Photosynthetically elevated pH in acid waters with high nutrient content and its significance for the zooplankton community

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Abstract

The pH of undisturbed surface waters in the New Jersey Pine Barrens is very acidic (pH 3.5–4.5). Surface waters disturbed by residential and agricultural development typically exhibit significantly elevated pH. Detailed analyses of a disturbed and undisturbed pond showed that the elevated pH of the disturbed pond was primarily the result of enhanced primary productivity. At night and during the winter, when productivity was reduced, the pH dropped to levels more characteristic of the undisturbed pond. The phenomenon of fluctuating pH had significant implications for the zooplankton in the disturbed pond. Though nutrients were significantly greater in the disturbed pond, zooplankton species composition and general abundance patterns were nearly identical in the two ponds. Thus, in these and other poorly buffered waters, it is hypothesized that the lowest pH values were the ones effectively regulating the zooplankton community.

Introduction

Interest in the limnology of acidic waters ($pH < 5.5$) has grown considerably over the past decade (e.g. Haines, 1981). Two areas of particular concern are the regulation of pH in these (usually) poorly buffered waters (cf. Schindler *et al.*, 1980) and pH control of the aquatic biota (Haines, 1981).

Many factors, both biological and chemical, can alter the pH of an acidic lake, including numerous redox reactions (particularly iron oxidation and reduction; Singer & Stumm, 1970), humic and fulvic acid production via decomposition (Crerar *et al.*, 1981), cation exchange with sediments (Oliver & Kelso, 1983), and various watershed reactions (Krug & Frink, 1983). Kelley *et al.* (1982) provide a comprehensive review of these and other relevant processes. Photosynthesis is another factor that can alter lake pH (Talling, 1976). The usual mechanism results in elevated pH by a photosynthetically induced reduction in pCO_2. In acidic lakes, total DIC is very small, so a photosynthetic change in pCO_2 has relatively little effect on pH (cf. Stumm & Morgan, 1981). However, CO_2 removal is not the only way photosynthesis can alter pH. Laboratory studies have shown that algal NO_3^- and NO_2^- uptake results in a stoichiometric production of OH^- in the external medium, while NH_4^+ uptake produces H^+ Brewer & Goldman, 1976; Goldman & Brewer, 1980).

To date, demonstration of the effect of elevated photosynthesis on the pH of acidic lakes is rare. One example appears to be Crosson Lake, Ontario, Canada, where the epilimnetic pH rose from 5.1 to 6.6 during the summer (Zimmerman & Harvey, 1979). Since all inflow waters were at or below pH 5.3, primary productivity appeared the only factor capable of raising the pH. NO_3^- levels declined significantly during the period suggesting that nitrogen uptake was the mechanism responsible for the increase (NRCC, 1981). This finding and the experiments of Brewer & Goldman (1976) suggest that, even in acidic lakes, primary productivity may play a critical role in pH regulation. The purpose of this paper is to provide further documentation of the

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effect of elevated photosynthesis on pH in a naturally acidic lake, and to examine its significance to an important component of the lake biota, the zooplankton.

Study area

The Pine Barrens occupy most of the southern half of the State of New Jersey, USA (see Forman, 1979 for a comprehensive treatment). The region is mostly forested, and is underlain by thick coastal plain sands which form droughty, nutrient poor, acidic soils. The vegetation is dominated by pitch pine (*Pinus rigida*) and a variety of oaks (*Quercus*). Surface waters are fed primarily from groundwater discharge (Rhodehamel, 1979), and are typically nutrient poor, stained brown, and acidic (Morgan, 1984). Although bogs and swamps form the only natural standing bodies of water in the region, numerous streams have been dammed, creating small, shallow reservoirs. Some portions of the Pine Barrens have experienced heavy agricultural and residential development over the past several decades. Watershed development typically results in surface waters with greatly elevated nutrients and pH (Pinelands Commission, 1980; Morgan, 1984).

The studies reported here were carried out on two impounded ponds, Oswego and Nescochague lakes, located within the Mullica River drainage, in the center of the Pine Barrens (Fig. 1). Both ponds exhi-

