

The influence of whole lake aeration on the limnology of a hypereutrophic lake in central Florida

Bruce C. Cowell, Clinton J. Dawes, William E. Gardiner & Sandra M. Sceda
Department of Biology, University of South Florida, Tampa, FL 33620, USA

Keywords: lake restoration, artificial destratification, limnology, subtropical lake

Abstract

To determine the influence of a multiple inversion aeration system upon the limnology of a small sinkhole lake, we monitored physical-chemical and biological parameters for 15 months prior to starting aeration and for 24 months thereafter. Aeration eliminated thermal stratification and dissolved oxygen concentrations of bottom waters increased significantly. Secchi disk transparency increased during aeration while turbidity, pH, alkalinity, total nitrogen, hydrogen sulfide and iron concentrations decreased significantly. Primary production and mean chlorophyll *a* did not change significantly during aeration but total phytoplankton cell volume decreased 2-fold. This decrease was caused by a marked reduction in blue-green algae which appears to be attributable to rapid mixing of the lake and to decreases in the pH. Cell volumes of green algae remained constant but numbers of taxa increased 70%. Densities of crustacean zooplankton were reduced markedly by aeration while densities of rotifers increased significantly during the first year but then returned to pre-aeration levels during the second year. Large-bodied cladocerans were replaced by small-bodied forms during aeration, and copepod populations became dominated by nauplii (97%). Densities of benthic macroinvertebrates declined 2-fold during aeration due to a marked reduction (10-fold) in the *Chaoborus* population which correlated strongly with decreases in crustacean zooplankton abundance. The total number of taxa collected on individual sample dates increased throughout the two year aeration period (from 12 to 25) and chironomids became the predominant group (70%).

The multiple inversion aeration system successfully eliminated many of the undesirable features of eutrophication (e.g., oxygen depletion, blue-green algal blooms, low benthic diversity), but it did not change the trophic state. Aeration of hypereutrophic lakes for multiple years may be necessary to maintain desired conditions.

Introduction

Many lakes throughout the world are undergoing accelerated aging or eutrophication due to man's activities (Dunst *et al.*, 1974). This includes the influences of agricultural, industrial and domestic pollution which lead to deteriorating water quality, phytoplankton blooms, oxygen deficits, fish kills, and sediment infilling. In recent years, limnologists have attempted to reverse eutrophication with lake restoration methods which limit fertility and sedimentation or attempt to control the consequences of eutrophication.

A variety of lake restoration techniques have been utilized: 1) curbing nutrient influx, 2) in-lake schemes to accelerate nutrient outflow or prevent recycling, and 3) lake management programs of chemical controls, aeration, dredging, sediment consolidation and other habitat manipulations (Dunst *et al.*, 1974). However, lake restoration techniques are in an early stage of development and there is need for detailed studies on a variety of lake types and geographic locations.

Typically, aeration is used to eliminate thermal stratification and density barriers by increasing circulation within the lake. This produces oxygenation

of bottom waters and leads to general increases in the rates of decomposition of bottom sediment and organic matter in the water column, and to reductions in the concentrations of reduced forms of iron, manganese, nitrogen, and sulfur (see Toetz *et al.*, 1972; Smith *et al.*, 1975; and Pastorok *et al.*, 1980). The increase in oxygen in bottom waters and the subsequent changes in redox reactions involving metals (iron, manganese and aluminum) also may partly determine the availability of nitrogen and phosphorus by regulating release from profundal sediments (Mortimer, 1941, 1942; Holdren & Armstrong, 1980).

The effects of aeration on biotic communities are not well documented, probably because of the lack of thoroughness of many of the previous studies. Dunst *et al.* (1974) stated that there is serious need for additional, thorough studies of the responses of phytoplankton, zooplankton and other fauna to aeration. However, a recent review by Pastorok *et al.* (1980) and a predictive model by Forsberg & Shapiro (1980) have characterized the responses of phytoplankton communities to aeration as being highly variable and attributable to multiple factors.

Our objective was to make a detailed study of the effect of a multiple inversion aeration system on the limnology of Lake Brooker, Florida, and to determine the potential of aeration for management and restoration of small, eutrophic lakes in the Tampa Bay area. We conducted: 1) a 15 month analysis of physical, chemical and biological properties of the lake prior to installation of the aeration system, and 2) a 2 year analysis of the same parameters during aeration.

Description of study area

Lake Brooker is located in northwest Hillsborough County, Florida (28°10'N Lat., 82°28'W Long.). It has a surface area of 10.5 ha and is composed of two sinkhole basins; the north basin is approximately 8 ha and the south basin is approximately 2.5 ha (Fig. 1). The mean depth is 4.0 m and maximum depth is 5.2 m. Below 3 m in depth, the bottom sediment is comprised principally of small-grained sand (<63 μm), silt and organic matter; above this depth larger-grained sand particles predominate. There are no aquatic macrophytes, because of the absence of a shallow littoral zone

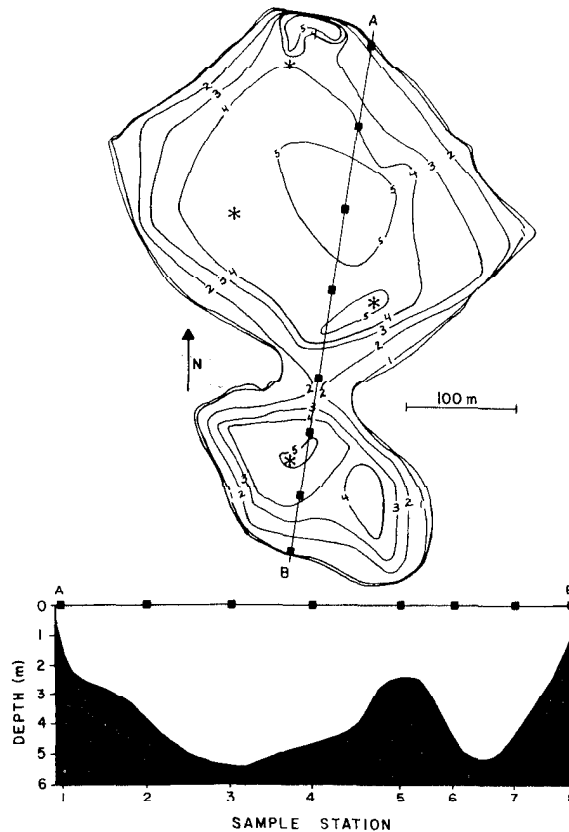


Fig. 1. Map of Lake Brooker, Florida showing locations of ceramic diffuser heads (*), benthic sampling stations (■), and a cross section profile. The vertical scale on the cross section profile is exaggerated.

(Fig. 1) and comparatively low transparency.

A small runoff ditch enters the lake along the northeast shoreline. During years of normal rainfall (approximately 131 cm yr⁻¹), runoff from the ditch is present only during the rainy season (May-October). Influx of nutrients and organic matter from a dairy feed lot in the late 1960's and early 1970's caused the lake to become hypereutrophic. In 1978, court action by local property owners terminated the dairy farm and its inflow, but runoff from former pastures still occurs after heavy rains.

Methods

A Clean-Flo Laboratories (4342 Shady Oak Road, Hopkins, MN 55343) multiple inversion aer-

ation system (Laing, 1974, 1979; Laing & Adams, 1975) was installed in Lake Brooker on 11 June 1981. This system is powered by four 0.5 hp pumps and has four ceramic diffuser heads located on the bottom at selected stations in deep water (see Fig. 1); three of the diffusers are in the north basin and one is in the south basin. The bubbles generated by this system can move between 1 800 000 and 2 700 000 liters of water, from the bottom to the surface, per hour (R. L. Laing, person. comm.). This is enough displacement to completely circulate the volume of Lake Brooker in 6 to 7 days.

Biweekly sampling was conducted from 19 March 1980 through 8 June 1981 to determine pre-aeration conditions and from 22 June 1981 through 8 June 1983 to monitor changes during aeration. All sampling was conducted during the morning hours to minimize the influence of time of collection.

At each sampling 17 chemical, 7 physical and 4 biological variables were measured. Water samples for most variables were composites, collected with a 4.2 l nonmetallic Kemmerer water bottle, from 2 deep water stations (> 5 m) located at opposite ends of the lake. Samples for all parameters except dissolved oxygen, carbon dioxide and hydrogen sulfide were collected at 1.5 m intervals from the surface to 3.0 m during pre-aeration and from the surface to 4.5 m during aeration; 4.5 m samples were collected for the above exceptions during pre-aeration. All water samples were placed on ice for transport to the laboratory and chemical samples were preserved in the field using EPA approved preservatives. Samples were analyzed within 24 h of collection or were stored in a cold room for a period not exceeding EPA recommended holding times (U.S. EPA, 1982).

Physical-chemical parameters

Water temperature and conductivity were measured at 1 m intervals using a Tri-R electric thermometer and a Beckman RB3-338 conductivity bridge. Light penetration was measured with a T.S.K. submarine illuminance meter and a Secchi disk. Turbidity was determined with a Hach 2100-A turbidimeter using nephelometric calibration (U.S. EPA, 1979). True color and apparent color were determined on a Hach DR/2 spectrophotometer. Hydrogen-ion concentration was determined with a

Corning Model 10, expanded scale pH meter. Dissolved oxygen concentrations were determined using the azide modification of the Winkler method (A.P.H.A., 1975). Alkalinity was determined by titrating with 0.02 N H₂SO₄ using phenolphthalein and methyl orange or bromocresol green indicators (A.P.H.A., 1975). Carbon dioxide concentrations were determined using a titrimetric method and 0.0454 N Na₂CO₃ prepared daily with carbon dioxide-free distilled water; phenolphthalein indicator was used (A.P.H.A., 1975).

