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NUTRIENT LIMITATION OF ALGAL STANDING CROPS IN SHALLOW PRAIRIE LAKES[1]

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Abstract. Environmental control of algal standing crops in two non-stratified prairie lakes in South Dakota and Minnesota, USA was investigated by season for 3 years. Multiple regression analysis was performed using chlorophyll *a* concentration and cell counts as dependent variables. In both lakes physical factors (light, temperature, wind stress and rainfall) were more frequently correlated with changes in algal standing crops than were nitrogen and phosphorous. Both lakes indicated occasional positive correlations with nitrogen. The correlations were greater in the deeper lake. Phosphorus was positively correlated during one season in the deeper lake, never in the shallower lake.

Multiple regression analyses using concentrations of nitrate, ammonia, and orthophosphate as dependent variables and physical factors, algal abundance and zooplankton abundance as independent variables showed positive correlations between increases in orthophosphate and nitrate and prior rainfall and wind stress. Ammonia showed strongest correlations with wind stress.

The correlations between wind stress and nutrient levels are assumed to result from recirculation of nutrients released at the sediment surface by circulation of the water column and by direct stirring of sediments in shallow water by wave action. The more extensive direct stirring of sediments in the shallower lake is assumed to partially account for the much higher levels of nutrients observed. Depth of lake relative to depth of wave action determines to what extent the sediments of a shallow lake are subject to direct stirring.

Key words: Algae; chlorophyll; eutrophication; Minnesota; nutrient limitation; nutrient regeneration; South Dakota; wind stress.

INTRODUCTION

The limiting factor concept has been useful in the understanding of lake algae dynamics because it has frequently indicated causes for changes in population density (Hutchinson 1944, Lund et al. 1963, Megard 1972). The concept has also had appeal for management agencies concerned with evaluating potential effects of nutrient limitation on lakes' troubles with algal blooms. An excellent discussion of the available methods of determining limiting nutrients is given by Goldman (1972). Two methods discussed by Goldman were used by this author (Haertel 1972): correlation of changes in standing crop with changes in levels of major nutrient elements and measurement of changes in production rates after addition of nutrients to natural phytoplankton populations.

This paper deals with the results obtained by correlating changes in algal standing crops with changes in suspected limiting nutrients, and physical factors. Population changes in nature can rarely be explained on the basis of only one factor (Hall 1971) and it is necessary to use methods of analysis which permit evaluation of several factors simultaneously. Newer statistical techniques such as multiple regression analysis make possible the simultaneous consideration of several suspected factors, and also the evaluation of relative importance of each factor.

The objectives of this study were to determine to what extent (1) algal abundance could be correlated with nutrient levels and physical factors, and (2) nutrient levels could be correlated with physical factors.

Lakes in the prairie region of the eastern Dakotas and western Minnesota are characterized by persistent blooms of blue-green algae. The natural, glacially-formed lakes are usually shallow, saucer-shaped depressions and are thoroughly mixed by the strong summer winds. The lakes do not exhibit summer thermal stratification. The shallowness and extensive mixing of the lakes and surrounding fertile soils create a situation in which limitation of algal populations by any nutrient element becomes questionable.

The two lakes selected for this study (Fig. 1) represent different extremes in the degree of eutrophication of prairie lakes. The larger of the two lakes, Lake Hendricks, is quite shallow (average depth 1.8 m) and drains a large watershed (14,827 ha). It consistently supported blooms of the blue-green alga *Aphanizomenon holsatica* (*A. flos-aquae*) during the course of this study. The blooms appeared in early to mid-June and persisted throughout the summer.

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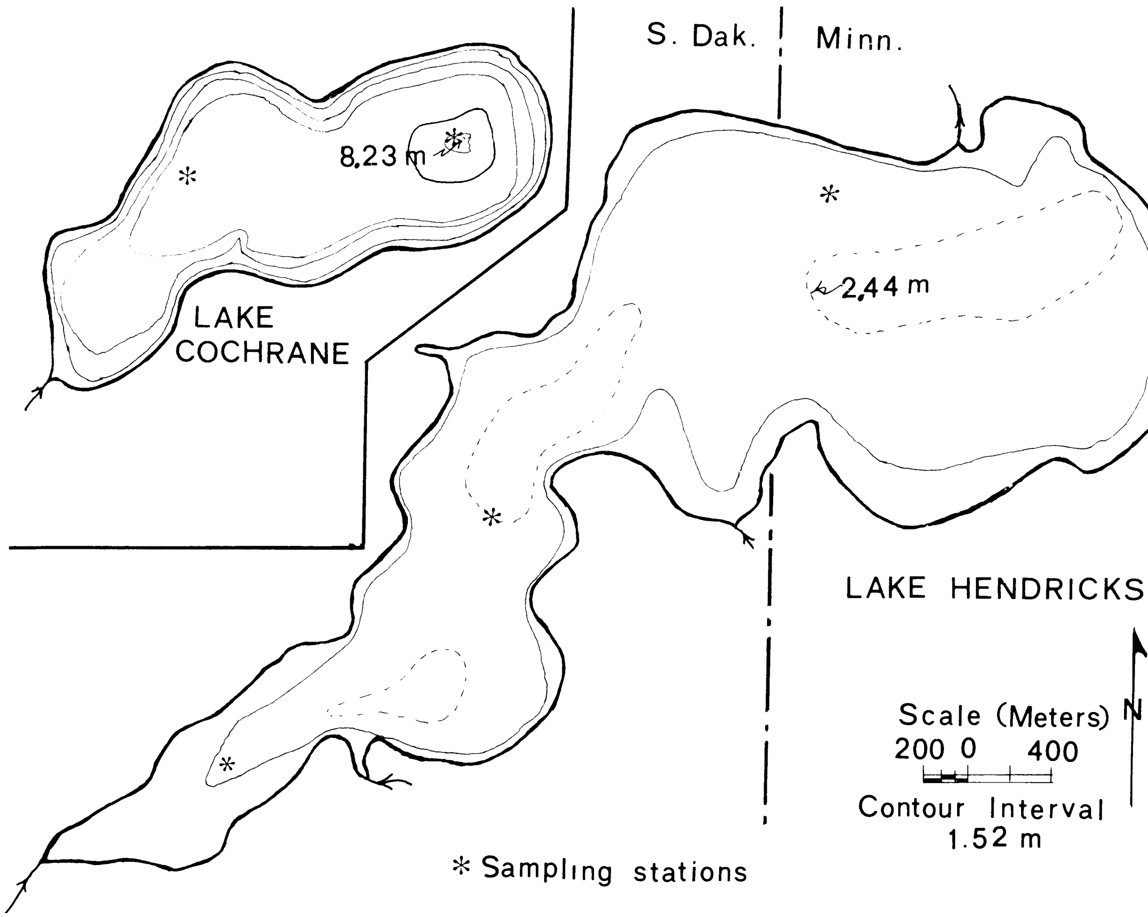

FIG. 1. Study lakes and location of sampling stations.