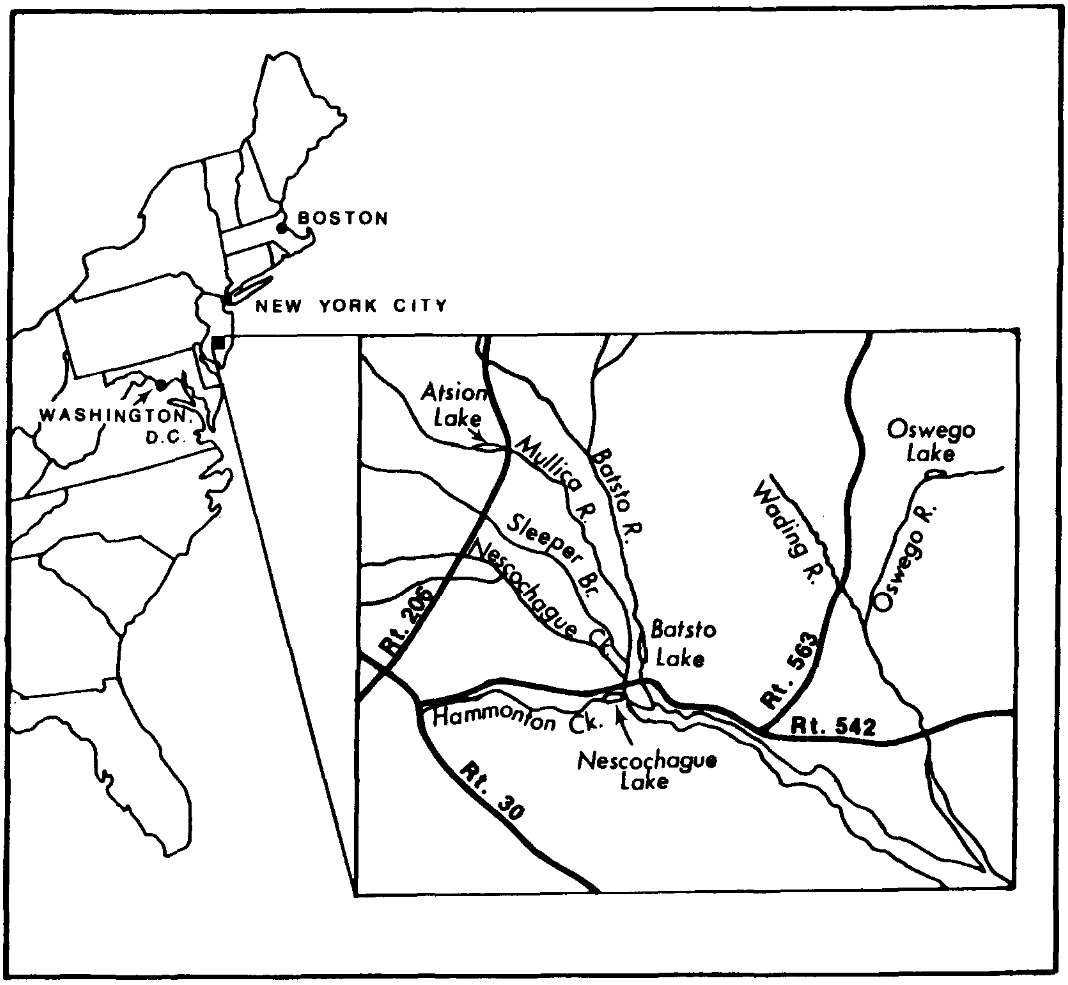

Fig. 1. Map of the Eastern United States showing the location of the New Jersey Pine Barrens. The detailed map shows the location of the study lakes within the Mullica River drainage.

Table 1. Comparison of the physical characteristics of Oswego and Nescochague lakes.

	Oswego	Nescochague
Approx. Surface Area	0.5 km^2	0.5 km^2
Mean Depth	1 m	1 m
Maximum Depth	2.5 m	2 m
Sediment Characteristics	Sand/Muck	Sand/Muck
Near Shore Vegetation	Pitch Pine forest/ Cedar Swamp	Pitch Pine forest/ Cedar Swamp/Residential[a]
Retention Time	2 – 3 days	2 – 3 days
Stratification	None except during ice cover[b]	None except during ice cover[b]
Maximum Temperature °C	30	30

[a] Including various non-native trees and shrubs.

[b] Except occasionally during moderately calm weather when strong absorption of solar radiation by the upper layer of these colored waters can result in a 4 – 5 °C temperature difference between the surface and the bottom at 2 m.

bited similar physical characteristics (Table 1), but differed in that the Nescochague Lake watershed was heavily developed for agricultural and residential uses, including a sewage treatment plant several kilometers upstream. The Oswego Lake watershed was mostly undisturbed.

Materials and methods

Routine pH, NO_3^--N, NH_4^+-N, total P, alkalinity, and Chl *a* measurements were taken from near-surface samples at two open water stations ($z = 2.0$–2.5 m) in each pond. pH was measured in the field with an Acumet 640 portable pH meter by gently stirring each sample, and then waiting until a stable reading was obtained. Water for NO_3^--N, NH_4^+-N, and total P analyses was collected in acid rinsed polyethylene bottles, returned to the laboratory, and analyzed immediately (for NH_4^+-N) or frozen at −20° C for later analysis of NO_3^--N and total P. Ammonium was determined by the phenate method, nitrate by cadmium reduction and total P by the ascorbic acid method following persulfate digestion (A.P.H.A., 1980). Total alkalinity was determined in the field by titration to a pH endpoint of 4.5 with 0.02 N H_2SO_4. The use of this endpoint tends to overestimate alkalinity in low alkalinity water (Faust, 1983), but the absolute magnitude of this error was considered small for these field measurements. The alkalinity of water below pH 4.5 was considered zero. Water column Chl *a* was extracted by filtering 200–1000 ml of lakewater through GF/C filters, which were then ground and allowed to stand overnight in 90% acetone. Chl *a* concentration was determined spectrophotometrically by use of the trichromatic equations (A.P.H.A., 1980).