Nutrient determinations were made using a Technicon AutoAnalyzer II and methodology outlined by the U.S. EPA (1979). Total Kjeldahl nitrogen was measured, after digestion with a Technicon BD-40 block digester, using the ammonia-salicylate complex method of McDaniel *et al.* (1967). Ammonium was determined using the same method. Nitrate+nitrite was analyzed using methodology described by Armstrong *et al.* (1967). Total phosphorus was determined after digestion using the Murphy & Riley (1962) phosphomolybdate blue modification and soluble reactive phosphorus was determined using a Technicon modification of this method. Silicate was determined with the colorimetric molybdosilicate method (A.P.H.A., 1975). Sulfate was measured with the methylthymol blue method utilizing an ion exchange column to remove interference from multivalent cations (see Lazarus *et al.* 1965).

A Perkin Elmer, Model 2280, atomic absorption spectrophotometer was used to determine concentrations of Fe, Mg, K, Na and Ca. Analysis procedures were modified from Fishman & Downs (1966). Samples for iron analyses received 4 ml of lanthanum oxide (50 g l⁻¹) per 100 ml of sample; 2 ml per 100 ml were used for other metals to suppress background interference.

Primary production

Primary production was determined at two month intervals using the oxygen light and dark bottle method. Water samples were collected from 0, 0.5, 1, 2, 3 and 4 m depths. Two replicates of light and dark bottles were prepared and samples for determining initial dissolved oxygen concentration and phytoplankton standing crop also were collected. Dissolved oxygen was determined with the azide modification of the Winkler method

(A.P.H.A., 1975), and conversion of mg oxygen evolved (mg l^{-1}) to carbon fixed (mg l^{-1}) was made using the formulae of Strickland & Parsons (1968) and a photosynthetic quotient of 1.25 (Ryther, 1956).

Chlorophyll a and phytoplankton

Chlorophyll *a* determinations were made using the method of Lorenzen (1967) and several of the modifications suggested by Holm-Hansen (1978). Under dim light, samples were mixed thoroughly and subsamples were filtered through glass fiber filter papers (Whatman GF/C). Filters were ground for 2 min in 2 ml of 90% reagent grade acetone, diluted to 10 ml with acetone, and placed in darkness for 2 h at room temperature. Following centrifugation, supernatant absorbances were read on a Gilford 250 spectrophotometer at 665 and 750 nm wavelengths, before and after acidification with 0.3 N HCl and subsequent neutralization with 250 mg of MgCO_3 .

Subsamples from the chlorophyll *a* samples also were used to determine the taxonomic composition and standing crops of phytoplankton. Live samples were examined under an inverted microscope to determine species compositions and samples preserved with modified Lugol's solution (Edmondson, 1959) were used to determine standing crops. Standing crops were measured using a modification of the Utermohl sedimentation technique and an inverted microscope (Hudson & Cowell, 1966), and were expressed as volume per liter ($\mu\text{l l}^{-1}$) using the techniques of Verduin (1960) and Cowell (1960).

Trophic states

Trophic state indices (TSI's) were calculated using the Baker *et al.* (1981) modification of Carlson's (1977) method. This procedure uses four separate univariate indices of trophic state (Secchi disk transparency, total phosphorus, total nitrogen and chlorophyll *a*) and an average value, combining the major physical, chemical and biological variables, is used for comparative and management purposes. For Florida lakes, Baker *et al.* (1981) recommended that the lesser value of the TSI's for total nitrogen and total phosphorus be averaged with the corresponding indices for Secchi disk and chlorophyll *a*.

Zooplankton

Rotifers and copepod nauplii were collected at 1.5 m depth intervals, from the surface to the bottom, with an 8.7 l Schindler-Patalas rotifer trap fitted with a 28 μm net. Samples were preserved with a 10% sugar-formalin solution (Haney & Hall, 1973) containing rose bengal stain. In the laboratory each sample was concentrated to 15 ml, mixed thoroughly, and a 1 ml subsample was placed in a Sedgwick-Rafter cell. All rotifers in 25, 50 or 100 haphazardly selected fields, depending upon density, were counted and identified under 40 \times magnification. After completing the rotifer count, the total number of copepod nauplii in the cell was determined with a dissecting microscope. The sample then was replaced in the concentrate, a new sample was withdrawn, and the procedure was repeated. If variability between the two counts was large, additional subsamples were counted.

Crustacean zooplankton were collected with a high-speed Miller sampler (Miller, 1961) equipped with a flowmeter and a 158 μm net. An oblique tow was made beginning approximately 1 m off the bottom and ascending at 1 m intervals every 30 seconds; each tow filtered approximately 1000 to 2000 l of water and covered a distance of 250–400 m. Samples were preserved in 10% sugar-formalin solution with rose bengal stain. In the laboratory samples were diluted to a known volume and two replicate subsamples were counted in a modified rotary chamber (Ward, 1955). Subsample size was considered adequate when 150 individuals (excluding copepod nauplii) had been counted and identified. Additional replicates were counted if subsample variability was large.

Benthos

A transect with eight sample stations was established in Lake Brooker (see Fig. 1). Samples were collected, bimonthly from May 1980 through May 1983, with a 232 cm^2 Ekman dredge. The samples were sieved with a 23.6 mesh/cm (234 μm openings) screen and were preserved with 10% formalin-rose bengal mixture (Mason & Yevich, 1967). First and second instars of small species of Chironomidae are not retained by this sieve. However, in a previous study (Cowell & Vodopich, 1981) we noted that excluding these early instars did not change species composition or relative abundance of each species; only absolute densities were affected.

Organisms were separated from sediment and detritus by flotation in sugar solution of 1.12 sp. gr. (Anderson, 1959). Organisms which did not float or which became trapped in organic materials were picked by examining the bottom of the picking dish, under $7\times$ magnification, after decanting most of the sugar solution. The efficiency of this procedure has been validated (Cowell, 1984). All organisms were preserved in 70% ethanol. Slides and identification of larval chironomids were made using the keys and techniques of Beck (1975, 1976). Other organisms were identified with keys of Penak (1978), Merrit & Cummins (1978) and Usinger (1963).

Statistical analyses

We used the SAS (Statistical Analysis System) computer software system and an IBM 3033 computer for data analyses. The Burr-Foster Q test (Anderson & McLean, 1974) was used to check for homogeneity of variances before conducting analyses of variance (ANOVA's) and transformations were used to satisfy normality assumptions. Most chemical data and phytoplankton cell volumes were assumed to be normally distributed but numbers of zooplankton and benthic organisms were transformed using $\ln(Y+1)$. Student-Newman-Keuls' test, which protects against Type I errors, was used for comparisons of annual means between sample depths and for multiple comparisons between pre-aeration (year 1) and during aeration (years 2 and 3) means. Nonparametric statistics were used if satisfaction of assumptions was questionable.

Results

Vertical distributions of physical-chemical parameters

During the 15 month period before the aeration system was installed only 4 of the physical-chemical variables (temperature, dissolved oxygen, carbon dioxide and hydrogen sulfide) showed significant vertical stratification ($p < 0.05$). In the warmer months (March-November) thermal stratification and clinograde dissolved oxygen profiles were common, but in winter (December-February) windy conditions caused homothermal conditions and or-

thograde dissolved oxygen profiles. Temperature differences, from surface to the bottom, ranged from $4-5^{\circ}\text{C}$ during the spring and fall, and from $8-10^{\circ}\text{C}$ during the summer; winter differences ranged between $0-1^{\circ}\text{C}$. Dissolved oxygen concentrations usually exceeded 100% saturation at the surface but concentrations near the bottom (4.5 m) were close to 0 mg l^{-1} at all times of the year except winter when they generally were $>4\text{ mg l}^{-1}$. Carbon dioxide and hydrogen sulfide concentrations were significantly greater at the 4.5 m sample depth in all seasons except winter and differences were greatest, ranging from 1 to 2 orders of magnitude, during the summer.

During the first year of aeration there were no significant differences between depths for any of the physical-chemical parameters. The second year of aeration showed vertical patterns similar to the first year except for dissolved oxygen and iron concentrations. Dissolved oxygen showed minor stratification during the summer (1982) and spring (1983) but both were caused by malfunctions of one of the 0.5 hp pumps; when the pump was fixed, stratification was eliminated. Mean iron concentration at the surface (0.132 mg l^{-1}) was significantly lower ($p < 0.05$) than at other depths (1.5 m = 0.154, 3.0 m = 0.168 and 4.5 m = 0.182 mg l^{-1}).

Influence of aeration on physical-chemical parameters

Because so few of the physical-chemical parameters showed significant vertical stratification, daily means will be presented to show the influence of aeration on each parameter except dissolved oxygen; both surface and 4.5 m oxygen profiles will be presented. Table 1 gives the annual means (for all depths) for 22 physical-chemical variables and shows statistical comparisons between years. Year 1, which actually represents 15 months of pre-aeration data, is compared with years 2 and 3 to assess the impact of aeration.

Aeration produced profound changes in only a few physical-chemical factors, dissolved oxygen and Secchi disk transparency increased ($p < 0.05$) and turbidity, pH, alkalinity, total nitrogen, hydrogen sulfide and iron concentrations decreased ($p < 0.05$). Other parameters (carbon dioxide, conductivity, nitrate + nitrite, total phosphorus, soluble reactive phosphorus, calcium, sodium and mag-

nesium) showed significant change during the first year of aeration but returned to pre-aeration levels during the second year.