During the bloom season other species were practically nonexistent. The second lake, Lake Cochrane, is somewhat deeper (mean depth 3.0 m) and drains a much smaller watershed (202 ha). It first major bloom of blue-green algae was recorded during the 2nd year of this study. The major bloom species, *Anacystis cyanea* (*Microcystis aeruginosa*) and *Anacystis incerta* had been present in low concentrations in the lake the year preceeding the bloom along with other dominant species, principally dinoflagellates (*Peridinium bipes*, *Ceratium hirundinella*) and diatoms (*Chaetoceras Elmorei*). Other blue-green species were present in Lake Cochrane during the 1971 and 1972 blooms. *Agmenellum* spp. (*Merismopodia* ssp.) appeared in 1971 and *Gomphosphaeria* ssp in 1972. Both were an order of magnitude less abundant than *Anacystis*.

Lake Cochrane is a closed basin lake during most of the year and is slightly brackish (average salinity 2,214 ppm). Major ions are magnesium and sulfate. Lake Hendricks exhibits more typical prairie lake salinity (average 483 ppm) with calcium, bicarbonate, and sulfate the major ions.

METHODS

Environmental data

Sampling was conducted from 30 April 1970 in Lake Cochrane and from 15 July 1970 in Lake Hendricks, through 2 August 1972 in both lakes. The lakes were sampled weekly during the summer, approximately biweekly during the spring, and approximately monthly during the winter. Longer intervals between sampling were necessary during the period of formation and breakup of winter ice cover. During the season of open water, four samples were taken in each lake on each sampling date. Two stations were sampled at two depths (just below the surface and just above the bottom) in Lake Cochrane, and three stations (the middle station at two depths) in Lake Hendricks. Samples for water chemistry, chlorophyll *a* analysis and algal cell counts were taken out of the same Van Dorn bottle cast. Zooplankton were sampled on most dates with a Clarke-Bumpus sampler with a #12 mesh net. Under ice cover, only one to two stations were sampled in each lake, and zooplankton were not sampled.

Temperature was determined at all locations with a bucket thermometer. Water transparency was measured with a Secchi disk.

The following chemical parameters were measured on each sampling date: sodium and potassium (atomic absorption), carbonate and bicarbonate (calculated from alkalinity titration) silicate (heteropoly blue), nitrate-nitrogen (brucine) ammonia-nitrogen (direct nesslerization), organic nitrogen (total Kjeldahl) orthophosphate-phosphorus (stannous chloride), acid-hydrolyzable phosphate phosphorus (acid hydrolysis) and oxygen (azide modification of winkler technique). In addition, the following measurements were taken once a month: manganese and copper (atomic absorbtion) iron (phenanthroline), calcium (EDTA titrimetric), magnesium (EDTA hardness minus calcium), chloride (mercuric nitrate), and sulfate (turbidimetric). All methods were according to American Public Health Association (1971). Chlorophyll *a* was measured using the Strickland and Parsons (1968) method. Samples for cell counts were preserved in Lugol's solution and concentrated, when necessary, in a plankton centrifuge. One milliliter of preserved sample was placed on a Sedgwick-Rafter slide, inverted, and allowed to settle. Fields were randomly counted at 400× on an inverted stage microscope until 100 of the most numerous species were recorded (Lund et al. 1958). A filament of *Aphanizomenon holsatica* or a colony of *Anacytis cyanea*, the two dominant species, were counted as one unit. The number of cells in 10 randomly selected filaments or colonies of *Aphanizomenon* and *Anacystis* were then counted on a conventional microscope under an oil immersion objective to estimate average filament or colony size, and these were used to determine final counts as cells per milliliter. Zooplankton were counted using the method described by Haertel and Osterberg (1967).

Statistical analysis

Sampling dates were divided according to the following biological seasons:

1) Spring—defined as the period after ice breakup until the water temperature reached ≈ 20°C, usually early to mid-June;
2) Early Summer—defined as a period of ≈ 1 mo, from mid-June to mid-July when blue-green algae numbers were greatest; and
3) Late Summer—defined as mid-July to early September, the period of consistently high algae blooms.

TABLE 1. Annual average values of physical, chemical, and biological variables in Lake Cochrane, South Dakota. To convert langleys (ly) to megajoules per square meter (MJ/m^2) multiply by 0.4184

	Season of open water			Under ice cover	
	1970	1971	1972	1970–1	1971–2
Wind stress[a] (cm/s^2)	0.13	0.09	0.06	----	----
Solar radiation[a] (ly/day)	496	491	416	----	----
Rainfall[a] (cm/day)	0.28	0.26	0.51	----	----
Water chemistry (ppm)					
Salinity[b]	2,380	2,161	2,113	2,760	2,359
Na	106	108	107	137	112
K	51	55	45	70	46
Ca[b]	100	108	111	161	130
Mg[b]	361	343	305	350	398
Cl[b]	16	16	15	16	18
SO_4[b]	1,578	1,291	1,284	1,774	1,381
HCO_3	106	190	196	221	170
CO_3	61	51	47	27	97
Si	2.7	2.9	6.1	4.6	9.1
Fe[b]	0.08	0.08	0.05	0.50	0.02
Mn[b]	0.01	0.02	0.00	0.00	0.30
Cu[b]	0.00	0.02	0.00	0.03	0.01
ortho PO_4-*P*	0.013	0.021	0.005	0.098	0.046
Acid hyd. PO_4-P	0.026	0.097	0.022	0.101	0.061
NO_3-N	0.045	0.034	0.023	0.09	0.04
NH_3-N	0.060	0.017	0.000	0.10	0.05
N:P[c]	8.1:1	2.4:1	4.6:1	1.9:1	2.0:1
Organic N	1.12	1.55	1.35	2.08	1.10
Chlorophyll *a* (ppb)	10	19	18	4	13
Anacystis (cells/l)	39,500	791,000	1,220,000	1,790	7,480
Total zooplankton (N/m^3)	96,100	107,000	93,500	----	----

[a] Averages of values recorded 7 days prior to sampling dates (fall sampling dates not included as the fall season was only sampled in 1971).
[b] Measured only once a month.
[c] Calculated as the ratio of NH_3-N + NO_3-N : ortho PO_4-P.

Fall and winter samples were not included in the statistical analysis because few samples were available.