Algal primary productivity was estimated by an in situ incubation with $NaH^{14}CO_3$ in the summer of 1981. Algae were collected from 4–5 discrete depths at an open water station in each pond. One dark and two light bottles were filled with lakewater, injected with ^{14}C, and resuspended at the collection depth for 3–4 h. At the end of the incubation the bottle contents were filtered on 0.45 μm Millipore filters and prepared for scintillation counting. Calculation of carbon fixed followed standard methods (A.P.H.A., 1980).

Crustacean zooplankton were collected approximately every three weeks at one or two open water stations in each pond from June 1981–May 1983. Samples were collected by towing a 25 cm diameter, 116 μm mesh, nylon plankton net from the bottom to the surface. If zooplankton densities were low, two such tows were pooled into a single sample. Tows generally ranged from 1.5–2.0 m long. Usually, two replicate tows were taken at each station. All samples were preserved in sucrose-Formalin.

An in situ manipulation of pH was carried out in Nescochague Lake during the summer of 1982 using open topped, 1 m^3 polyethylene enclosures. Two bags were filled with lakewater and anchored, floating, at an open water station. One bag was acidified with dilute (approx. 0.02 N) H_2SO_4 to bring the pH down to between 4.0 and 4.5, which is the pH typical of undisturbed waters in the Pine Barrens. The other bag was unaltered. The pH in both bags was monitored every 2–4 days for three and a half weeks. Additional acid was added to the acidified enclosure on three occasions to bring the pH back down to the 4.0–4.5 range. Additional NO_3^--N (2 mgl^{-1}) was added to both enclosures on day 11 to prevent nutrient limitation of the algae.

The effect of photosynthesis on lakewater pH was also examined in the laboratory. In August 1983, Nescochague Lake water was filtered to remove zooplankton and acidified to pH 4.5 by the addition of dilute HCl. The water was distributed in 150 ml aliquots among two sets of four flasks. One set of flasks was treated with DCMU to a final concentration of 50 μmol DCMU. This concentration is sufficient to stop photosynthesis in many algal species (Calvayrac *et al.*, 1979). Excess NO_3^--N (0.5 mgl^{-1}) was added to each flask so that photosynthesis could continue unimpeded throughout the experiment. All flasks were placed in a growth chamber under constant illumination. The temperature was maintained close to that experienced in the field (26° C), and the light intensity was equivalent to that at 0.5 m depth at midday (250 μEinst $m^{-2}s^{-1}$). The experiment ran for three days and the pH was recorded every 8–16 h. Midway through the first day of the experiment, a ^{14}C uptake experiment was performed on both treated and untreated water to verify that photosynthesis had ceased in the treated flasks. The viability of the algae in both sets of flasks was also monitored at this time by microscopic examination.

Results and discussion

The impact of watershed disturbance on surface water pH was clearly evident in Nescochague Lake (Fig. 2). Nescochague Lake pH exceeded the pH observed in Oswego Lake by at least 1 pH unit on most occasions. From June 1981–June 1984, Nescochague Lake pH averaged 5.0 (based on H^+ concentration) compared with 4.2 in Oswego Lake. However, there was a great deal of seasonal variation in Nescochague Lake pH. During the warm season (May–October), pH was significantly elevated ($\bar{x}$= 5.9), and declined in the cold season (November–April) to levels closer to those found in Oswego Lake ($\bar{x}$ = 4.7). This pattern was evident in each of the three years studied. Despite the elevated summer pH, alkalinity in Nescochague Lake remained extremely low (Table 2).

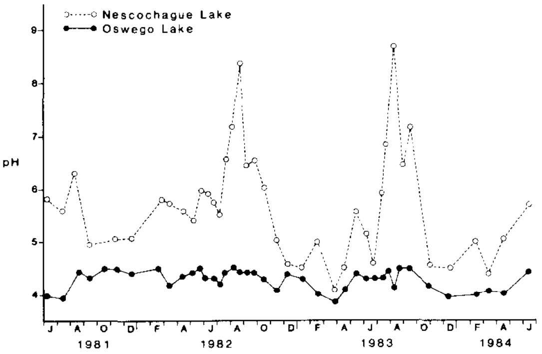

Fig. 2. Oswego and Nescochague lakes near surface daytime pH from June 1981 – June 1984.

Table 2. Comparison of chemical and biological characteristics of Nescochague and Oswego Lakes. Values reported are mean (range) of NH_4^+-N, total P, and alkalinity from March 1982 – June 1984. Summer is defined as May – October and Winter as November – April. Chl *a* values are mean (range) from June – August, 1982 and 1983. Primary productivity data are single measurements on 13 August, 1981 in Nescochague Lake and 30 July 1981 in Oswego Lake.

