dinobryon bavarium</i>	<1	<1
<i>D. cylindricum</i>	1.2	17.1
<i>D. sertularia</i>	<1	<1
<i>D. sociale</i>	<1	<1
<i>Mallomonas</i> sp.	6.9	1.0
<i>Synura</i> sp.	12.1	14.1
Cryptophyta		
<i>Cryptomonas</i> sp.	15.4	6.5
<i>Rhodomonas minutum</i>	3.7	1.5
Pyrrhophyta		
<i>Peridinium limbatum</i>	1.3	3.8
<i>P. pusillum</i>	1.8	<1
<i>P. wisconsinense</i>	0	<1
Misc. <i>Peridinium</i>	<1	<1
Euglenophyta		
<i>Phacus</i> sp.	<1	0
<i>Trachelemonas</i> sp.	<1	0

ing between 50-100 $\text{mmol C m}^{-3} \text{d}^{-1}$. The early peak in June corresponded to a bloom of *Synura*.

Phytoplankton species composition and phenology differed between the lakes (Table 4, Fig. 7). In Paul Lake, phytoplankton biovolume increased in late June, declined somewhat in July, and began to increase again in early August. The chrysophytes *Mallomonas* and *Synura* bloomed in late June, while *Chryso-sphaerella longispina* peaked in late August. *Oocystis* species and various microflagellates dominated chlorophyte biovolumes, although a bloom of *Gloeocystis* contributed to an early summer maximum and a bloom of *Sphaerocystis schroeteri* contributed to the August maximum. Cyanophytes increased throughout the summer with *Merismopedia tenuissima* dominating the earlier period and *Anabaena circinalis* dominating later. The cryptophytes *Cryptomonas* and *Rhodomonas minutum* also increased throughout the summer. A few *Peridinium* species appeared in June and July. Peter Lake had phytoplankton maxima in early June and late August. Among the chrysophytes, the early bloom consisted of *Synura* and *Dinobryon cylindricum*, while the later bloom was *Chryso-sphaerella longispina*. Chlorophytes increased in late June (*Oocystis*) and again in late August (*Cosmarium* and *Sphaerocystis schroeteri*). The cyanophytes, particularly *Chroococcus limneticus*, increased in late June, while *Anabaena planctonica* increased in late August. The cryptophytes *Cryptomonas* and *Rhodomonas minutum* were most common in early June. *Peridinium limbatum* appeared briefly in early August.

Both lakes had similar zooplankton species (Table 5), although Paul Lake had greater zooplankton biomass (Fig. 8). Biomass in unlimed Paul Lake was dominated by the cladocerans *Daphnia pulex*, *D. rosea* and *Holopedium gibberum*. *Daphnia rosea* accounted for most of the early season biomass; *H. gibberum* dominated in late July and early August, while *D. pulex* increased in late August. *Orthocyclops modestus* dominated the cyclopoid biomass, while calanoids were uncommon throughout the sampling period. Sev-