Aeration, other than breaking up thermal stratification, had little effect on seasonal temperature patterns. Maximum temperatures for each year were between 30 and 32°C and usually occurred in July. Minimum values of 10–14°C occurred in January. Annual means ranged from 23.2 to 24.7°C and the average temperature for the entire 39 months of the study was 23.7°C.

Aeration had marked influence on the dissolved oxygen concentrations (Fig. 2). During pre-aeration surface concentrations ranged from 5.5 to 15 mg l⁻¹ with peaks often being associated with high densities of phytoplankton. Concentrations at the 4.5 m sample depth were low, usually between 0 and 4.0 mg l⁻¹, during periods of thermal stratification (March–October), and were higher, usually >4.0 mg l⁻¹, during winter homothermy. Differences in dissolved oxygen concentrations, between the surface and 4.5 m, decreased markedly commensurate with the start of aeration, and concentrations at both depths were equivalent throughout the remainder of the study, except during periods of equipment failure (Fig. 2).

Aeration produced an increase in Secchi disk transparency and a decrease in turbidity (Table 1). Mean transparency for the pre-aeration year was

0.91 m and during aeration (2 years) it was 1.11 m. Turbidity decreased 58%, pre-aeration and during-aeration means were 5.2 and 3.0 NTU's respectively. Variability in Secchi disk transparency and turbidity also decreased with aeration. Standard errors for both parameters were reduced over the course of the study (Table 1), and because differences in sample sizes between years were small, these reductions reflect similar changes in both ranges and standard deviations. The changes in transparency and turbidity appear to be associated with changes in phytoplankton standing crops (autochthonous turbidity, see Phytoplankton section).

Variability and peak concentrations of both apparent and true color were greater in years 1 and 2 than in year 3, but the annual means for year 3 were significantly higher ($p < 0.05$) than those for years 1 and 2 (Table 1). Additional comparisons of the ratios of apparent to true color showed a decrease with time; the ratios for years 1, 2 and 3 were 2.47, 2.04 and 1.44 respectively. These changes appear to be indicative of reductions in autochthonous turbidity (phytoplankton cell volumes) within the lake and to increases in true color from inflow contributions.

The pH of Lake Brooker declined steadily following installation of the aeration system (Table 1). During the pre-aeration year (year 1) daily mean pH ranged from 5.6–9.4 and peak values often

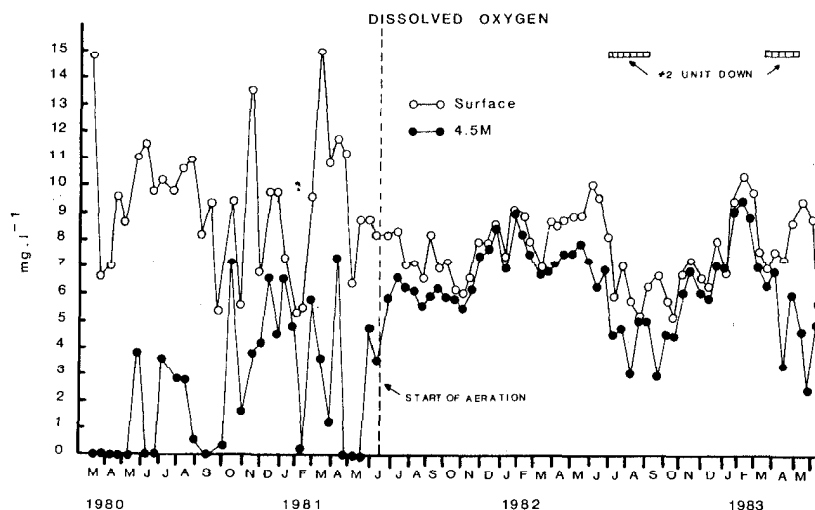


Fig. 2. Dissolved oxygen concentrations at the surface and 4.5 m sample depths in Lake Brooker, Florida during three years of a lake aeration study. Start of aeration is indicated by a vertical line.

Table 1. Chemical characteristics of a small, hypereutrophic Florida lake during three years of a lake aeration study. Year 1 represents 15 months of pre-aeration data and years 2 and 3 represent during aeration. Concentrations are expressed as annual means (for all sampling depths) \pm 1 standard error, and numbers of sample dates are indicated in parentheses. Statistical comparisons between years, using Student-Newman-Keuls' Test, also are given; years underscored by the same line are not significantly different.

Variable	Year 1 3/80 – 5/81	Year 2 6/81 – 5/82	Year 3 6/82 – 6/83	Ranking of means by year and significance of SNK Test	
				high	low
Secchi Disk Transparency (m)	0.91 \pm 0.06 (32)	1.16 \pm 0.05 (26)	1.06 \pm 0.03 (27)	<u>2</u>	<u>3</u> 1
Turbidity (NTU)	5.2 \pm 0.6 (32)	3.2 \pm 0.2 (25)	2.8 \pm 0.1 (27)	<u>1</u>	<u>2</u> 3
Apparent Color (Pt-Co Units)	70.6 \pm 4.6 (32)	64.6 \pm 5.6 (26)	86.6 \pm 2.8 (27)	3	<u>1</u> <u>2</u>
True Color (Pt-Co Units)	28.6 \pm 3.7 (32)	31.7 \pm 4.1 (26)	60.2 \pm 3.1 (27)	3	<u>2</u> <u>1</u>
pH	7.40 \pm 0.17 (30)	6.84 \pm 0.05 (26)	6.55 \pm 0.06 (27)	1	<u>2</u> <u>3</u>
Alkalinity (mg l ⁻¹ CaCO ₃)	37.4 \pm 1.1 (32)	22.5 \pm 2.3 (26)	12.9 \pm 0.2 (27)	1	<u>2</u> <u>3</u>
Carbon dioxide (mg l ⁻¹)	8.47 \pm 0.97 (27)	3.63 \pm 0.33 (26)	7.37 \pm 0.70 (27)	<u>1</u>	<u>3</u> <u>2</u>
Conductivity (μ S cm ⁻¹)	170.4 \pm 3.5 (25)	205.6 \pm 2.9 (26)	170.0 \pm 3.1 (27)	2	<u>1</u> <u>3</u>
Total Nitrogen (mg l ⁻¹)	1.63 \pm 0.08 (32)	1.22 \pm 0.03 (26)	1.15 \pm 0.04 (27)	1	<u>2</u> <u>3</u>
Nitrate + Nitrite (μ g l ⁻¹)	7 \pm 1 (32)	17 \pm 5 (25)	2 \pm 1 (27)	2	<u>1</u> <u>3</u>
Ammonium (μ g l ⁻¹)	407 \pm 52 (32)	372 \pm 41 (26)	291 \pm 32 (27)	<u>1</u>	<u>2</u> <u>3</u>
Total Phosphorus (mg l ⁻¹)	0.24 \pm 0.04 (32)	0.06 \pm 0.01 (26)	0.23 \pm 0.01 (27)	<u>1</u>	<u>3</u> <u>2</u>
Soluble Reactive Phosphorus (μ g l ⁻¹)	34 \pm 4 (32)	17 \pm 2 (26)	46 \pm 5 (27)	3	<u>1</u> <u>2</u>
TN to TP ratio ¹	6.89	21.02	5.09		
Silicate (mg l ⁻¹)	0.88 \pm 0.09 (31)	0.68 \pm 0.10 (25)	0.69 \pm 0.07 (24)	<u>1</u>	<u>3</u> <u>2</u>
Sulfate (mg l ⁻¹)	26.53 \pm 0.89 (31)	34.77 \pm 1.09 (25)	22.74 \pm 1.30 (24)	2	<u>1</u> <u>3</u>
Hydrogen sulfide (mg l ⁻¹)	0.176 \pm 0.069 (24)	0.026 \pm 0.002 (26)	0.022 \pm 0.001 (26)	1	<u>2</u> <u>3</u>
Iron (mg l ⁻¹)	0.32 \pm 0.05 (32)	0.14 \pm 0.03 (26)	0.16 \pm 0.01 (27)	1	<u>3</u> <u>2</u>
Potassium (mg l ⁻¹)	6.72 \pm 0.25 (32)	7.01 \pm 0.04 (26)	5.70 \pm 0.15 (27)	2	<u>1</u> <u>3</u>
Calcium (mg l ⁻¹)	11.10 \pm 0.40 (32)	12.06 \pm 0.20 (26)	10.17 \pm 0.33 (27)	2	<u>1</u> <u>3</u>
Sodium (mg l ⁻¹)	6.62 \pm 0.22 (32)	8.14 \pm 0.29 (26)	7.08 \pm 0.13 (27)	2	<u>3</u> <u>1</u>
Magnesium (mg l ⁻¹)	3.54 \pm 0.08 (32)	4.51 \pm 0.09 (26)	3.29 \pm 0.10 (27)	2	<u>1</u> <u>3</u>

¹ Total Nitrogen to Total Phosphorus ratios were computed using annual mean concentrations.

were associated with phytoplankton blooms. This variability was reduced after aeration started (range = 5.7–7.3) and the annual mean pH decreased significantly ($p < 0.05$) from 7.40 during pre-aeration to 6.55 during the second year of aeration. Alkalinity also declined significantly ($p < 0.05$) over the course of the study (Table 1).