Parameter	Lake			
	Nescochague			Oswego
	Year Round	Summer	Winter	
Alkalinity (μeql^{-1})	26	34 (0 – 80)	16 (0 – 40)	0
NH_4^+-N (μgl^{-1})	32	36 (14 – 70)	27 (0 – 62)	10 (0 – 24)
Total P (μgl^{-1})	402	415 (255 – 600)	376 (240 – 515)	8 (3 – 11)
Primary Productivity ($mgC \cdot m^{-2} \cdot h^{-1}$)	277			36
Chl *a* ($mg\ m^{-3}$)		21 (5 – 70)		2 (1 – 3)

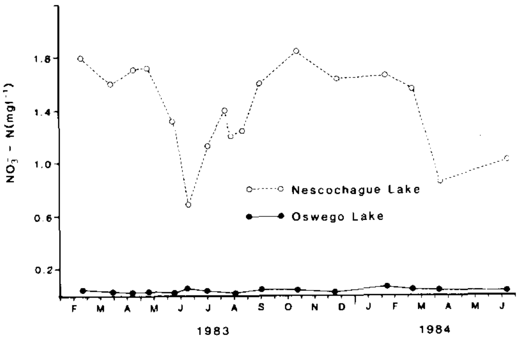

Fig. 3. NO$_3$-N in Oswego and Nescochague lakes from 1983 February – June 1984.

The effect of disturbance was also evident in ambient nutrient concentrations. NO$_3$-N was very high in Nescochague Lake, averaging 1.4 mgl^{-1} between February 1983 and June 1984 (Fig. 3). As with pH, nitrate varied significantly with the seasons, being lowest in the summer ($\bar{x} = 1.21$ mgl^{-1}) and highest in the winter ($\bar{x} = 1.56$ mgl^{-1}). Total P was also extremely elevated, but did not show any obvious seasonal trends (Table 2). NH$_4^+$-N, on the other hand remained very low throughout the year. As is characteristic of undisturbed Pine Barrens waters, concentrations of all nutrients in Oswego Lake were barely detectable and showed no obvious seasonal trends (Fig. 3, Table 2). Nescochague Lake summer Chl *a* and primary productivity values, as a result of the elevated nutrients, were nearly an order of magnitude greater than the very low values observed in Oswego Lake (Table 2).

The factors controlling the pH in Oswego Lake appeared relatively straightforward. Numerous watershed processes and anthropogenic inputs in the Pine Barrens result in very acidic soil, ground, and surface waters with pH's in the 3.5–4.5 range (Tedrow, 1979; Morgan, 1984). These acidic source waters appeared to flow through Oswego Lake largely unaffected by processes within the lake itself. Thus, the lake pH remained low and fairly uniform throughout the study period (Fig. 2).

The control of pH was much more complex in Nescochague Lake. pH values tended to approach those of the undisturbed Oswego Lake during the winter, but increased and considerably diverged during the growing season. A likely explanation of this trend would be a change in the inflow.

Three sources must be considered when characterizing the inflow into Nescochague Lake; surface stream inflow, groundwater discharge, and direct atmospheric inputs. Although surface inflow may be dominant in most lakes, the high water table and porous soils of the Pine Barrens combined with rapid turnover suggest that groundwater and direct inputs are very important in Pine Barrens ponds. For instance, measurements at both Nescochague and Oswego Lakes revealed that only about 75% of the outflow could be accounted for by the stream inflow. The complexity of the inflow into Nescochague Lake precluded quantification of inputs, but data exist that suggest all three sources were very acid even in the warm season. For instance, Durand & Zimmer (unpubl. data) reported a mean stream inflow pH of 4.95 (n = 12) and 5.01 (n = 11) for the warm and cold seasons, respectively, in 1978 and 1979. These values are very close to ones I obtained in scattered sampling during the summers of 1982 and 1983 (pH = 4.8, n = 5). Durand & Zimmer also reported a mean pH of 4.7 for near surface well water just upstream of Nescochague Lake. Crerar *et al.* (1981) reported similarly low values (mean pH = 4.4) for nearby shallow wells. Finally, year-round bulk precipitation measurements in this region in the early 1980s averaged about pH 4.1 (Morgan, 1984). Thus, water entering Nescochague Lake was uniformly acidic, so the elevated summer pH must have resulted from internal processes.

Two sets of field observations suggested that primary productivity was the most likely process capable of elevating pH. First, Chl *a*, as a marker for primary productivity, and pH were significantly and positively correlated over the study period (Fig. 4; r = 0.782, p < 0.01). There was no significant correlation between pH and Chl *a* in Oswego Lake. Second,

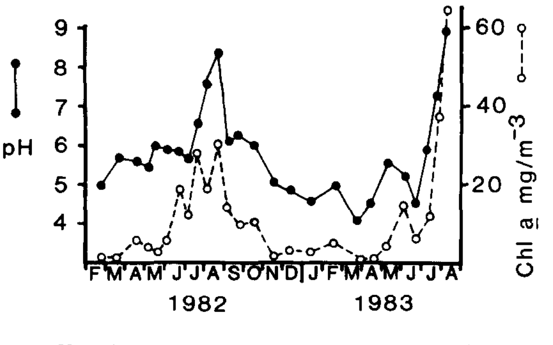

Fig. 4. pH (solid dots) and chlorophyll *a* (open circles) in Nescochague Lake from February 1982 – August 1983.