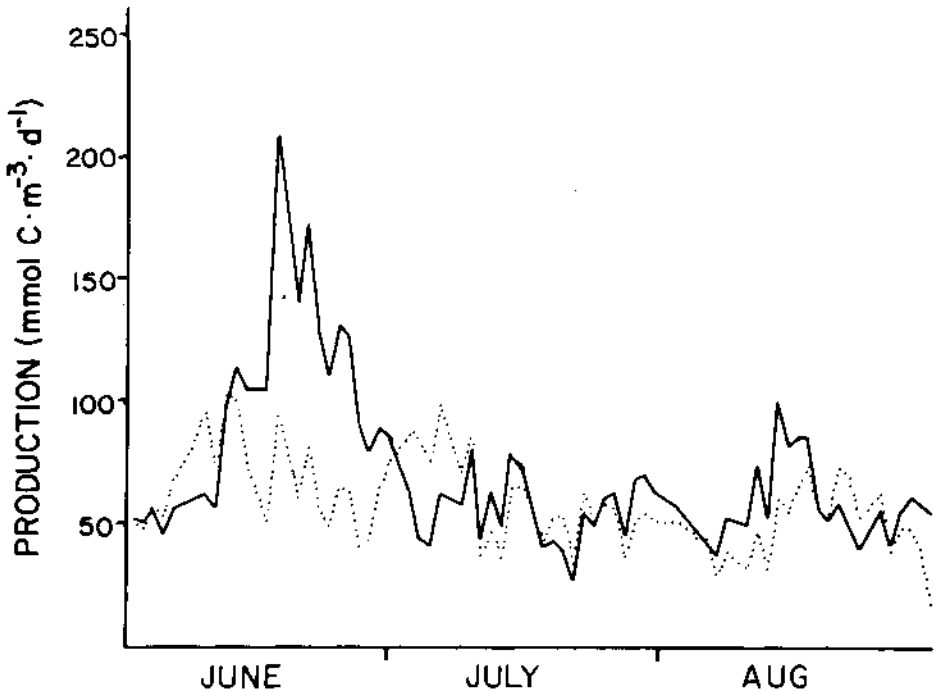


Fig. 6. — Daily volumetric productivity ($\text{mmol C m}^{-3} \text{d}^{-1}$) for Paul Lake (solid line) and Peter Lake (dotted line)

eral rotifer populations peaked in early July, including *Asplanchna*, colonial *Conochilus* and *Filinia terminalis*. The cladoceran biomass in limed Peter Lake was dominated by *Daphnia pulex* and *Holopedium gibberum*, but they contributed a much smaller proportion to total zooplankton biomass than in Paul Lake. The calanoids were dominated by *Diaptomus oregonensis*, while *Cyclops varicans rubellus* dominated the cyclopoids. *Asplanchna* and *Gastropus stylifer* contributed to the early rotifer maximum. Total zooplankton biomass in Peter Lake peaked in the early summer and declined to a fairly stable level, whereas in Paul Lake, the biomass fluctuated over the entire sampling period. The fluctuations in Paul Lake result from seasonal changes in the dominant Cladocera.

DISCUSSION

Liming of Peter Lake has caused several major changes in the lake compared to unlimed Paul Lake. Alkalinity, pH and DIC values, recorded over the years since the initial liming, have remained consistently higher in Peter Lake than Paul Lake. In 1984,