Concentrations of free carbon dioxide in Lake Brooker were low, generally less than 15 mg l⁻¹. Aeration caused a significant decrease ($p < 0.05$) in carbon dioxide during year 2; daily mean concentrations averaged 3.63 mg l⁻¹ and were 2-fold lower than in year 1 (Table 1). The mean carbon dioxide concentration increased significantly ($p < 0.05$) during year 3 (years 1 and 3 were not significantly different), but this increase appears to be associated with aeration equipment failures (July-

September 1982 and March-May 1983).

Mean conductivity of Lake Brooker ranged from 125–230 μ S cm⁻¹ and averaged 182 μ S cm⁻¹. The annual mean for year 2 was significantly higher ($p < 0.05$) than the means for years 1 or 3 (Table 1). Conductivity increased markedly from September 1980 to May 1982, and subsequently decreased in the latter part of 1982 and 1983. These changes correlated positively ($r > 0.80$) with changes in sulfate and magnesium concentrations.

Aeration produced a 25–30% decrease in total nitrogen concentrations (Table 1). Most of the decrease was attributable to a decline in organic nitrogen (presumably phytoplankton) since concentrations of the inorganic nitrogen compounds were either comparable or statistically higher ($p < 0.05$) during the aeration years. Total nitrogen during the

pre-aeration year (year 1) ranged from 0.8–2.75 mg l⁻¹ and averaged 1.63 mg l⁻¹. Variability was less during aeration ranging from 0.6–1.6 mg l⁻¹ and mean concentrations were 1.22 and 1.15 mg l⁻¹ during years 2 and 3 respectively. Large variability in ammonium concentrations with depth caused differences between years to be nonsignificant ($p > 0.05$), but there was a trend toward progressively lower mean concentrations following the start of aeration (Table 1). The mean concentration of nitrate+nitrite for year 2, 17 $\mu\text{g l}^{-1}$, was significantly greater ($p < 0.05$) than that for year 1, 7 $\mu\text{g l}^{-1}$, but year 3, 2 $\mu\text{g l}^{-1}$, was not different from the pre-aeration mean (Table 1).

Total phosphorus and soluble reactive phosphorus (SRP) concentrations showed great variability with depth and over the course of the study. During pre-aeration daily mean concentrations of total phosphorus ranged from 0.80 to 0.024 mg l⁻¹ and the annual mean was 0.24 mg l⁻¹ (Table 1). Concentrations remained low during the first year of aeration (year 2), ranging from 0.003–0.138 mg l⁻¹, and the annual mean for year 2 (0.06 mg l⁻¹) was significantly lower ($p < 0.05$) than that of year 1; most of the depth variability disappeared also. Values in year 3 showed a steady increase (ranging from 0.012 mg l⁻¹ in June 1982 to 0.35 mg l⁻¹ in April 1983) and the annual mean (0.23 mg l⁻¹) was not different ($p > 0.05$) from year 1. Daily mean concentrations of soluble reactive phosphorus during pre-aeration ranged from 2–115 $\mu\text{g l}^{-1}$ and the annual mean was 34 $\mu\text{g l}^{-1}$. Concentrations declined steadily during year 2 and the annual mean (17 $\mu\text{g l}^{-1}$) was significantly lower than that of year 1. SRP concentrations increased markedly in year 3 and the annual mean of 46 $\mu\text{g l}^{-1}$ was significantly greater ($p < 0.05$) than the means for years 1 or 2.

Based on annual means, total nitrogen to total phosphorus ratios (TN/TP) for Lake Brooker were low, indicative of eutrophic conditions (Table 1). But ratios for individual sample dates showed marked variability between years. TN/TP ratios were less than 30 on all but four dates during year 1. During the first year of aeration (year 2) TN/TP showed peaks ranging from 50 to 470 which were attributable to low total phosphorus concentrations; the annual mean was 21.02. In year 3, TN/TP ratios decreased and the annual mean of 5.09 was similar to that for year 1 (6.89).

There were no significant differences ($p > 0.05$) in silicate concentrations between years (Table 1). Peak concentrations ($> 1.0 \text{ mg l}^{-1}$) tended to occur in the early spring (March–April) and/or summer and fall (July–November), and low concentrations ($< 0.2 \text{ mg l}^{-1}$) usually occurred in the winter (January) and/or late spring (May).

Sulfate concentrations were significantly different ($p < 0.05$) for all years of the study (Table 1). There was a steady increase in the daily mean sulfate concentration from March 1980 to July 1982; concentrations doubled from approximately 20 to 40 mg l⁻¹. This was followed by two periods (July–November, 1982 and February–May, 1983) of decreasing concentrations which occurred during periods of high rainfall; 100.8 cm for the first interval and 55.5 cm for the second.

Hydrogen sulfide concentrations were highly variable during year 1, ranging from 0.015–0.28 mg l⁻¹. The annual mean for pre-aeration was significantly greater ($p < 0.05$) than means during aeration (Table 1). During aeration mean concentrations (for all depths, 0–4.5 m) ranged from 0.01–0.06 mg l⁻¹; these concentrations are at or below the lower limits of sensitivity (0.05 mg l⁻¹) for the colorimetric method employed.

There was a significant reduction ($p < 0.05$) in iron concentrations following the installation of the aeration system (Table 1). During the pre-aeration year (year 1) daily mean concentrations were highly variable, ranging from 0–0.96 mg l⁻¹, but during aeration (years 2 and 3) concentrations usually were close to the lower limit of sensitivity for the atomic absorption spectrophotometric technique (0.03 mg l⁻¹).

The other cations (K, Ca, Na and Mg) did not show changes attributable to aeration. Annual mean concentrations for all four cations were highest in year 2, the first year of aeration (Table 1). Statistical comparisons of annual means for calcium, sodium and magnesium showed that concentrations during year 2 were higher ($p < 0.05$) than those of years 1 and 3. For potassium year 1 was not significantly different from year 2 ($p > 0.05$) but there was a significant decrease for year 3. Variability between depths and between dates was low for all cations.

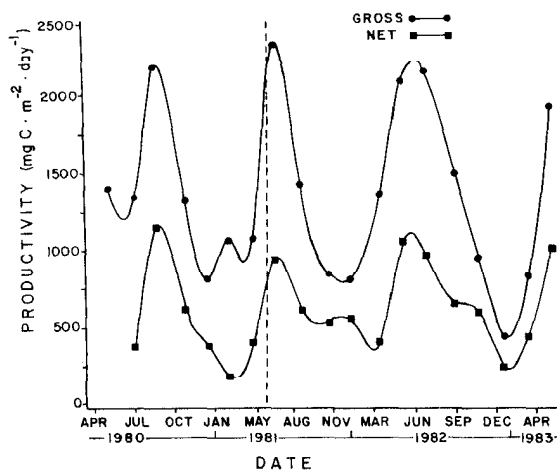


Fig. 3. Gross and net primary productivity of Lake Brooker, Florida during three years of a lake aeration study. Start of aeration is indicated by a vertical line.

Primary production

The primary productivity of Lake Brooker, on a $\text{mg C m}^{-2} \text{ day}^{-1}$ basis, was high with pronounced seasonal fluctuations (Fig. 3). Gross productivity ranged from 418 to $2349 \text{ mg C m}^{-2} \text{ day}^{-1}$ and showed peaks ($>2000 \text{ mg C m}^{-2} \text{ day}^{-1}$) during the summer and fall (July or September) and minimum values ($<1000 \text{ mg C m}^{-2} \text{ day}^{-1}$) in the winter (January). Aeration did not appear to have an

effect on productivity; annual mean productivity rates, both gross and net, were not statistically different between years ($p > 0.05$). In addition, there were no significant correlations between observed carbon assimilation rates and standing crops of phytoplankton or concentrations of major nutrients (nitrogen and phosphorus compounds) and cations (Ca, Mg, Na, K or Fe).

Vertical distribution of phytoplankton

Comparisons of the vertical distributions of chlorophyll *a*, total phytoplankton and the dominant classes (Cyanophyceae, Chlorophyceae, Cryptophyceae, Bacillariophyceae and Dinophyceae) of phytoplankton showed little variation with depth. The only significant difference among annual means was for total phytoplankton in year 3 when the surface cell volume was significantly greater ($p < 0.05$) than that at 4.5 m. No significant differences were recorded for chlorophyll *a* or for individual classes of phytoplankton (see Cowell & Dawcs, 1984). Thus, daily means of the 3 or 4 sample depths will be used in subsequent between year comparisons.

Influence of aeration on phytoplankton

There were no significant differences ($p > 0.05$) in chlorophyll *a* concentrations between years (Table 2). The only noticeable changes during aeration

Table 2. Mean chlorophyll *a* concentrations and phytoplankton cell volumes in Lake Brooker during three years of a lake aeration study. Statistical comparisons between years, using Student-Newman-Keuls' Test, are given also; years underscored by the same line are not significantly different. Year 1 represents pre-aeration and years 2 and 3 were during aeration. Numbers of sample dates are indicated in parentheses.