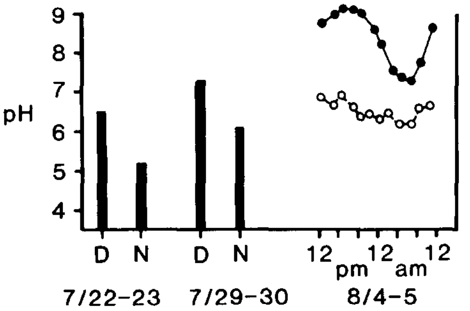

Fig. 5. Midday (D) and before dawn (N) pH in Nescochague Lak in July 1983. Also depicted is a diurnal plot of pH near the surface (solid dots) and at 1.5 m depth (open circles) in August 1983.

three sets of diurnal pH measurements in July and August, 1983, showed that surface pH values were at least 1.2 pH units higher during the day than just before dawn the next morning (Fig. 5). This is just what would be expected if primary productivity were controlling pH. In addition, the lake was temporarily stratified at the time of the August sampling, and diurnal pH readings taken near the bottom at 1.5 m did not fluctuate consistently over the 24 h period (Fig. 5). Since this depth corresponded to the compensation point in this lake (Morgan, 1983), primary productivity was the most probable process that could account for the elevated surface, but not bottom, pH in this system.

The direct control of Nescochague Lake pH by elevated primary production was confirmed by a laboratory and field experiment. The pH of acidified (to pH 4.5) Nescochague Lake water (initial pH 7.1) rose to pH 8.0 within three days under constant illumination in a growth chamber (Fig. 6A). In contrast, the pH of acidified DCMU-treated lakewater remained essentially constant, never going above pH 5.0. Microscopic examination of the DCMU-treated algae after 24 h revealed that these organisms were still apparently healthy; chloroplasts were green and motile forms were still swimming. The DCMU only affected carbon uptake as confirmed by the ^{14}C uptake experiment (Table 3). The in situ enclosure experiment gave similar results (Fig. 6B). The pH of the acidified enclosure consistently approached the pH of the control even following several further additions of acid to lower the pH. Elevated pH via high rates of primary productivity was again the most probable process that could satisfactorily account for these results.

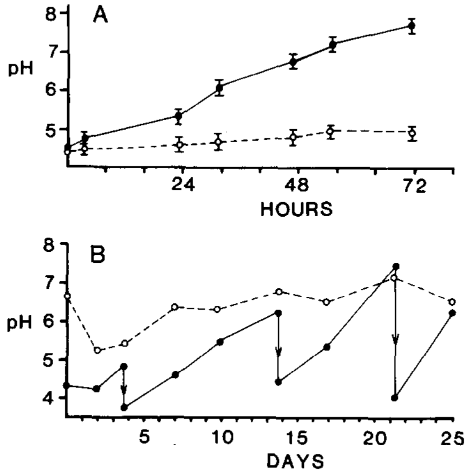

Fig. 6. A) pH of experimental flasks containing Nescochague Lake water after acidification to pH 4.5 under constant illumination (solid dots) and with illumination plus DCMU (open dots). The vertical bars represent ± 1 S.E. B) pH of the control enclosure (open dots) and the acid enclosure (solid dots) in Nescochague Lake in August 1982. Arrows represent addition of acid to the acid enclosure.

The mechanism by which primary productivity raised the pH of Nescochague Lake water appeared to be related to nitrogen transfers. Nitrate assimilation (plus nitrite), denitrification and nitrate reduction will raise pH, while ammonium assimilation and nitrification will reduce it (cf. Brewer & Goldman, 1976; Kelley *et al.*, 1982). Considering the rapid turnover of Nescochague Lake and the high nitrate and low ammonium concentrations (Table 2), algal uptake of nitrate would appear to be the dominant process affecting pH. Although a complete nitrogen budget for Nescochague Lake could not be calculated, the data available support this conclusion. For example, if the mean winter pH of 4.7 is considered the baseline pH for the lake, then an elevation to the mean summer pH of 5.9 would require the net con-

Table 3. Results in counts per minute (c.p.m.) of ^{14}C uptake experiment on acidified and acidified + DCMU treated Nescochague Lake water.

	c.p.m.	
	Average Light	Dark
Acidified Only	3841	175
Acidified + DCMU	120	88

sumption of about 20 μeql^{-1}H^+, assuming no significant buffering (cf. Table 2). Because there should be a 1 : 1 relationship between H^+ consumption and NO_3^- uptake, this would be equivalent to removal of 280 μgl^{-1} of NO_3^--N. The average winter–summer difference in NO_3^--N was about 350 μgl^{-1}. Because it is the net NO_3^- uptake versus other acidifying processes that is important, this difference is very close to the expected.