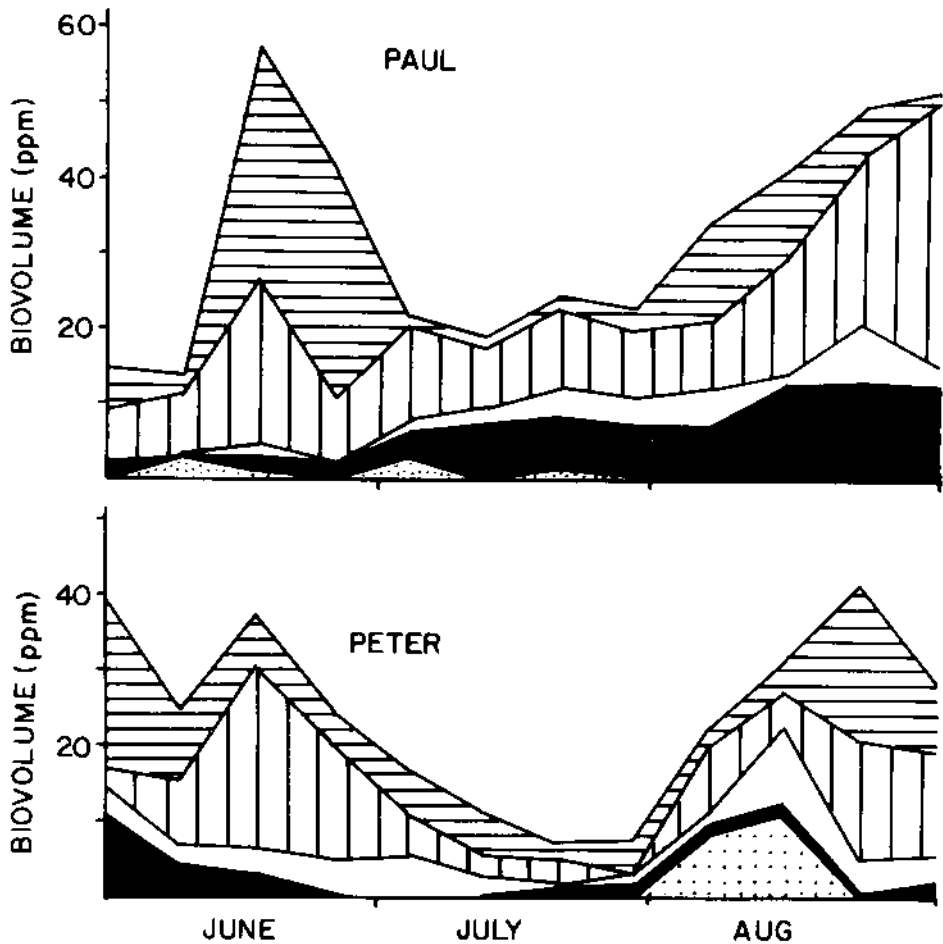


Fig. 7.—Phytoplankton biovolume (ppm) in Paul and Peter lakes for June-August, 1984. Pyrrhophyta and Euglenophyta (dotted), Cryptophyta (solid black), Cyanophyta (solid white), Chlorophyta (vertical hatching), Chrysoophyta (horizontal hatching)

alkalinity and DIC values were 3-3.5 times higher in Peter Lake. This difference was similar to that recorded after the initial liming in 1951. A review of the historical data indicates that a variety of methods to determine alkalinity and DIC values were used, thereby masking any possible year-to-year trends within each lake. The valid comparisons are, therefore, those between Peter Lake (the experimental lake) and Paul Lake (the reference lake) for each year of data.

Most liming studies indicate that liming is useful for short-term management and increased alkalinity can only be maintained by periodic lime applications (Hasselrot and Hultberg, 1984). Limestone (CaCO_3) is the most commonly used liming agent and consequently many studies have focused on its effectiveness in neutralizing acidified waters. Some investigators suggest that CaCO_3 becomes nonreactive in a few weeks and can be inhibited by organic materials (Driscoll *et al.*, 1982; Fraser and Britt, 1982), while others suggest that this is not the case (Hillbricht-Ilkowska *et al.*, 1977; DePinto *et al.*, 1980; Hongve and Abrahamsen, 1984). Dolomitic hydrated lime ($\text{Ca}(\text{OH})_2 \cdot \text{MgO}$) was used to lime Peter Lake. Several studies suggest that hydrated lime materials are more effective neutralizing agents than CaCO_3 (Blake, 1981; Britt and Frazer, 1983) although pH values above 9 may result (Driscoll *et al.*, 1982). Magnesium carbonate is apparently less soluble than calcium carbonate (Stross and Hasler, 1960; Britt and Frazer, 1983). In Peter Lake, however, Stross and Hasler (1960) reported that 5 years

TABLE 5.—Abundance of zooplankton species for Paul and Peter lakes expressed as percentage of total population for June-August 1984

Species	Paul	Peter
Cladocerans		
<i>Bosmina longirostris</i>	<1	<1
<i>Daphnia pulex</i>	9	4
<i>D. rosea</i>	6	<1
<i>Holopedium gibberum</i>	12	2
Cyclopoid copepods		
<i>Cyclops varicans rubellus</i>	<1	3
<i>Mesocyclops edax</i>	<1	<1
<i>Orthocyclops modestus</i>	3	1
Calanoid copepods		
<i>Diaptomus oregonensis</i>	<1	13
<i>Epischura lacustris</i>	<1	<1
<i>Skistodiaptomus pallidus</i>	0	<1
Rotifers		
<i>Ascomorpha eucaudis</i>	<1	<1
<i>Asplanchna</i> sp.	2	<1
<i>Conochiloides dossuaris</i>	22	0
<i>Conochilus unicornis</i>	3	3
<i>Filinia terminalis</i>	14	15
<i>Gastropus stylifer</i>	<1	7
<i>Kellicotia</i> sp.	<1	6
<i>Keratella cochlearis</i>	10	7
<i>K. testudo</i>	2	<1
<i>Polyarthra vulgaris</i>	9	14
<i>Synchaeta</i> sp.	0	<1
<i>Trichocerca cylindrica</i>	4	0

after the initial lime addition the amounts of calcium and magnesium retained in solution from the initial liming were 50% and 96%, respectively. They also recorded high levels of bicarbonate in Peter Lake at that time (Stross and Hasler, 1960). These observations coupled with the alkalinity and DIC differences between Paul and Peter lakes which have been maintained for long periods of time without further lime additions, suggest that lime additions to Peter Lake did cause the long-term increase in alkalinity.