Phytoplankton variable or group	Annual mean \pm 1 standard error			Ranking of means by year and significance of SNK Test	
	Year 1 (32)	Year 2 (25)	Year 3 (27)	high	low
Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	53.11 ± 5.34	42.06 ± 3.66	51.78 ± 3.06	1	3 2
Total Phytoplankton ($\mu\text{l l}^{-1}$)	8.11 ± 1.11	3.87 ± 0.87	3.47 ± 0.42	1	2 3
Cyanophyceae ($\mu\text{l l}^{-1}$)	5.36 ± 1.15	0.51 ± 0.11	0.83 ± 0.15	1	3 2
Chlorophyceae ($\mu\text{l l}^{-1}$)	1.60 ± 0.36	1.53 ± 0.33	1.90 ± 0.32	3	1 2
Cryptophyceae ($\mu\text{l l}^{-1}$)	0.38 ± 0.12	0.43 ± 0.13	0.13 ± 0.04	2	1 3
Bacillariophyceae ($\mu\text{l l}^{-1}$)	0.21 ± 0.13	0.89 ± 0.61	0.15 ± 0.03	2	1 3
Dinophyceae ($\mu\text{l l}^{-1}$)	0.08 ± 0.05	0.31 ± 0.22	0.09 ± 0.03	2	3 1
Miscellaneous ¹ ($\mu\text{l l}^{-1}$)	0.48	0.20	0.37		

¹ Includes: Euglenophyceae, Chrysophyceae, Prasinophyceae and unidentifiable components. Standard errors were not calculated for this grouping.

were the elimination of peaks in excess of $100 \mu\text{g l}^{-1}$ (there were 5 such peaks in year 1 but none in years 2 or 3), and the reduction of variability (standard errors were markedly lower) between sample dates (Fig. 4, Table 2).

Total phytoplankton standing crops ($\mu\text{l l}^{-1}$) were reduced significantly ($p < 0.05$) by aeration. Mean cell volume during year 1 was more than 2-fold greater than during years 2 and 3 (Table 2). The principal cause of the reduction in total phytoplankton was a significant decrease ($p < 0.05$) in the volumes of Cyanophyceae (Table 2). Blue-green algae comprised 66% of the total cell volume

during year 1 but only 13% and 24% respectively during years 2 and 3. Peaks of heterocystic blue-green algae, during the spring and summer months of year 1, were in excess of $10 \mu\text{l l}^{-1}$ and often were monospecific in composition. During aeration peaks never exceeded $3 \mu\text{l l}^{-1}$ (Fig. 4) and species composition generally was more diverse; non-heterocystic forms occurred more frequently.

The Chlorophyceae showed no significant differences ($p > 0.05$) between years (Table 2), but percent composition increased during years 1–3 from 20% to 40% to 55% respectively of the total phytoplankton. The frequency of occurrence of taxa of Chlorophyceae also increased during aeration. Mean numbers of chlorophycean taxa per sample date, for years 1–3, were 4.6, 14.7 and 21.0 respectively. Most of these taxa (75–81%) were Chlorococcales which usually occurred with daily mean cell volumes of less than $0.1 \mu\text{l l}^{-1}$.

No significant differences between years were observed for any of the other classes of algae found in Lake Brooker (Table 2). However, there were increases in the frequencies of occurrence of some classes. Chrysophyceae and Cryptophyceae both had more frequent occurrences, at low cell volumes, during aeration while Bacillariophyceae, Dinophyceae and Euglenophyceae showed no increases. Numbers of taxa, for all classes except Chlorophyceae, remained fairly constant throughout the study. Numbers of chlorophycean taxa increased approximately 70% (from 38–65 taxa) following the start of aeration.

Trophic state indices

Annual means (see Tables 1 and 2) were used to calculate the univariate indices of trophic state. During each year of the study, total nitrogen indices were lower than total phosphorus indices so total nitrogen was used to calculate the average trophic state index (TSI). Aeration had little effect on the average TSI; values for years 1 to 3 were 64.2, 60.8 and 61.7 respectively and are indicative of eutrophic conditions.

Vertical distribution of zooplankton

Vertical distributions of rotifers and copepod nauplii showed only slight variations with depth. For rotifers, multiple contrasts between sums of

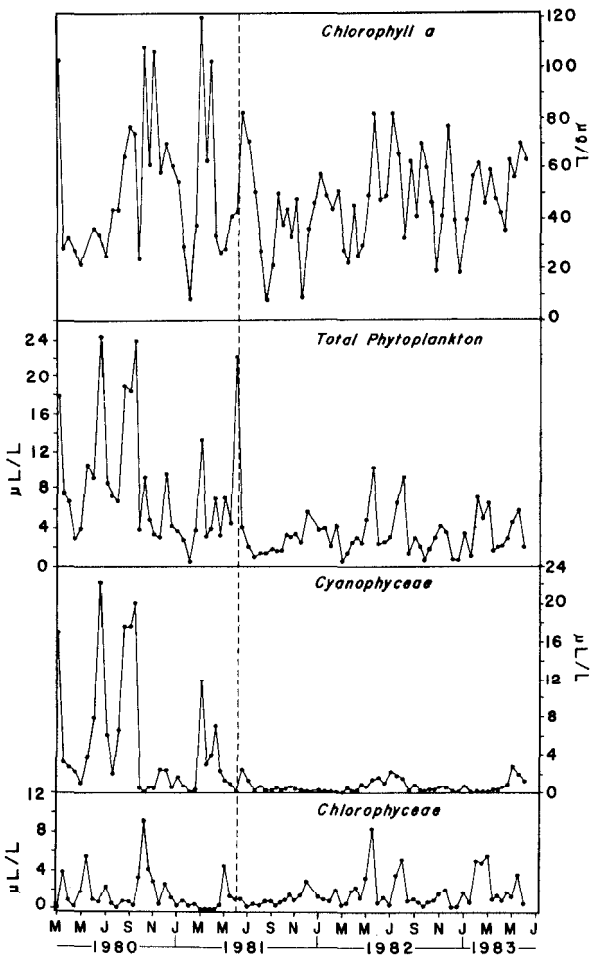


Fig. 4. Mean chlorophyll α concentrations, mean phytoplankton cell volumes and mean cell volumes of Cyanophyceae and Chlorophyceae in Lake Brooker, Florida during three years of a lake aeration study. Start of aeration is indicated by a vertical line.

ranks showed that the 3.0 m sample depth was significantly lower than those for 0 and 1.5 m during year 1, and in year 3 the 4.5 m sum of ranks was significantly different from that at 1.5 m. Copepod nauplii sums of ranks for the 1.5 and 3.0 m sample depths were significantly higher than at the surface (0 m) during year 1, and during years 2 and 3 there were less nauplii ($p < 0.05$) at 0 m than at other depths; 1.5, 3.0 and 4.5 m values were not significantly different ($p > 0.05$). Because the above comparisons only showed significant differences for one sample depth, subsequent comparisons of years are based on daily means of the 3 or 4 sample depths.

Influence of aeration on zooplankton

Aeration had profound effects on the zooplankton community. Densities of crustacean zooplankton, both Copepoda and Cladocera, declined significantly ($p < 0.01$) following the start of aeration, while densities of Rotifera increased significantly ($p < 0.05$) during year 2 but then returned to pre-aeration levels during year 3. Annual mean crustacean zooplankton densities for years 2 and 3 were 36 and 42 l^{-1} respectively, and compared to year 1, 476 l^{-1} , represent decrease of 91–92%; differences between years 2 and 3 were not significant. The decrease in total crustaceans was marked and occurred commensurate with the start of aeration (Fig. 5); on 8 June 1981, three days before the start of aeration, the density was 618 l^{-1} but it dropped to 170 l^{-1} on 22 June and to 9 l^{-1} by 8 July. Densities of total crustaceans remained low, usually less than 85 l^{-1} , for the next 22 months.

Mean densities of Copepoda, which over the three year study period comprised 64% of the crustacean zooplankton, decreased approximately 88% ($p < 0.01$) following the start of aeration (Fig. 5), but differences between the two years of aeration (years 2 and 3) were not significant. The composition of the copepod populations shifted from about equal proportions of nauplii (56.3%) and larger copepodid and adult stages (43.7%) during year 1, to one dominated by naupliar stages (97.2%) during year 3. Species composition of the Copepoda did not change with aeration.

Densities of Cladocera were high ($> 200 l^{-1}$) during the winter and spring month of year 1, but they declined markedly commensurate with the

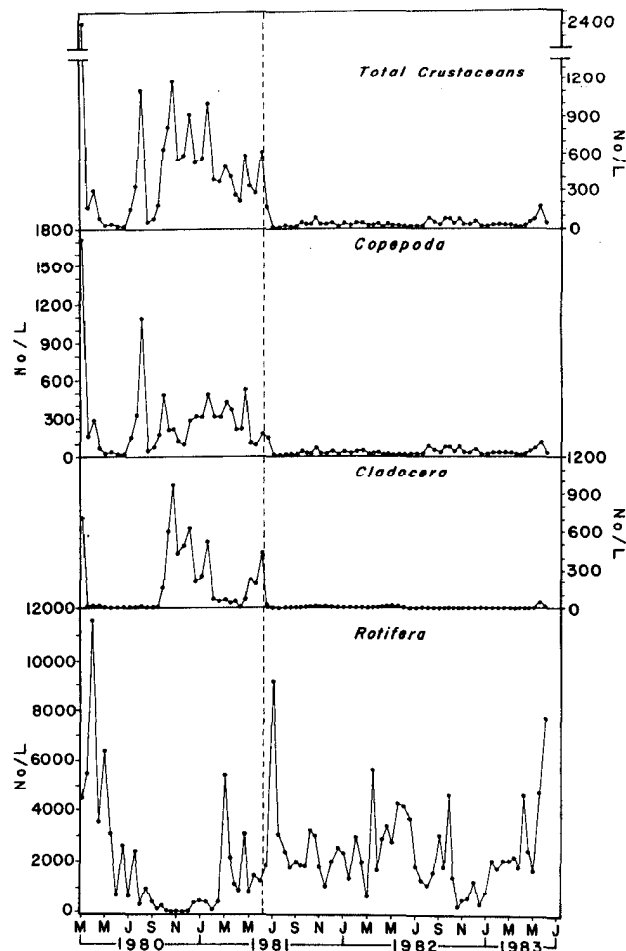


Fig. 5. Densities of total crustacean zooplankton, Copepoda, Cladocera and Rotifera in Lake Brooker, Florida during three years of a lake aeration study. Start of aeration is indicated by a vertical line.