An important assumption in this argument is that there were no seasonal differences in inflow pH or NO_3^-. The diversity of inflow sources make validation of this assumption difficult, but data from this and a 1977–1979 study by Durand & Zimmer (unpubl. data) on the surface inflow showed no significant seasonal differences in pH or NO_3^- (eg. from Durand & Zimmer: May–October NO_3^--N $\bar{x} = 1.17$ mgl^{-1}, $s = 0.59$, $n = 19$; November–April $\bar{x} = 1.09$ mgl^{-1}, $s = 0.69$, $n = 18$; seasonal pH data are given above).

The 350 μgl^{-1} NO_3^--N difference between winter and summer converts to a 175 μgl^{-1}d^{-1}rate of uptake, assuming a two day turnover of the lake. Based on a C : N ratio of 6.3 for phytoplankton, this would translate into 1.1 mgl^{-1}d^{-1} POC produced, or 2.2 g m^{-2}d^{-1} for a water column 2 m deep. The measured rate of primary productivity at 2 m depth in Nescochague Lake was 0.277 g m^{-2}h^{-1} (Table 2) or 2.7 g m^{-2}d^{-1} assuming a 12 h day. Because there were other nitrogen sources available, these values are consistent with the rate of nitrate uptake necessary to raise the pH.

One further check on the role of nitrate uptake can be made based on the laboratory and field experiments. In the laboratory experiment, the change in pH from 4.5–8.0 required the consumption of about 32 μeql^{-1} H^+ which would mean a net uptake of 448 μgl^{-1} NO_3^--N. Since the flasks were spiked before the experiment with 500 μgl^{-1}, sufficient nitrate was available to raise the pH the required amount. In fact, a preliminary experiment without a spike did not significantly raise the pH. In the field experiment, the total consumption of H^+ was about 300 μeql^{-1}. This would necessitate an uptake, over the course of the experiment, of 4.2 mgl^{-1} NO_3^--N. Unfortunately, reliable estimates of nitrate concentrations in the bags are not available. However, the bags probably started with about 1.2 mgl^{-1} (the summer average for this lake). To this, an additional 2.0 mgl^{-1} NO_3^--N were added to each bag on day 11 of the experiment. Thus, sufficient nitrate was available to account for all but about 71 μeql^{-1} of the H^+ consumed. The unaccounted for H^+ is not great if one considers the effect of small errors in pH measurement at these low pH levels. For instance, an underestimation of the lowest pH values in Fig. 6B of just 0.1 pH units would result in a total error of 63 μeql^{-1}. Since these measurements were made in the field with a portable pH meter, errors of this magnitude are not unreasonable. The data from the bag experiment, therefore, are consistent with the importance of nitrate uptake in elevating pH.

At pH levels above 5.5, DIC derived solely from $CO_2(g)$ would become significant in Nescochague Lake. When this occurred, photosynthetic and respiratory effects on $CO_2(g)$ could significantly alter pH (Stumm & Morgan, 1981). It should be remembered, however, that pH changes will occur only when pCO_2 is altered. For the most part, Nescochague Lake was well mixed. Thus, any changes in pCO_2 would have been short-lived, and therefore, could not account for the observed prolonged elevation in lake pH.

Productivity induced seasonal and diurnal fluctuations in pH may have significant implications for the assessment of acidic lake biota. The pH of a productive acidic lake, depending on when it is measured, may turn out to be much higher than the pH controlling the biota. For instance, the elevated nutrients and summer pH in Nescochague Lake suggest that the zooplankton communities in Nescochague and Oswego lakes should be quite different. In fact, this was not the case. Crustacean zooplankton collections in Nescochague Lake revealed a fauna essentially identical to that found in Oswego Lake (Table 4). Twenty nine species were observed in Nescochague Lake, all of which were also found in Oswego Lake. Six species were found unique to Oswego Lake. Even for those species considered common (found in at least 25% of the samples), all were common in both lakes, except for *Eurycercus* sp. in Nescochague Lake and *Acroperus* sp. and *Epischura nordenskioldi* in Oswego Lake.

As would be expected from its greater nutrient content, total zooplankton abundance in Nescochague Lake exceeded the levels in Oswego Lake (Fig. 7). However, the patterns of abundance in the two lakes were very similar. The same species, *Bosmina coregoni,* dominated both lakes and accounted for most of the major fluctuations in total abundance (Fig. 7). The only major exception was a large pulse of cyclopoid copepods (mostly *Eucyclops agilis*) in

Table 4. Crustacean zooplankton species present in Oswego and Nescochague lakes based on 27 collections from June 1981 – May 1983. Common species are defined as those occurring in more than 25% of all samples. * = species collected by D. G. Frey (pers. commun.) in August 1982, but not yet recorded from the open water stations.