All samples for a given season were run through linear correlation analysis to determine which biological, chemical, and physical variables were related. Correlation analyses included the following weather data: rainfall (cm/day) as the prior 7-day average; solar radiation (langleys/day) as both the prior 3-day average and the prior 7-day average; and wind stress (t) as both the prior 7-day average and the effective displacement index (EDI). EDI and t were calculated by the method in Small (1963). Weather data were obtained from the National Weather Service Station at Brookings, South Dakota

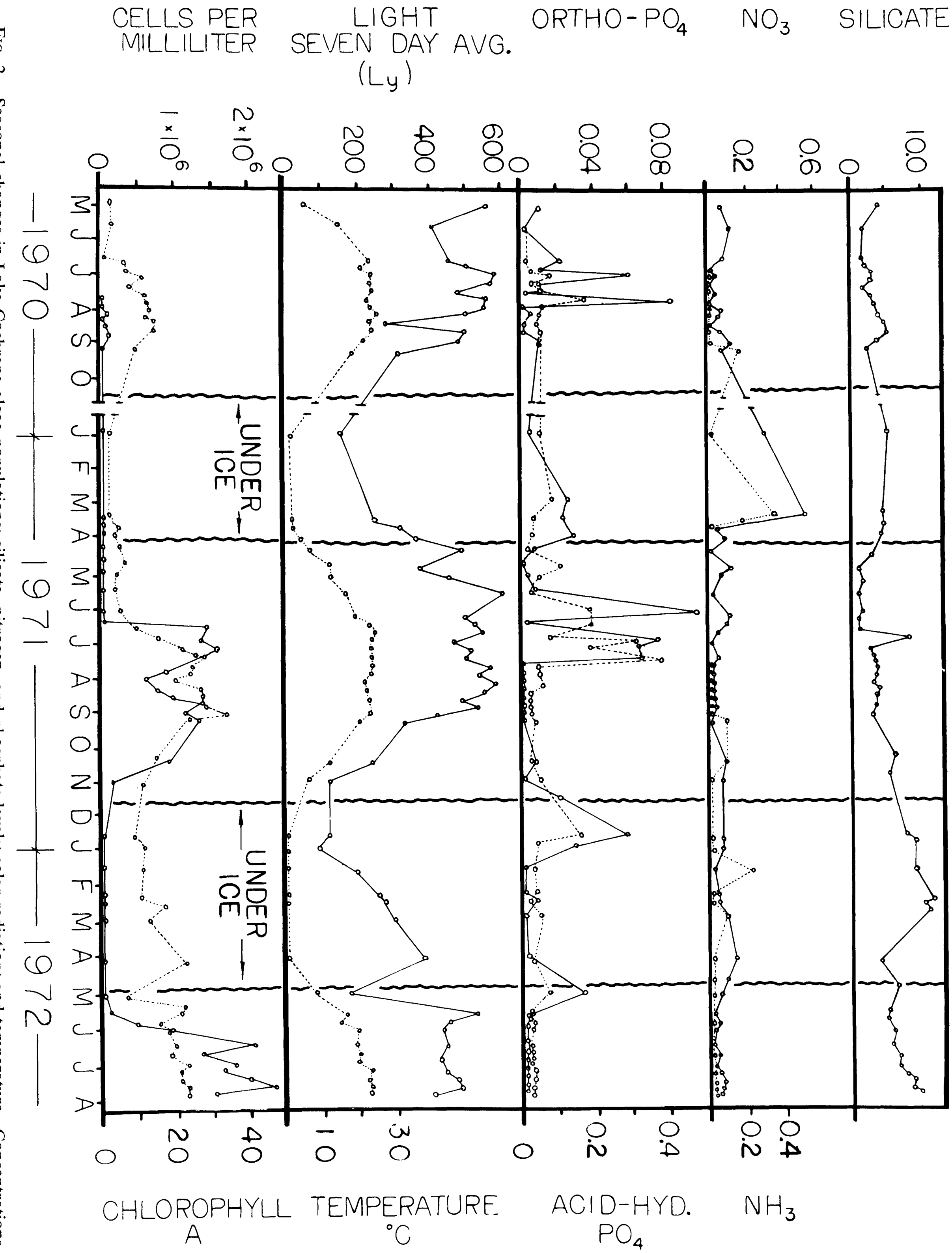

FIG. 2. Seasonal changes in Lake Cochrane algae populations; silicate, nitrogen, and phosphate levels; solar radiation; and temperature. Concentrations are in parts per million except chlorophyll *a* (parts per billion). Left-hand variable designated by solid line.

TABLE 2. Annual average values of physical, chemical, and biological variables in Lake Hendricks, South Dakota

	Season of open water			Under ice cover	
	1970[d]	1971	1972	1970–1	1971–2
Wind stress[a] (cm/s^2)	0.14	0.09	0.06		
Solar radiation[a] (ly/day)	483	490	446		
Rainfall[a] (cm/day)	0.09	0.28	0.39		
Water chemistry (ppm)					
Salinity[b]	519	475	492	666	648
Na	6	7	7	30	10
K	12	10	8	11	12
Ca[b]	99	107	98	221	142
Mg[b]	55	23	27	33	45
Cl[b]	5	5	5	12	16
SO_4[b]	161	120	125	165	156
HCO_3	133	154	181	156	203
CO_3	30	32	25	15	58
Si	18	17	15	23	17
Fe[b]	0.38	0.16	0.14	0.15	0.07
Mn[b]	0.005	0.003	0.00	0.00	0.00
Cu[b]	0.00	0.01	0.00	0.00	0.00
ortho PO_4-P	0.13	0.18	0.13	0.21	0.43
Acid hyd. PO_4-P	0.16	0.30	0.21	0.35	0.58
NO_3-N	0.22	0.13	0.09	0.05	0.30
NH_3-N	0.18	0.05	0.02	0.03	0.21
N:P[c]	3.1:1	1:1	0.9:1	0.4:1	1.2:1
Organic N	1.77	2.60	2.15	2.40	1.81
Chlorophyll *a* (ppb)	20	58	38	3	16
Aphanizomenon (cells/l)	288,000	165,000	187,000	22	36
Total zooplankton (N/m$_3$)	121,000	153,000	118,000	----	----

[a] Averages of values recorded 7 days prior to sampling dates.
[b] Measured only once a month.
[c] Calculated as the ratio of NH_3-N + NO_3-N : ortho PO_4-P.
[d] Not sampled prior to 15 July 1970.

located ≈ 32.2 km from Lake Hendricks and 88.5 km from Lake Cochrane.

After a correlation matrix was determined, stepwise multiple regression (Little 1966) was performed on certain variables to determine which independent variables explained the variation in the dependent variables. Dependent variables were: algal standing crops (determined as both chlorophyll *a* and cell counts of the most abundant species), inorganic nitrogen, and inorganic phosphorus. Multiple regression was separately performed for each season and year.

RESULTS AND DISCUSSION

Environmental changes

Summer algae blooms in Lake Cochrane increased during the course of this study (Fig. 2, Table 1). Late summer 1971 cell counts increased more than twenty-fold over 1970 late summer populations, and 1972 cell counts were slightly higher than 1971 populations. Chlorophyll *a* concentrations also showed increases from 1970 to 1971 but the increase was not as dramatic as the cell count increases, probably because substantial numbers of *Peridinium bipes* present in 1972, which were absent from the 1971 and 1972 counts. Individual *Peridinium* cells (diam 38–55 μm) would be expected to contain much larger quantities of chlorophyll than the *Anacystis cyanea* cells (diam 3–4.5 μm) which dominated the 1971 and 1972 cell counts.