start of aeration (Fig. 5). There was a shift in the species compositions and sizes of the predominant cladocerans between the pre-aeration (year 1) and during aeration (years 2 and 3) sampling periods. During year 1 the numerically dominant species of Cladocera (99.7%) were *Ceriodaphnia lacustris* (mean density = 127.4 l^{-1}) and *Daphnia ambigua* (61.3 l^{-1}). During aeration these species were replaced by two smaller cladocerans, *Bosmina longirostris* (3.3 l^{-1}) and *Eubosmina tubicen* (1.2 l^{-1}) which comprised 86.7% of the Cladocera (Fig. 6). Eleven more species of Cladocera were found during the course of the study, but most of these oc-

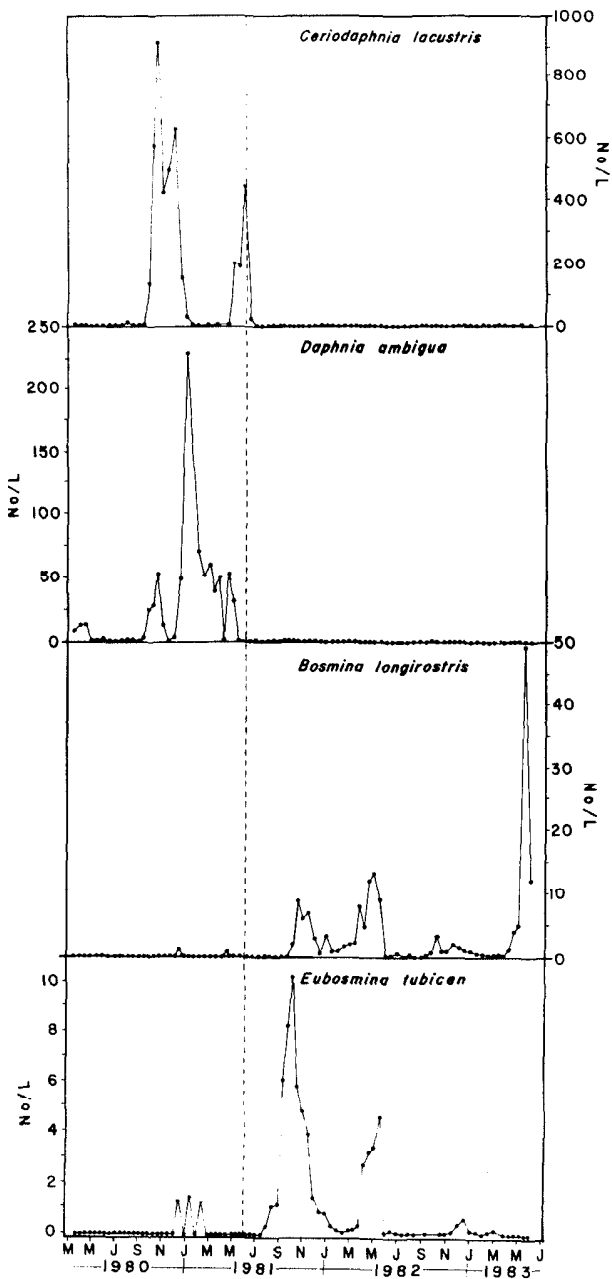


Fig. 6. Densities of four species of Cladocera in Lake Brooker, Florida during three years of a lake aeration study. Start of aeration is indicated by a vertical line.

occurred in low densities, usually $<0.1 \text{ l}^{-1}$. The number of cladoceran species increased with time, numbers of species during years 1, 2 and 3 were 7, 11 and 19 respectively.

Rotifer densities in Lake Brooker showed marked variability between sampling dates and pronounced seasonal changes (Fig. 5). During pre-aeration peak standing crops occurred in the spring ($>5000 \text{ l}^{-1}$), but densities declined through the summer and were less than 500 l^{-1} during the fall and winter months. An initial peak in rotifer density (9237 l^{-1}) occurred in July 1981 following the start of aeration, but throughout the remainder of year 2 variability was reduced and densities did not decline in the fall and winter (Fig. 5). The annual mean density for year 2 was 2714 l^{-1} and this represents a 47% increase ($p < 0.05$) compared to the year 1 mean of 1851 l^{-1} . Annual mean rotifer abundance declined 16% from year 2 to year 3. Mean density for year 3 was 2290 l^{-1} and it did not differ significantly ($p > 0.05$) from the means of years 1 or 2.

A total of 36 taxa of rotifers was found in Lake Brooker during this three year study but only 7 taxa showed significant differences ($p < 0.05$) in densities between years. Mean differences between years for the remaining 29 taxa often were large but high variances (because these taxa occurred infrequently but often at high densities) caused the comparisons to be nonsignificant. Temporal changes in the frequency of occurrence and/or abundance for the rotifer taxa showed that following the start of aeration: 1) few taxa were eliminated (*Brachionus havanaensis*, *B. havanaensis trahea*, *Cephalodella* sp. and *Kellicottia bostoniensis*); 2) a few previously unrecorded taxa occurred (e.g., *Dipleuchlanis propatula*, *Epiphanes* sp. and *Monostyla* sp.); 3) many taxa showed only small changes in densities or times of occurrence (e.g., *Conochilus unicornis*, *Hexarthra* sp., *Keratella cochlearis*, and *Polyarthra vulgaris*); and 4) some taxa showed significant increases in densities (*Anuraeopsis fissa*, *Ptygura libera*, *Synchaeta* spp. and *Trichocerca* sp.).

Influence of aeration on benthic invertebrates

Similarity analyses

Classification of site data may be used to produce discrete groups or patterns of species co-occurrence. We used Czekanowski's Quantitative Index (Field and MacFarlane, 1968), based on natural log transformed data ($\ln Y+1$), and group average clustering for normal classification. This hierarchical grouping of sites shows two groups for each

sample period (before and during aeration) which reflect depth and sediment characteristics: 1) deep (>4.0 m) stations where the substrata were comprised primarily of small-grained sand (<125 μm), silt and organic matter (Stations 2, 3, 4, 6 and 7), and 2) shallow (<2.5 m) stations with large-grained sand (>125 μm) substrata (Stations 1, 5 and 8). The deep stations showed high similarity during both sample periods. Similarity before the start of aeration was 92% and during aeration it was 81%, but the similarity of these groups of stations between sample periods was only 49%. Similarity at the shallow stations was 61% before aeration, 43% during aeration, and only 20% between sample periods. Comparisons between the two groups of stations show that the deep stations during aeration were more similar to the shallow stations before aeration. During aeration the shallow stations were markedly dissimilar from other groupings (only 20% similarity). These data indicate that aeration had profound effects upon the taxonomic composition and abundance of benthic invertebrates at each sample station.

Changes at sample stations

Fig. 7 shows the total density, in number per Ekman grab, of benthic invertebrates at each sample station over the three years of the study. Before aer-

ation densities usually were greater at the deep stations (2, 3, 4, 6 and 7), but during aeration densities were greater at the shallow stations (1, 5 and 8). Seasonal abundance before aeration was greatest in the winter when oxygen deficits in hypolimnetic waters were absent (see Physical-Chemical Results); fluctuations in density were less pronounced during aeration.

The numerically dominant benthic invertebrate before aeration was the phantom midge, *Chaoborus punctipennis*, which was significantly more abundant ($p < 0.05$) at deep water stations. Aeration caused marked reductions in densities of *C. punctipennis* and abundances remained comparatively low throughout the remainder of the study (Table 3).

Members of the Family Chironomidae (Insecta: Diptera) were the second most abundant taxon before aeration (Table 3). Chironomids were more abundant at shallow stations, and usually were absent or present in small densities (<3 grab⁻¹) at deep stations at all times of the year except January when oxygen was present at these stations. Aeration caused densities to increase at all stations, but it was more noticeable at the shallow stations where densities, principally *Glyptotendipes paripes*, generally were in excess of 200 grab⁻¹. Two other species of chironomids, *Cladotanytarsus* sp. and

Total Density of Benthic Invertebrates

as Number per Ekman Grab

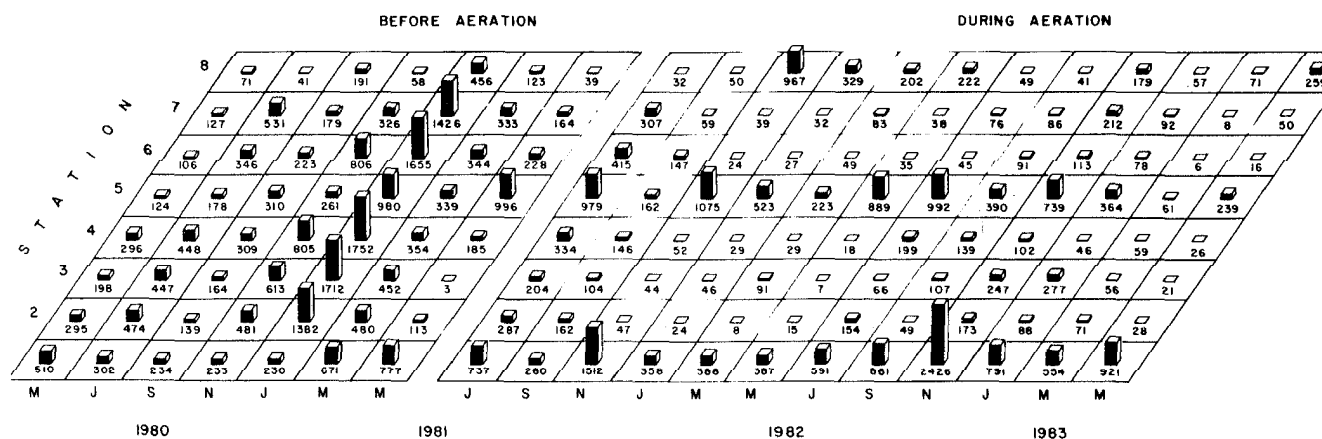


Fig. 7. Block chart of benthic invertebrate abundance at all sample stations over three years of a lake aeration study. The space in the block chart indicates the start of aeration. Station numbers are those of Figure 1.