Oswego Lake	Nescochague Lake
Common Species	
Cladocera	Cladocera
Bosmina coregoni	_Bosmina coregoni_
Daphnia ambigua	_Daphnia ambigua_
Polyphemus sp.	_Polyphemus_ sp.
Chydorus brevilabris	_Chydorus brevilabris_
C. linguilabris	_C. linguilabris_
Alona intermedia	_Alona intermedia_
Acantholeberis curvirostris	_Acantholeberis curvirostris_
Acroperus sp.	_Eurycercus_ sp.
Copepoda	Copepoda
Eucyclops agilis	_Eucyclops agilis_
Tropocyclops prasinus mexicanus	_Tropocyclops prasinus mexicanus_
Epischura nordenskioldi	
Other Species	
Cladocera	Cladocera
Scapholeberis sp.	_Scapholeberis_ sp.
Ceriodaphnia sp.	_Ceriodaphnia_ sp.
Simocephalus sp.	_Simocephalus_ sp.
Alona rustica	*_Monospilus dispar_
A. quadrangularis	_Alona rustica_
A. affinis	_A. quadrangularis_
Pleuroxus denticulatus	_A. affinis_
*_P. laevis_	_Pleuroxus denticulatus_
P. striatus	_P. striatus_
Graptoleberis testudinaria	_Disparalona acutrostris_
*_Chydorus piger_	*_Chydorus piger_
*_Monospilus dispar_	_Acroperus_ sp.
*_Pseudochydorus globosus_	_Diaphanosoma_ sp.
Eurycercus sp.	_Latona setifera_
Disparalona acutrostris	_L. parviremis_
Rhynochotalona falcata	_Ilyocryptus_ sp.
Diaphanosoma sp.	
Latona setifera	
L. parviremis	
Ofryoxus gracilis	
*_Macrothrix_ sp.	
Ilyocryptus sp.	
	Copepoda
Copepoda	_Mesocyclops edax_
Mesocyclops edax	_Macrocyclops albinus_
Macrocyclops albinus	_Epischura nordenskioldi_

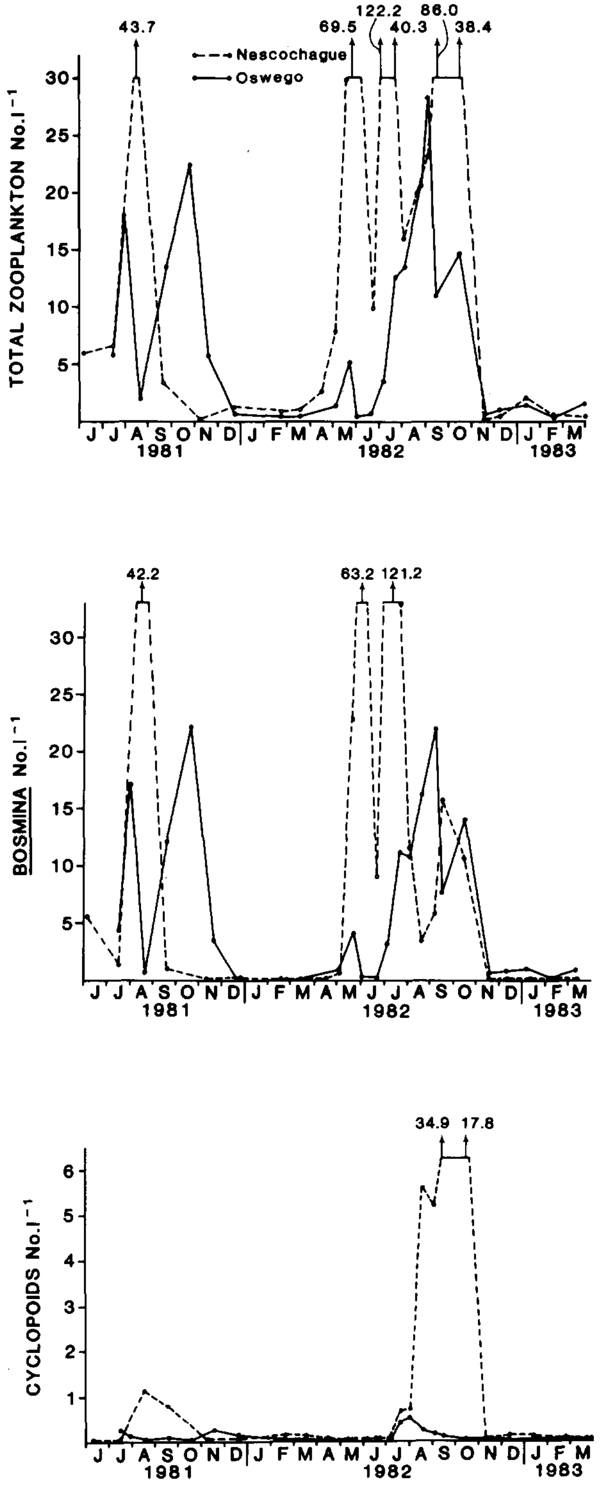

Fig. 7. Zooplankton abundance in Nescochague and Oswego lakes from June 1981 - March 1983.

the fall of 1982 in Nescochague Lake.