Paralleling the increase in algae between 1970–1971 were the following chemical changes (Fig. 2, Table 1). The average level of ammonia-nitrogen plus nitrate-nitrogen decreased by a factor of 2, both under the ice and during the open water season possibly due to the greater uptake by the larger amounts of algae present. The average levels of phosphorus showed a great increase, particularly in acid-hydrolyzable phosphate (which includes orthophosphate and condensed phosphate, but not most of the organic phosphorus present). A possible source of some of the unusually high 1971 phosphates might have been construction operations; several cottages were constructed, and one cottage builder actually bulldozed a portion of his soil into the lake in late June 1971, just before the *Anacyostis* bloom began. The 1970 to 1971 difference in ortho- and acid-hydrolyzable phosphate levels is particularly noticeable in Fig. 2, phosphate levels are particularly enriched in spring and early summer 1971 when the algae bloom is building up, and show complete depletion in late summer 1971, undoubtedly because of uptake by the increased biomass of algae.

Measured levels of phosphate and inorganic nitrogen were much lower in 1972. Despite this algae populations remained high. Zooplankton abundance was remarkably constant during the 3 yr of the study.

Lake Hendricks algal populations (as measured by cell counts) did not undergo the same dramatic increase between 1970 and 1971 (Fig. 3, Table 2) that was observed in Lake Cochrane populations, even though changes in Lake Hendricks' water chemistry between 1970 and 1971 were similar to those in Lake Cochrane; both forms of phosphate increased in 1971, and nitrate and ammonia nitrogen decreased over the 3-yr period (Table 2, Fig. 3). Phosphate levels in Lake Hendricks were almost an order of magnitude higher than in Lake Cochrane during all 3 yr and would not be expected to limit algal populations at any time. Inorganic nitrogen levels were also much higher. As in Lake Cochrane, zooplankton densities were similar during all 3 yr of the study.

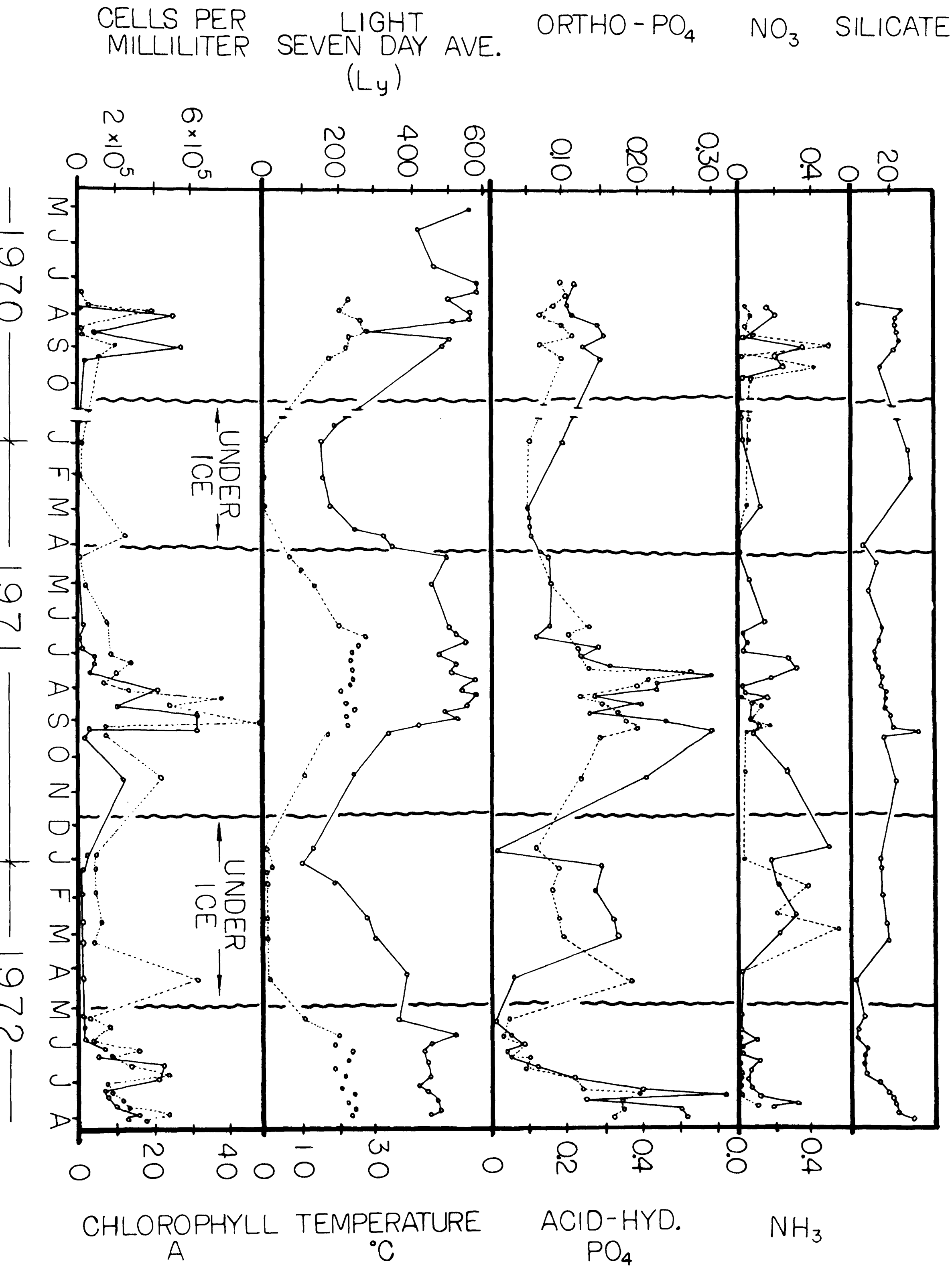

FIG. 3. Seasonal changes in Lake Hendricks algae populations; silicate, nitrogen, and phosphate levels; solar radiation; and temperature. Concentrations are in parts per million except chlorophyll *a* (parts per billion). Left-hand variable designated by solid line.

Correlation and regression analyses of algae populations

Multiple regression was performed using chlorophyll *a* concentrations and cell counts as dependent variables. Nutrients included in the regression analyses were nitrate, ammonia (the latter only for those seasons when data was available and ammonia was measurable), orthophosphate (acid-hydrolyzable phosphate for late summer 1971 in Lake Cochrane when no orthophosphate was measureable), bicarbonate, and in chlorophyll *a* analyses, silicate.

The results of the simple correlation and multiple regression analyses of algal standing crops are shown in Tables 3-4.