In the original experiment, lime was added to Peter Lake to increase the euphotic-zone depth of the lake and thereby create more suitable habitat for trout. Transparency in Peter Lake did increase following the initial liming while transparency in Paul Lake was unchanged. This difference in transparency has been maintained between the lakes and appears to be caused by the increased alkalinity in Peter Lake. Changes in heat content and dissolved oxygen content in Peter Lake as compared to Paul Lake also resulted from the increased transparency.

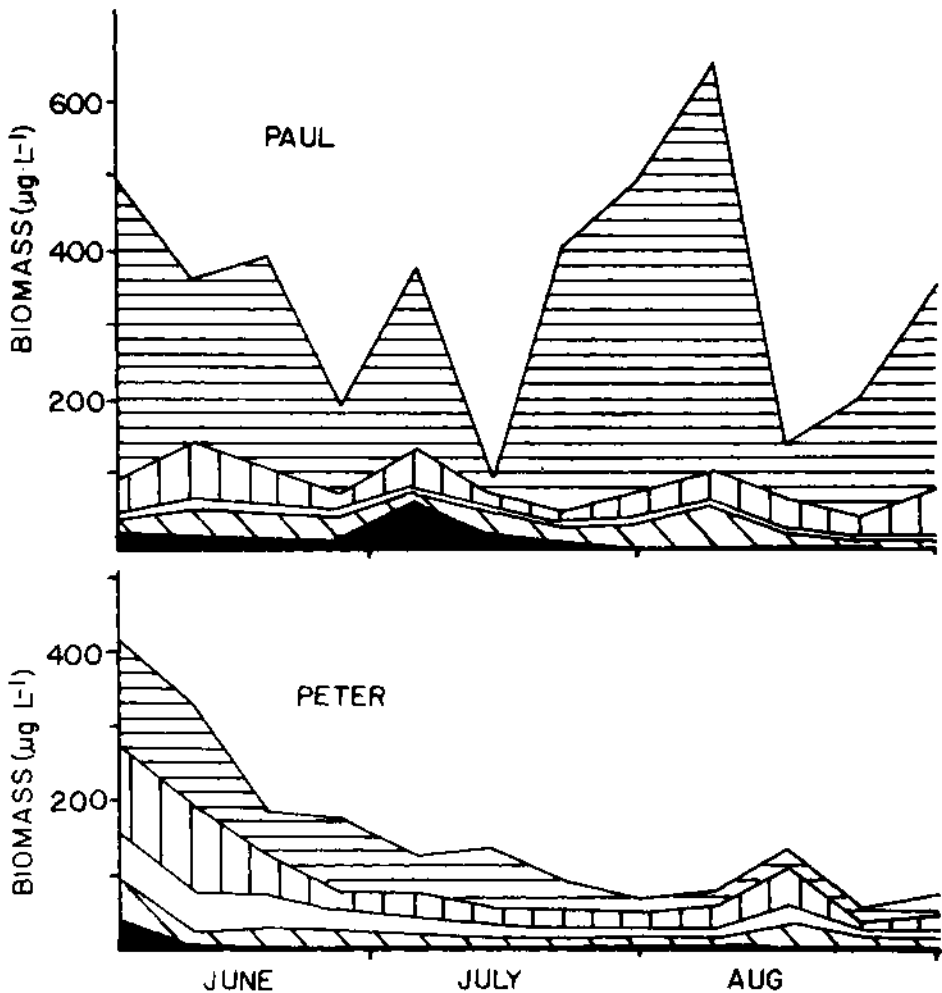


Fig. 8. — Zooplankton biomass ($\mu\text{g L}^{-1}$) in Paul and Peter lakes for June-August, 1984. Rotifers (solid black), cyclopid copepods (diagonal hatching), calanoid copepods (solid white), copepodites and nauplii (vertical hatching), cladocerans (horizontal hatching)

The effect of liming on transparency depends on the relative importance of organic and mineral acids in the acidity of the lake. Lime additions to humic lakes such as Peter Lake have generally increased their transparency (Fraser and Britt, 1982; Hasler *et al.*, 1951). However, heavy applications of lime can also stimulate phytoplankton blooms in humic lakes (Water, 1957; Waters and Ball, 1957), and in such cases no net change in transparency results because light extinction by algae replaces light extinction by humic substances. In lakes dominated by mineral acids, liming has generally decreased transparency by enhancing algal growth (Fraser and Britt, 1982; Hasselrot and Hultbert, 1984; Henriksen *et al.*, 1985).