An explanation for the surprising similarity of the zooplankton communities in these two lakes may be related to the photosynthetically influenced seasonal and diurnal fluctuations in Nescochague Lake pH. The periodic lowering of pH to near that found in Oswego Lake can be viewed as a filter that allows only acid tolerant species to survive. A similar effect of fluctuating photosynthetically elevated pH was reported by O'Brien & de'Noyelles (1972), except in that case, photosynthesis raised the pH so high that non-alkaline tolerant species could not survive. Consequently, in these and other poorly buffered and productive waters, the pH measured in routine sampling and the ecologically effective pH may be quite different.

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References

American Public Health Association, 1980. Standard methods for the examination of water or wastewater. 15th Edn A.P.H.A., Inc., N.Y. 1193 pp.

Brewer, P. G. & J. C. Goldman, 1976. Alkalinity changes generated by phytoplankton growth. Limnol. Oceanogr. 21: 108-117.

Calvayrac, R., J. L. Bomsel & L. M. Danielle, 1979. Analysis and characterization of 3-(3,4-Dichlorophenyl)-1, 1-Dimethylurea (DCMU)-resistant *Euglena*. Pl. Physiol. 63: 857-865.

Crerar, D. A., J. L. Means, R. F. Yuretich, M. P. Borcsik, J. L. Amster, D. W. Hastings, G. W. Knox, K. E. Lyon & R. F. Quiett, 1981. Hydrogeochemistry of the New Jersey Coastal Plain 2. Transport and deposition of iron, aluminium, dissolved organic matter, and selected trace elements in stream, ground- and estuary water. Chem. Geol. 33: 23-44.

Faust, S., 1983. Total alkalinity versus buffer value (capacity) as a sensitive indicator for fresh waters receiving acid rain. J. envir. Sci. Hlth A18: 701-711.

Forman, R. T. T. (ed.), 1979. Pine Barrens: Ecosystem and landscape. Academic Press, N.Y., 601 pp.

Goldman, J. C. & P. G. Brewer, 1980. Effect of nitrogen source and growth rate on phytoplankton mediated changes in alkalinity. Limnol. Oceanogr. 25: 352-357.

Haines, T. A., 1981. Acidic precipitation and its consequences for aquatic ecosystems: A review. Trans. am. Fish. Soc. 111: 669-707.

Kelley, C. A., J. W. M. Rudd, R. B. Cook & D. W. Schindler, 1982. The potential importance of bacterial processes in regulating rate of lake acidification. Limnol. Oceanogr. 27: 868-882.

Krug, E. C. & C. R. Frink, 1983. Acid rain on acid soils: A new perspective. Science 221: 520-525.

Morgan, M. D., 1984. Acidification of headwater streams in the New Jersey Pinelands: A reevaluation. Limnol. Oceanogr. 29: 1259-1266.

Morgan, M. D., 1983. Impact of changing acidity on the trophic dynamics of Pine Barrens plankton communities. Cent. Cst. Envir. Stud., Rutgers Univ., 38 pp.

National Research Council Canada, 1981. Acidification in the Canadian Aquatic Environment. Natn. Res. Coun. Can, Publ. 18475, 369 pp.

O'Brien, W. J. & F. deNoyelles, Jr. 1972. Photosynthetically elevated pH as a factor in zooplankton mortality in nutrient enriched ponds. Ecology 53: 605-614.

Oliver, G. G. & J. R. M. Kelso, 1983. A role of sediments in retarding the acidification of headwater lakes. Wat. Air Soil Pollut. 20: 379-389.

Pinelands Commission, 1980. New Jersey Pinelands comprehensive management plan. N. Jersey Pinelands Comm., New Lisbon, N.J., 446 pp.

Rhodehamel, E. C., 1979. Hydrology of the New Jersey Pine Barrens. In R. T. T. Forman (ed.), Pine Barrens: Ecosystem and landscape. Academic Press, N.Y.: 147-167.

Schindler, D., R. Wagemann, R. Cook, T. Ruszczynski & J. Prokopowich, 1980. Experimental acidification of Lake 223, Experimental Lakes Area: Background data and the first three years of acidification. Can J. Fish. aquat. Sci. 37: 342-354.

Singer, P. C. & W. Stumm, 1970. Acidic mine drainage: The rate determining step. Science 167: 1121-1123.

Stumm, W. & J. J. Morgan, 1981. Aquatic Chemistry. Wiley-Interscience, N.Y. 780 pp.

Talling, J. E., 1976. The depletion of carbon dioxide from lakewater by photosynthesis. J. Ecol. 64: 79-121.

Tedrow, J. C. F., 1979. Development of Pine Barrens Soils. In R. T. T. Forman (ed.), Pine Barrens: Ecosystem and landscape. Academic Press, N.Y.: 61-79.

Zimmerman, A. P. & H. H. Harvey, 1979. Sensitivity to acidification of waters of Ontario and neighboring states. Final Rep. Ont. Hydro, Univ. Toronto, 118 pp.

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