The results of multiple regression of the algae populations as chlorophyll *a* and numbers of cells of the dominant species present in Lake Cochrane showed variable success in explaining observed variations (Table 3). Results ranged from as low as 21% to as high as 87% of the variation in the dependent variable explained (early summer 1971 chlorophyll *a* concentrations). The early summer 1971 results are particularly interesting in Lake Cochrane, not only because relatively high fractions of the variability in algal populations were explained, but also because this was the season of the buildup of the first recorded bloom of blue-green algae in that lake. Major significant independent variables from both statistical tests included wind stress, silicate, and phosphate for chlorophyll *a*, and phosphate, temperature, and wind stress for *Anacystis*. Phosphate was correlated with immediate increases in cell numbers, with 47% of the variation in cell numbers explained by variations in phosphate concentrations measured on the same day. This close correlation is also shown in Fig. 2. Prior high levels of phosphate were not correlated with algal increases, possibly because the water temperature was too low for optimal blue-green growth. Late summer populations of *Anacystis* might have been maintained despite the absence of measurable orthophosphate in the water due to regeneration of phosphate by animals and bacteria, and/or because of "luxury storage" of phosphate by the algae (Ketchum 1939, Gerloff and Skoog 1954).

Some general trends may be noted from the analyses of Lake Cochrane algal populations for other seasons. Nitrogen was the nutrient most frequently significantly correlated. Chlorophyll *a* showed significant correlation with nitrates in many seasons. Nitrogen was the major factor explaining the variations in the *Anacystis* population in late summer 1970 and 1971. However, the effect of nitrogen availability on algal abundance may never have been very great. The average fraction of variation in cell numbers and chlorophyll *a* explained by nitrate in the nine multiple regression analyses in which it was statistically significant was only 18%. Not shown in Table 3 is the analysis of *Peridinium bipes* (late summer 1970) in which 45% of the variation in abundance was significantly explained by variations in nitrate and *Agmenellum* ssp. (late summer 1971) in which 33% of the variation in abundance was significantly explained by variations in ammonia. Silicate was occasionally positively correlated with chlorophyll *a* increases in spring and early summer, seasons during which diatoms were occasionally abundant. The occasional correlations with phosphate from seasons other than spring and early summer 1971, were negative and may simply indicate that phosphate was being depleted as the algae increased, but was not limiting. Planktonic algae have generally been assumed to require nitrogen and phosphorus in a ratio of 7.2:1 (by weight) (Redfield 1934, Richards and Vaccaro 1956), and assuming that they do, phosphorus would not be expected to be a limiting element in Lake Cochrane after 1970 although nitrogen might be limiting (Table 1).

Combining the multiple regression results from all seasons, physical factors accounted for a larger fraction of the variability in algae populations than did nutrient levels. Light and/or temperature was significantly correlated with either cells or chlorophyll *a* during the spring season of all 3 yr. Negative correlations with wind stress (early summer 1970 and spring 1972, linear regression only) might also suggest light limitation. However, wind stress was positively correlated with algal populations, perhaps due to its effect on either nutrient recycling (early summer 1971), or its effect of keeping algae circulated away from high light intensities at the surface (late summer 1971). Positive correlations with rainfall (late summer 1971 and 1972) may result from runoff water contributing a limiting nutrient (in both seasons, nitrogen might be implicated).

Algae populations in Lake Hendricks (Table 4) showed frequent significant correlations with orthophosphate. In all cases the correlation was negative, suggesting that phosphate was being depleted as the algae population increased. Phosphate levels were very high in Lake Hendricks and phosphate inhibition might also be a possibility. Significant positive correlations with nitrogen were found in only a few seasons (spring and late summer 1971, early summer 1972). The N:P ratio in Lake Hendricks was always $< 7.2:1$; however, nitrogen levels were so much higher in Lake Hendricks than in Lake Cochrane that nitrogen limitation would be expected to be a less frequent phenomenon.

As in Lake Cochrane physical factors accounted for a larger fraction of the variation in algal standing crops than changes in nutrients. Wind stress and rainfall showed positive correlations in spring and tive correlations with rainfall frequently occurred together with positive correlations with nitrogen.

Correlations and regression analyses of nutrient concentrations

Multiple regression was performed using levels of nitrate, ammonia and orthophosphate as dependent variables and solar radiation, water temperature, wind stress, and rainfall as independent variables.

Analysis of nitrate gives inconclusive results in both lakes (Tables 5 and 6). However, rainfall is frequently significantly correlated and the effect can be either positive or negative, suggesting that runoff water may sometimes but not always, carry large amounts of dissolved nitrates. Differing agricultural practices in the watershed at different seasons may account for some of the differences. Also, the effect of rainfall on nitrates may not be linear; a sudden heavy rainfall may transport more nitrate than the same amount of rain distributed over a longer period of time. Positive correlations between wind stress and nitrate might implicate recycling of nitrates previously regenerated in the sediments (spring; early summer 1970; late summer 1971; spring 1972, Table 5; and early summer 1971, Table 6). Negative correlations between nitrate and light levels suggest photosynthetic uptake. A significant portion of the nitrate input may result from groundwater recharge. Lack of groundwater data may be one reason such a low fraction of the nitrate variation can be explained.

Wind stress shows the greatest positive correlation with ammonia in both lakes (Tables 5 and 6). Presumably this is by recycling ammonia regenerated in the sediments. Negative correlations between ammonia and light suggest photosynthetic uptake.

Both rainfall and wind are frequently positively correlated with orthophosphate in both lakes (Tables 7 and 8). Rainfall may also show a negative correlation with orthophosphate, suggesting that runoff waters may not always carry large amounts of phosphates. Again, changing land use patterns in the watershed and variation in intensity of rainfall may account for the variability in the data. Wind stress undoubtedly affects orthophosphate levels in the same way as it affects nitrate and ammonia levels, by recycling of phosphates regenerated in the sediments back into the water column. The negative correlations observed between light and phosphate during all seasons in Lake Hendricks (Table 8) suggest photosynthetic uptake. Positive correlations between light and phosphate (early summer 1972, both lakes, may result from high solar radiation causing increased water temperatures and subsequently increased rates of regeneration by bacteria (Hutchinson 1957, Harrison et al. 1972).

Potential for nutrient limitation

Significant correlations between nutrients and algal abundance do not prove causal relationships between nutrients and increases in algae. However, recent studies by Dillon and Rigler (1974) and Jones and Bachman (1976) demonstrate a high level of success in predicting algal blooms from levels of incoming phosphorus and early spring levels of phosphorus in lake water, respectively. Lakes Cochrane and Hendricks definitely do not show such a clear-cut correlation with phosphorus as a limiting element. In Lake Cochrane the nutrient most frequently correlated with algae is nitrogen. As the ratio of available N:P (Table 1) is less than the ratio normally found in plankton (Redfield 1934, Richards and Vaccaro 1956, Vollenwieder 1968) it is logical to suspect that future variations in available nitrogen might be accompanied by variations in algae. However, the potential importance of phosphate is also indicated by early summer 1971 when 47% of the variation in cells could be explained by variations in that element (multiple regression analysis, (Table 4).