Although chlorophyll concentrations were similar in the two lakes, their phytoplankton composition differed. Larger populations of *Anabaena*, *Dinobryon* and *Cosmarium* were present in Peter Lake, while Paul Lake had larger numbers of *Merismopedia*, *Gloeoecystis*, *Quadrigula* and *Cryptomonas*. In an earlier study Malueg (1963) found only 13 species in Paul Lake and 31 species in Peter Lake. Our more extensive species list (Table 4) is probably the result of more intensive sampling rather than any real changes in the lakes. Temporal differences in algal blooms between the two lakes were observed, with blooms in limed Peter Lake occurring in early June and blooms in unlimed Paul Lake occurring in late June. The differing timing of the spring blooms probably reflects the increased transparency and heat content of Peter Lake which permits earlier phytoplankton growth.

Since 1951, zooplankton biomass and species composition have been much more variable in limed Peter Lake than in unlimed Paul Lake. In Paul Lake, 1984 biomass, species composition and phenology data were very similar to those of Stross *et al.* (1961) for 1954-1956, except that *Daphnia rosea* had increased in importance. In Peter Lake, however, considerable fluctuations have occurred. *Diaptomus* replaced *Holopedium* immediately after the initial liming, but in some years *Holopedium* reappeared as a dominant zooplankton for a few weeks (Stross *et al.*, 1981). *Daphnia pulex* was replaced by *D. rosea*, and eventually by *Bosmina* (Kitchell and Kitchell, 1980; Stross *et al.*, 1961). By 1984, this trend had reversed: *Bosmina* was absent and *D. pulex* was again an important member of the zooplankton community (Fig. 8). Bergquist (1985) reported much higher *D. pulex* biomass in 1982 and 1983 in Peter Lake than we found in 1984. Kitchell and Kitchell (1980) attribute the striking variability of Peter Lake zooplankton to changing fish communities coupled with increased transparency, which allowed zooplanktivores to forage more efficiently.

The food web effects induced by the liming and clarification of Peter Lake are the opposite of the responses observed when lime is applied to lakes acidified by mineral acids. In such lakes, liming increases algal biomass and thereby decreases transparency, which decreases the effectiveness of zooplanktivores. This, in turn, leads to increases in zooplankton biomass and in the relative density of large zooplankton (Henriksen *et al.*, 1985). Nevertheless, in both humic lakes and mineral acid lakes the major biological consequences of liming are secondary and result from changes in predation by fishes due to changes in water clarity.

Two major conclusions can be drawn from this study. The primary conclusion is that lime additions to Peter Lake have increased its alkalinity, DIC and transparency, and these changes have persisted for 33 years. Although Peter Lake and Paul Lake are not located in regions heavily affected by acidic deposition, they normally have very little natural buffering capacity and the maintenance of high alkalinity in Peter Lake can only be a result of the lime applications. The exact mechanisms of these effects are not clear and further study of the hydrology and sediments would be useful. Secondly, the increased transparency associated with the liming of Peter Lake has had major effect on the ecosystem. Increased light penetration has increased the heat content of Peter Lake and may have allowed its phytoplankton to bloom earlier in the summer than similar species in Paul Lake. The increased euphotic-zone depth due to the precipitation of humic substances has led to deeper oxygenated zones which may have resulted in lower

winter fish mortalities. Finally, increased transparency has increased the efficiency of visual predation by zooplanktivores, which has altered the zooplankton community composition. As a result of these biological interactions, the zooplankton community of Peter Lake has been more variable than that of Paul Lake. This temporal variability in the plankton of Peter Lake contrasts with the relative stability of physical and chemical conditions that followed liming.

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