Table 3. Annual mean densities of the predominant taxa of benthic invertebrates in Lake Brooker, Florida during a lake aeration study. Year 1 represents pre-aeration and Years 2 and 3 were during aeration. Statistical comparisons of years, using $\ln(Y + 1)$ transformed data, are given; ranks underscored by the same line are not different.

Taxon	Mean density in number per Ekman grab			Ranking of means by year and results of SNK multiple comparison test	
	Year 1 (n = 56)	Year 2 (n = 48)	Year 3 (n = 48)	high	low
Oligochaeta	17.07	3.75	24.35	<u>3</u>	<u>1</u> <u>2</u>
Hirudinea	0.11	0.69	0.38	<u>2</u>	<u>3</u> <u>1</u>
Amphipoda					
<i>Hyaella azteca</i>	0.38	17.56	3.56	2	<u>3</u> <u>1</u>
Insecta					
Ephemeroptera					
<i>Caenis diminuta</i>	0.52	5.58	11.10	<u>3</u>	<u>2</u> <u>1</u>
Odonata ¹	0.02	0.14	0.37	<u>3</u>	<u>2</u> <u>1</u>
Trichoptera ¹	0.02	0.73	0.66	2	<u>3</u> <u>1</u>
Diptera					
Chaoboridae					
<i>Chaoborus punctipennis</i>	330.96	35.77	39.44	1	3 2
Ceratopogonidae					
<i>Palpomyia-Bezzia</i> complex	0.57	3.96	6.35	<u>3</u>	<u>2</u> <u>1</u>
Chironomidae					
<i>Procladius</i> sp.	12.73	3.44	4.81	1	<u>3</u> <u>2</u>
<i>Tanypus stellatus</i>	0.91	5.08	2.52	<u>2</u>	<u>3</u> <u>1</u>
<i>Goeldichironomus carus</i>	42.41	8.10	11.06	<u>1</u>	<u>3</u> <u>2</u>
<i>Cryptochironomus fulvus</i>	0.34	2.42	2.21	<u>2</u>	<u>3</u> <u>1</u>
<i>Glyptotendipes paripes</i>	9.70	143.75	101.71	<u>2</u>	<u>3</u> <u>1</u>
<i>Cladotanytarsus</i> sp.	3.68	24.29	46.45	<u>3</u>	<u>2</u> <u>1</u>
<i>Tanytarsus</i> sp.	24.38	0.06	0.77	1	<u>3</u> <u>2</u>
Other species ¹	3.39	1.19	5.27	3	<u>1</u> <u>2</u>
Total Chironomidae	97.54	188.33	174.80	<u>2</u>	<u>3</u> <u>1</u>
Total organisms	447.19	256.51	261.01	1	<u>3</u> <u>2</u>

¹ See Cowell & Dawes (1984) for a list of species.

Cryptochironomus fulvus, showed increases at the shallow stations similar to *G. paripes*, but densities of these species were markedly lower (Table 3).

A second pattern of distribution change following the start of aeration was exhibited by two species of Tanypodinae (Diptera: Chironomidae). *Procladius* sp. and *Tanypus stellatus* were found principally at shallow stations before aeration, but during aeration distributions shifted to deeper stations. During aeration the frequency of occurrence for both species increased from approximately 20% to 50% at the deep stations.

Some chironomids showed no distribution changes following the start of aeration. *Goeldichironomus carus* occurred at both shallow and deep stations; it was found in 46% of the before

aeration samples and in 53% of the during aeration samples. *Tanytarsus* sp. occurred principally at shallow stations both before and during aeration; frequencies of occurrence were similar for both phases of the study but densities tended to be higher before aeration.

Other abundant taxa included: 1) Ceratopogonidae (Diptera), 2) *Caenis diminuta* (Ephemeroptera), 3) *Hyaella azteca* (Amphipoda) and 4) Oligochaeta. A ceratopogonid midge of the *Palpomyia-Bezzia* complex showed distributed changes with aeration similar to those of *Glyptotendipes paripes*. The mayfly, *Caenis diminuta*, was found sporadically in shallow samples before aeration (29%), but during aeration there were large increases in densities (10- to 20-fold) and fre-

quencies of occurrence (86%) at the shallow stations. The amphipod, *Hyalella azteca*, showed similar increases in density and frequency of occurrence at the shallow stations. Mean density increased 10- to 50-fold and frequencies of occurrence before and during aeration were 19% and 47% respectively. Before aeration *Oligochaeta* were present in 57% of the shallow station samples and only occurred at deep stations in January when oxygen deficits were absent. During aeration frequencies of occurrence increased for both groups of stations but densities remained low.

The final comparison for individual sample stations involves numbers of taxa (Fig. 8). Before aeration the mean number of taxa per grab was 3.75 but shallow stations had more taxa than deep stations; ranges of the two groups were 1–17 and 1–9 taxa respectively. Except in January when oxygen concentrations were high, deep stations never had more than three taxa. During aeration the mean number of taxa per grab increased to 6.4 and differences between shallow and deep stations were small at all times of the year except summer (especially July).

Between year changes

Annual mean densities of benthic invertebrate taxa were calculated using the data from all sample

stations (transect mean) and statistical comparisons between years were made for those taxa comprising more than 1% of the total density. Table 3 shows a 2-fold reduction in the density of total organisms following the start of aeration (years 2 and 3 were not statistically different but both differed from year 1). This decrease was attributable principally to a marked decline ($p < 0.05$), approximately 90%, of *Chaoborus punctipennis*. In contrast, densities of total chironomids increased approximately 2-fold following the start of aeration; years 2 and 3 were significantly higher than year 1 ($p < 0.05$). During year 1, *Chaoborus* and total chironomids comprised 74.0% and 21.8% respectively of total organisms, but during aeration these values switched to 14.5% and 70.2% respectively.

Abundances of individual species of chironomids were affected differently by aeration. Three species showed significant increases during aeration (*Glyptotendipes paripes*, *Cladotanytarsus* sp., and *Cryptochironomus fulvus*). *Tanytus stellatus* increased significantly only during year 2 ($p < 0.05$); year 3 was not different from years 1 or 2. The three remaining species of abundant chironomids, *Goeldichironomus carus*, *Procladius* sp. and *Tanytarsus* sp., all were more abundant before aeration (Table 3).

Densities of ceratopogonid midges (*Palpomyia-*

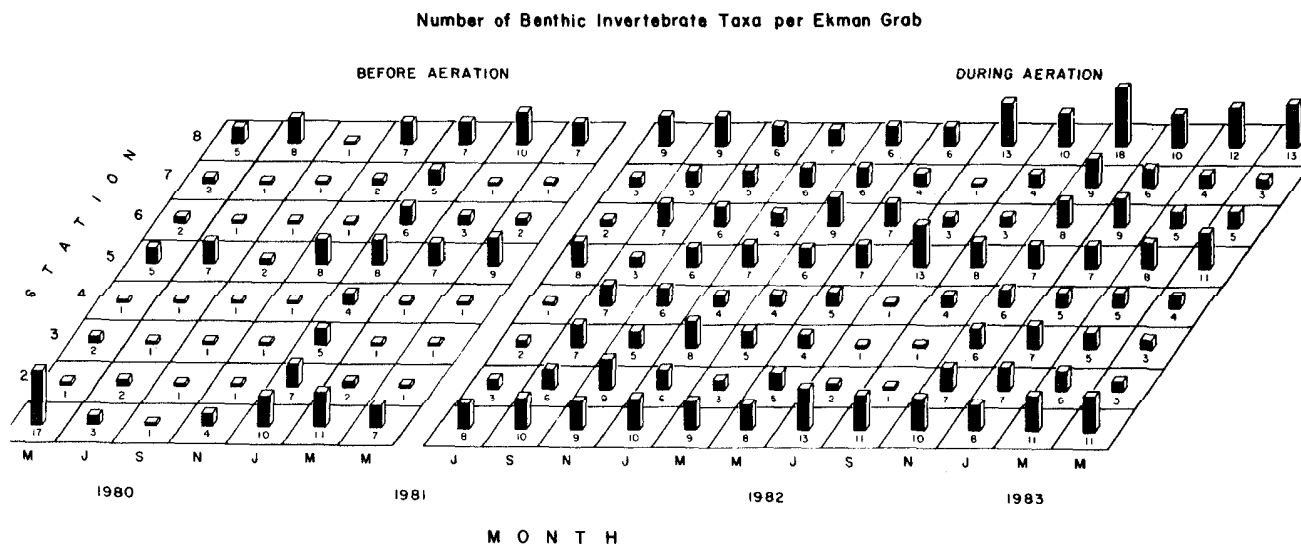


Fig. 8. Number of taxa of benthic invertebrates at eight sample stations in Lake Brooker, Florida during three years of a lake aeration study. The space in the block chart indicates the start of aeration.