Nutrient limitation is less likely in Lake Hendricks than in Lake Cochrane, undoubtedly because of the much higher levels of nitrogen and phosphorus in Lake Hendricks (Tables 1 and 2). No positive correlations between algae and phosphorus were found in Lake Hendricks (Table 4). Occasional correlations between algae and nitrogen were noted for Lake Hendricks, despite the fact that the major bloom species present has been repeatedly demonstrated to be able to fix nitrogen (Stewart et al. 1968, Horne and Fogg 1970, Granhall and Lundgren 1971, Horne and Goldman 1972). Without direct measurement of nitrogen fixation, or counts of heterocysts, it is impossible to say whether or not the *Aphanizomenon* in Lake Hendricks fixed nitrogen during this study.

Rainfall and wind stress are both correlated with increases in nitrate or orthophosphate in both lakes. Wind stress is implied to be far more important than rainfall in replenishing levels of ammonia in both lakes. Inasmuch as the processes of replenishment should be similar in both lakes, the reason for the strikingly higher levels of nutrients in Lake Hendricks need to be examined. Due to a large watershed (14,827 ha in Lake Hendricks as opposed to 202 ha for Lake Cochrane) it is likely that more nutrients will be brough in by runoff water in Lake Hendricks than in Lake Cochrane. Because wind stress, in addition to rainfall, accounts for some of the increases in nitrate and phosphate and most of the increases in ammonia, input from a larger watershed cannot explain all the difference. Wind stress may replenish nutrients by distribution of nutrients released at the sediment surface by wind-

TABLE 3. Regression analysis 1. Algae populations in Lake Cochrane. Abbreviations: L = light, T = temperature, W = wind stress, R = rainfall, P = orthophosphate, ahP = acid hydrolyzable phosphate, NH_3 = ammonia, Si = silicate. * Statistically significant correlations (0.05)

Dependent variable	Year	1970					1971					1972		
	Season	Spring	Early Summer		Late Summer		Spring	Early Summer		Late Summer		Spring	Early Summer	
	Dates	30/4–24/6	24/6–15/7		22/7–11/9		22/4–15/6	15/6–15/7		22/7–9/9		4/5–6/6	23/6–25/7	
	N	14	18		25		18	18		16		16	20	
	Treatment[a]	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.
Chlorophyll *a*	Simple linear	L 0.61*	L 0.19	L 0.58*	L 0.20	L 0.20	L 0.45	L −0.46	L −0.47	L −0.47*	L −0.30	L 0.50*	L −0.22	L −0.12
	correlation	T −0.07	T 0.01	T 0.71*	T 0.15	T 0.23	T −0.50*	T −0.41	T 0.48*	T 0.38	T 0.28	T 0.57*	T 0.26	T 0.31
	coefficient	W −0.50	W −0.67*	W −0.54*	W −0.21	W −0.25	W 0.45	W 0.88*	W 0.24	W 0.45*	W 0.28	W −0.20	W −0.19	W −0.29
	(*r*)	R −0.55*	R −0.61*	R −0.61*	R −0.08	R −0.08	R 0.25	R −0.22	R −0.22	R 0.61*	R 0.61*	R −0.17	R −0.12	R −0.12
		N 0.26	N −0.24	N 0.33	N 0.51*	N 0.46*	N 0.22	N 0.19	N −0.41	N 0.23	N 0.38*	N −0.32	N 0.12	N 0.34
		P −0.43	P −0.41	P 0.11	NH_3 −0.45*	NH_3 −0.15	P 0.13	P 0.68*	P −0.03	NH_3 −0.19	NH_3 −0.19	P −0.27	P −0.28	P −0.06
		Si 0.08	Si 0.62*	Si 0.75*	P 0.00	P 0.01	Si 0.19	Si 0.31	Si 0.55*	ahP 0.00	ahP −0.35	Si −0.41	Si 0.09	Si 0.14
	Multiple	L 0.37*	W 0.44*	Si 0.56*	N 0.26*	N 0.21*	T 0.25*	W 0.78*	Si 0.30*	R 0.38*	R 0.38*	T 0.32*	P 0.08*	N 0.12*
	regression:	N 0.23*					R 0.21*	L 0.10*	T 0.12				T 0.12*	T 0.06*
	Variance (r^2)						Si 0.11		W 0.23*				L 0.21*	L 0.16*
	explained by								N 0.06*					P 0.22*
	variables in								L 0.06*					
	order of								R 0.10*					
	importance[b]	0.60*	0.44*	0.56*	0.26*	0.21*	0.47*	0.87*	0.87*	0.38*	0.38*	0.32*	0.41*	0.55*
Anacystis	Simple linear	Not measured			L 0.20	L 0.28	L 0.40	L −0.32	L −0.12*	L −0.47*	L −0.56*	L 0.62*	L −0.24	L 0.21
(no. cells/l)	correlation				T 0.18	T 0.19	T 0.36	T −0.10	T 0.65*	T −0.13	T 0.03	T 0.66*	T 0.01	T 0.29
	coefficient				W −0.35	W −0.42*	W −0.53*	W 0.58*	W 0.58*	W 0.06	W 0.46*	W −0.82*	W 0.22	W 0.28
	(*r*)				R −0.35	R −0.35	R 0.62*	R −0.03	R −0.03	R 0.41*	R 0.41*	R −0.83*	R 0.51*	R 0.51*
					N 0.32	N 0.48*	N −0.02	N 0.05	N −0.31	N 0.54*	N 0.54*	N −0.32	N −0.10	N 0.12
					NH_3 −0.36	NH_3 −0.20	P 0.46	P 0.68*	P −0.31	NH_3 0.41	NH_3 0.42*	P −0.19	P −0.44*	P −0.06
					P −0.07	P −0.20				ahP −0.10	ahP −0.38*			
	Multiple				NH_3 0.13*	N 0.23*	R 0.39*	P 0.47*	T 0.42*	N 0.29*	L 0.31*	R 0.69*	R 0.26*	R 0.26*
	regression:				R 0.21*	W 0.07*				L 0.10*	N 0.07			
	Variance (r^2)					R 0.14*				W 0.06*				
	explained by									R 0.18*				
	variables in									T 0.07*				
	order of													
	importance				0.34*	0.44*	0.39*	0.47*	0.42*	0.70*	0.31*	0.69*	0.26*	0.26*

[a]Treatment: t.d. means independent variables used are those measured that day (exceptions are light—average of prior 3 days used, wind stress E.D.I. used rain—average of prior 7 days used); p.w. means independent variables used are the averages of the prior week.
[b] An r^2 value of 0.75 would indicate that 75% of the variation in the dependent variable can be explained by the independent variable listed.

TABLE 4. Regression analysis 2. Algae populations in Lake Hendricks

Dependent variable	Year	1970		1971					1972		
	Season	Late Summer		Spring	Early Summer		Late Summer		Spring	Early Summer	
	Dates	22/7–11/9		4/5–15/6	15/6–15/7		22/7–9/9		9/5–6/6	20/6–25/7	
	N	21		12	20		25		16	24	
	Treatment	t.d.	p.w.	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.
Chlorophyll *a*	Simple linear	L 0.37	L 0.19	L −0.96*	L −0.49*	L −0.14	L 0.21	L 0.24	L 0.11	L 0.07	L −0.35
	correlation	T 0.23	T 0.01	T −0.36	T −0.54*	T 0.21	T 0.36	T 0.31	T −0.06	T −0.04	T 0.24
	coefficient	W −0.10	W 0.09	W 0.08	W 0.57*	W 0.59*	W −0.19	W −0.31	W −0.21	W 0.26	W 0.57*
	(r)	R −0.25	R −0.25	R 0.95*	R −0.10	R −0.10	R −0.10	R −0.10	R 0.04	R 0.64*	R 0.64*
		N −0.24	N 0.03	N 0.82*	N 0.01	N −0.27	N 0.17	N 0.05	N 0.13	N 0.60*	N 0.56*
		NH_3 −0.31	NH_3 −0.11	P 0.48	P 0.13	P 0.09	NH_3 0.43*	NH_3 0.22	P 0.17	P −0.07	P −0.17
		P −0.44*	P −0.45*	Si 0.34	Si −0.21	Si −0.56*	P −0.52*	P −0.53*	Si 0.18	Si −0.07	Si −0.02
	Multiple	P 0.19*	P 0.20*	L 0.92*	W 0.33*	W 0.34*	P 0.27*	P 0.28*	NS	R 0.41*	R 0.41*
	regression:					R 0.21*				N 0.18*	N 0.19*
	Variance (r^2)					N 0.11*					
	explained by					L 0.08*					
	variables in										
	order of										
	importance	0.19*	0.20*	0.92*	0.33*	0.74*	0.27*	0.28*	0	0.59*	0.59*
Aphanizomenon (no. cells/l)	Simple linear	L 0.31	L 0.20	L −0.52	L −0.72*	L 0.45*	L 0.17	L 0.22	L 0.41	L −0.02	L −0.25
	correlation	T 0.28	T 0.15	T 0.11	T −0.54*	T 0.01	T 0.42	T 0.35	T 0.29	T −0.16	T 0.04
	coefficient	W −0.24	W −0.16	W −0.31	W 0.62*	W 0.66*	W −0.21	W −0.33	W −0.45	W 0.30	W 0.51*
	(r)	R −0.23	R −0.23	R 0.65*	R 0.16	R 0.16	R −0.11	R −0.11	R 0.06	R 0.48*	R 0.48*
		N −0.36	N −0.14	N 0.63*	N −0.05	N −0.18	N 0.13	N 0.06	N 0.06	N 0.41*	N 0.38
		NH_3 −0.36	NH_3 −0.23	P −0.07	P −0.11	P −0.05	NH_3 0.44*	NH_3 0.23	P 0.28	P −0.21	P −0.31
		P −0.40	P −0.35				P 0.61*	P −0.57*			
	Multiple	NS	NS	R 0.42*	L 0.52*	W 0.44*	P 0.37*	P 0.33*	NS	R 0.23*	W 0.26*
	regression:				R 0.03*	T 0.07*	NH_3 0.12*				
	Variance (r^2)				N 0.09*	P 0.04*					
	explained by				W 0.01*	R 0.05*					
	variables in				P 0.10*	L 0.20*					
	order of										
	importance	0	0	0.42*	0.75*	0.80*	0.49*	0.33*	0	0.23*	0.26*

TABLE 5. Regression analysis 3. Inorganic nitrogen in Lake Cochrane

Dependent variable	Year	1970					1971					1972		
	Season Dates N	Spring 30/4–24/6 14	Early Summer 24/6–15/7 18		Late Summer 22/7–11/9 25		Spring 22/4–15/6 18	Early Summer 15/6–15/7 18		Late Summer 22/7–9/9 28		Spring 4/5–6/6 16	Early Summer 23/6–25/7 20	
	Treatment	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.
Nitrate	Simple linear correlation coefficient (r)	L −0.31 T −0.22 W 0.36 R −0.03	L 0.07 T 0.04 W 0.38 R 0.35	L −0.22 T −0.40 W 0.39 R 0.35	L 0.00 T −0.34 W −0.09 R −0.33	L 0.05 T −0.26 W −0.08 R −0.33	L −0.35 T −0.17 W 0.26 R 0.27	L 0.29 T 0.26 W −0.01 R −0.19	L 0.15 T 0.02 W −0.23 R −0.19	L −0.33 T −0.25 W 0.00 R 0.36	L −0.51* T −0.06 W 0.38* R 0.36	L −0.64* T −0.69* W 0.46 R 0.43	L 0.37 T 0.19 W −0.29 R −0.23	L 0.29 T 0.19 W −0.18 R −0.23
	Multiple regression: Variance (r^2) explained by variables in order of importance	NS 0	NS 0	NS 0	NS 0	R 0.11* T 0.04* W 0.20* 0.35*	NS 0	L 0.09* T 0.28* 0.36*	NS 0	R 0.13* T 0.18* W 0.26* L 0.08* 0.64*	L 0.26* 0.26*	T 0.47* 0.47*	L 0.14* R 0.04* 0.18*	L 0.08* R 0.16* W 0.05* 0.30*
Ammonia	Simple linear correlation coefficient (r)		Not measured		L −0.28 T −0.51* W 0.56* R −0.24	L −0.23 T −0.70* W 0.77* R −0.24		Not measured		L −0.33 T −0.66* W −0.03 R −0.13	L −0.61* T −0.52* W 0.62* R −0.13	Not present in measurable quantities		
	Multiple regression: Variance (r^2) explained by variables in order of importance				W 0.32* L 0.08* R 0.15* T 0.09* 0.64*	W 0.60* L 0.09* 0.69*				T 0.44* L 0.09* 0.52*	W 0.39* 0.39*			

TABLE 6. Regression analysis 4. Inorganic nitrogen in Lake Hendricks

	Year	1970		1971					1972		
	Season Dates N	Late Summer 22/7–11/9 21		Spring 4/5–15/6 12	Early Summer 15/6–15/7 20		Late Summer 22/7–11/9 25		Spring 9/5–6/6 16	Early Summer 20/6–25/7 24	
Dependent variable	Treatment	t.d.	p.w.	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.
Nitrate	Simple linear correlation coefficient (r)	L –0.17 T –0.36 W 0.21 R –0.03	L –0.14 T –0.18 W 0.22 R –0.03	L –0.77* T –0.29 W 0.05 R 0.77*	L –0.11 T –0.36 W 0.51* R –0.52*	L –0.05 T –0.28 W –0.04 R –0.52*	L 0.05 T –0.02 W 0.25 R 0.04	L 0.01 T –0.18 W 0.10 R 0.04	L 0.34 T 0.08 W –0.32 R 0.38	L 0.26 T 0.23 W –0.10 R 0.31	L –0.06 T 0.32 W 0.19 R 0.31
	Multiple regression: Variance (r^2) explained by variables in order of importance	NS 0	NS 0	R 0.59* 0.59*	R 0.28* 0.50*	R 0.28* 0.49*	NS 0	NS 0	R 0.14* W 0.14* T 0.30* 0.57*	NS	NS
Ammonia	Simple linear correlation coefficient (r)	L –0.80* T –0.55* W 0.43 R –0.06	L –0.77* T –0.52* W 0.68* R –0.06		— Not measured —		L –0.39 T –0.30 W 0.40* R 0.40	L –0.19 T –0.23 W 0.05 R 0.40	Not present in measurable concentrations		
	Multiple regression: Variance (r^2) explained by variables in order of importance	L 0.65* 0.65*	L 0.60* W 0.11* T 0.03* R 0.06 0.80*				W 0.16* T 0.15* 0.31*	NS			

TABLE 7. Regression analysis 5. Inorganic phosphorus in Lake Cochrane

Dependent variable	Year	1970					1971					1972		
	Season Dates N	Spring 30/4–24/6 14	Early Summer 24/6–15/7 18		Late Summer 22/7–11/9 25		Spring 22/4–15/6 18	Early Summer 15/6–15/7 18		Late Summer 22/7–9/9 28		Spring 4/5–6/6 16	Early Summer 23/6–25/7 20	
	Treatment	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.
Ortho-phosphate	Simple linear correlation coefficient (r)	L −0.23 T 0.35 W 0.01 R 0.53	L 0.14 T 0.23 W 0.44 R 0.36	L −0.13 T −0.37 W 0.45 R 0.36	L 0.16 T −0.06 W 0.41* R 0.57*	L 0.24 T −0.03 W −0.04 R 0.57*	L 0.05 T 0.11 W −0.17 R 0.42	L −0.60* T −0.35 W 0.74* R 0.20	L −0.53* T 0.59* W 0.63* R 0.20				L 0.45* T 0.25 W −0.08 R −0.49*	L −0.29 T −0.07 W −0.24 R −0.49*
	Multiple regression: Variance (r^2) explained by variables in order of importance	NS	NS	NS	R 0.32* W 0.14* L 0.12*	R 0.32* L 0.24* T 0.11*	NS	W 0.54*	W 0.40*	Not present in measurable quantities		NS	R 0.24* L 0.18* W 0.23*	R 0.24* W 0.12* T 0.14* L 0.04*
		0	0	0	0.59*	0.67*	0	0.54*	0.40*				0.65*	0.54*

TABLE 8. Regression analysis 6. Inorganic phosphorus in Lake Hendricks

Dependent variable	Year	1970		1971					1972		
	Season Dates N	Late Summer 22/7–11/9 21		Spring 4/5–15/6 12	Early Summer 15/6–15/7 20		Late Summer 22/7–9/9 25		Spring 9/5–6/6 16	Early Summer 20/6–25/7 24	
	Treatment	t.d.	p.w.	t.d.	t.d.	p.w.	t.d.	p.w.	t.d.	t.d.	p.w.
Ortho-phosphate	Simple linear correlation coefficient (r)	L −0.57* T −0.38 W 0.08 R −0.28	L −0.52* T −0.20 W 0.25 R −0.28	L −0.62* T −0.44 W 0.34 R 0.51	L −0.03 T −0.48* W 0.53* R −0.32	L −0.16 T 0.04 W 0.02 R −0.32*	L −0.36 T −0.57* W 0.41* R 0.53*	L −0.43* T −0.24 W 0.43* R 0.53*	L 0.71* T 0.55* W −0.50* R 0.70*	L 0.50 T 0.63* W −0.14 R 0.09	L 0.19 T 0.51* W −0.23 R 0.09
	Multiple regression: Variance (r^2) explained by variables in order of importance	L 0.33*	L 0.27*	L 0.38*	W 0.29* L 0.36*	R 0.10* L 0.20* T 0.24*	T 0.32* R 0.33*	R 0.28* W 0.16*	L 0.51* R 0.28* W 0.08*	T 0.40 W 0.12* L 0.12* R 0.08*	T 0.26* R 0.10* W 0.17* L 0.15*
		0.33*	0.27*	0.38*	0.64*	0.53*	0.65*	0.43*	0.87*	0.72*	0.68*

generated circulation of the water and by direct stirring of sediments in shallow areas due to the action of wind generated waves. In shallow lakes this direct stirring may affect the entire lake bottom. When the wave period (the length of time between successive wave crests) is known, the depth at which the wave will feel bottom (critical depth) can be calculated from the following formula (Sverdrup et al. 1942)

$$h = (1/4)\ g\ T^2$$

where h is critical depth, T is wave period (in seconds), and g is the gravitational constant ($9.8\ m/s^2$). In most small lakes the wave period can easily be determined by observers standing on the shortline.

Critical depths for the two lakes were determined on 10 June 1972, a day when wind speeds averaged 26–29 km/h. Calculation of critical depth in Lake Hendricks gave $h = 4.3$ m, considerably more than the maximum lake depth. Therefore, waves could be assumed to be stirring sediments throughout the lake. Lake Cochrane lies in a sheltered basin, and on the same date developed much smaller waves with a critical depth of 1.2 m. Because $< 6\%$ of Lake Cochrane is shallower than 1.2 m, direct stirring of sediments and subsequent release of nutrients should be much less significant than in Lake Hendricks. The much greater agitation of sediments in Lake Hendricks is undoubtedly partially responsible for the higher levels of nutrients observed.

Lake management implications

When a typical summer wind can disturb lake bottom sediments and distribute released nutrients throughout the water column, efforts to curb algal blooms by restricting further nutrient input or by flocculating nutrients out of the water column are not likely to have more than temporary results. A period of high water temperatures together with the accumulation of organic matter on the sediment surface will stimulate bacterial release of sediment nutrients, and wind generated waves will assure their distribution into the water column. Because common blue-green bloom species are known to be able to concentrate phosphorus (and possibly nitrogen) at times of excess and continue growth at times of depletion (Ketchum 1939, Gerloff and Skoog 1954), temporary nutrient limitation may not affect the success of the bloom species. Also, in some lakes the contribution of nutrients from the sediments to the water column may greatly exceed the contribution of nutrients from runoff and other incoming sources; Harrison et al. (1972) calculated that the supply of nitrogen, phosphorus, and silicon in the upper 2.54 cm of sediments of Upper Klamath Lake, Oregon, was equivalent to the amount that would be brought into the lake in 60 yr of inflow. Barica (1974) also found prairie pothole lakes in Saskatchewan to be self-sufficient in nutrient supply. Significantly, both Upper Klamath Lake and the pothole lakes studied by Barica are dominated by blooms of the same species of algae as Lake Hendricks.

Lakes which are presently deep enough to prevent direct stirring of bottom sediments by waves may respond well to nutrient-limitation measures. In these lakes the fraction of algal abundance that may be presently ascribed to variations in suspected limiting nutrients can be estimated from multiple regression analysis to predict the future success of a nutrient limitation program. Efforts to control algae blooms by limiting incoming nutrients might best be concentrated on those lakes in which frequent nutrient correlations can be demonstrated, and in which wind generated waves will not frequently stir sediments over a large area of the lake.

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