Bezzia complex), mayflies (*Caenis diminuta*) and amphipods (*Hyalella azteca*) increased significantly during aeration (Table 3). Between years 1 and 3 densities of the *Palpomyia-Bezzia* complex increased 11-fold and *Caenis diminuta* increased approximately 20-fold; in both cases years 2 and 3 were not statistically different, but both differed ($p < 0.05$) from year 1. *Hyalella azteca* increased significantly ($p < 0.05$) from year 1 to year 2 but the increase was of short duration as the mean density in year 3 was not statistically different from year 1 (Table 3). Oligochaetes, the last of the numerically dominant taxa, were highly variable in occurrence and this caused the statistical comparisons to indicate no significant differences between years.

Fig. 9 shows a summary of changes in total density and number of taxa over the three years of this study. Mean densities during year 1 usually were greater than those at comparable times during years 2 and 3. Peak densities occurred during the late fall or early winter months in all three years; minimum densities occurred in the late summer of year 1 and in the early spring of years 2 and 3.

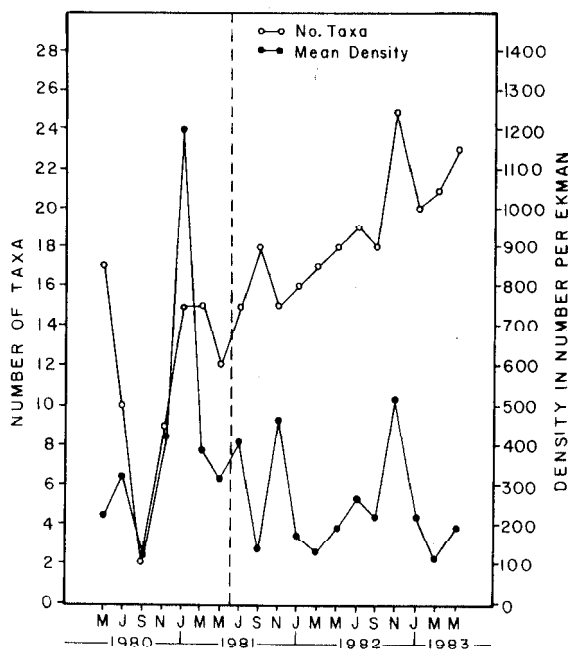


Fig. 9. Summary of changes in density and number of taxa in Lake Brooker, Florida during three years of a lake aeration study. Data represent means and totals respectively for all sampling.

Numbers of taxa were low (only 2) during the summer of year 1 when oxygen deficits were present, but thereafter numbers of taxa increased in almost a linear fashion. The number of taxa was still increasing at the end of the study.

Discussion

Physical-chemical parameters

Aeration or artificial mixing of stratified lakes generally improves water quality (Pastorok *et al.*, 1980; Toetz, 1979). The following trends usually are noted:

1) Dissolved oxygen concentrations of bottom waters increase immediately and the lake becomes isothermal (Hooper *et al.*, 1953; Irwin *et al.*, 1966; and Haynes, 1973).

2) As hypolimnetic waters are brought to the surface, gases such as CO_2 , H_2S and NH_3 are released into the atmosphere (Toetz *et al.*, 1972; Haynes, 1973).

3) The pH of the water column is lowered (Irwin *et al.*, 1966; Maleug *et al.*, 1973; Weiss & Breedlove, 1973).

4) Most chemical concentrations become isochemical with depth (Toetz *et al.*, 1972).

5) Concentrations of reduced forms of manganese and iron often decrease in the hypolimnion (Wirth & Dunst, 1967; Brezonik *et al.*, 1969) and internal nutrient cycles may be altered (Toetz *et al.*, 1972; Holdren & Armstrong, 1980).

Other variables, such as transparency (Secchi disk, turbidity and color) are highly variable and depend upon the intensity of mixing and the contributions of phytoplankton to turbidity levels before treatment (Pastorok *et al.*, 1980).

Dissolved oxygen at the 4.5 m sample depth in Lake Brooker showed an immediate increase commensurate with the start of aeration and thermal stratification was eliminated. During aeration, differences between the surface and 4.5 m sample depths were small except when equipment problems developed. However, the decreases in dissolved oxygen, associated with the failure of one of the 0.5 hp pumps, were large enough to indicate that turning off the aeration unit would cause conditions to revert back to pre-aeration values.

Aeration of Lake Brooker produced marked

reductions in hypolimnetic gases and pH. Concentrations of H_2S were reduced to trace amounts shortly after the start of aeration and CO_2 concentrations decreased 2-fold. Ammonium concentrations decreased each year but differences were non-significant because of high variability among samples. The pH decreased significantly following the start of aeration and variation between sample dates decreased. Pastorok *et al.* (1980) reported that lakes where pH decreased following circulation also showed an increase in the green to blue-green algal ratio; our study showed a similar response.

Aeration is expected to lower concentrations of reduced forms of iron and manganese, and lead to predictable nutrient cycling. Mortimer (1941, 1942, 1971) has shown that phosphorus is released from the sediment into the water during anoxic conditions and that low concentrations of oxygen will remove phosphorus by forming insoluble precipitates with oxidized ions of iron, manganese and magnesium. Clasen (1980) reported that if the oxygen of the microlayer at the mud-water interface was not allowed to drop below 3 mg l^{-1} , reduced ions and phosphorus ions would be prevented from being released into the free water zone. Graetz *et al.* (1973) reported that during anoxic conditions, ammonium was released into the water at a relatively constant rate, but during aeration bacterial oxidation caused rapid nitrification and increases in nitrate concentrations. Nitrate concentrations did not continue to increase under aerobic conditions, but rather decreased with time; this may be attributable to diffusion into the reduced sediments and to subsequent denitrification. In a hypolimnetic aeration experiment, McQueen & Lean (1984) found that concentrations of all forms of nitrogen (nitrate, nitrite, ammonia and total nitrogen) were higher in aerated enclosures than in control enclosures. They recommended that the optimum strategy for treating temperate lakes that stratify was to use hypolimnetic aeration in summer to maintain thermal stratification and to reduce phosphorus loads, and to use destratification (whole lake) aeration during the spring and fall to maximize nitrification. In Lake Brooker total nitrogen decreased significantly following aeration, ammonium decreased but not significantly, and nitrate + nitrite increased during year 2 and then decreased in year 3. These were close to the predicted responses. In contrast, total phosphorus and soluble reactive

phosphorus both decreased significantly during year 2 but then showed unexpected increases ($p < 0.05$) during year 3.

Garrell *et al.* (1977) working on a hypolimnetic aeration system noted similar unexpected nutrient cycles and concluded that substantial external loading of the study lake could mask aeration effects on the internal nutrient cycles. Nutrient inflows into Lake Brooker for total phosphorus, soluble reactive phosphorus and ammonium during year 3 were found to be much higher (up to 1–2 orders of magnitude) than lake concentrations (Cowell & Dawes, 1984) and may have been a contributing factor to the unusual nutrient cycles. Uttormark *et al.* (1974) pointed out that input from nonpoint sources also can overwhelm internal loading systems. Thus, when aeration is to be used as a restoration method in eutrophic lake systems, it is advisable to estimate loading of major nutrients from both point and nonpoint sources and to determine nutrient budgets. This will enable explanation of unusual nutrient concentrations and subsequent influences upon phytoplankton communities.

With the exceptions of finding decreases in iron and manganese during aeration, most studies have not addressed the other cations. Ashley (1983) found that hypolimnetic aeration vented accumulated CO_2 and decreased concentrations of calcium and magnesium via calcium carbonate – phosphate coprecipitation. Our data showed the expected reductions in iron concentrations but the other cations did not compare with the findings of Ashley. Our calcium, magnesium and sodium concentrations increased during the first year of aeration (year 2), as CO_2 decreased, but then decreased during year 3 when CO_2 concentrations increased. McQueen & Lean (1984) also cite examples where contrary results were obtained for amounts of phosphorus coprecipitated with calcium. There is need for additional studies of cation budgets and interactions with other chemicals.

Biological parameters

Relatively little information exists on changes in primary production of algal communities during aeration, and the few studies that have been done show contradictory results. Fast *et al.* (1973) found a 3-fold increase in primary production during the aeration (complete mixing) of Section Four Lake,

Michigan. LaBaugh (1979, 1980) using hypolimnetic aeration during two summers, found that primary production of Spruce Knob Lake, West Virginia, was not affected by aeration. Toetz *et al.* (1979), working on incomplete mixing of Arbuckle Lake, Oklahoma, observed a decrease in the ratio of gross production: community respiration, and predicted that lakes which are artificially mixed should have lower net primary productivities than those which are not mixed. Our study showed no change in primary production during aeration even though whole lake aeration was used.

The reasons for different responses to aeration or mixing appear to be related to the type of aeration system employed and to natural variability in limnological factors. Hypolimnetic aeration should have no direct impact upon primary production unless: 1) stratification is destroyed and nutrients are recirculated into the epilimnion, or 2) light penetrates below the thermocline and metalimnetic production, under high nutrient levels, ensues. In lakes undergoing artificial destratification or whole lake mixing, changes in light penetration, nutrient levels and algal standing crops may influence primary productivity, and both increases or decreases could occur. However, depth and the rate of mixing appear to be superimposed upon these factors. If the lake is deep and large volumes of epilimnetic waters are moved to the bottom rapidly, algae may spend long periods of time in suboptimal light, respiration would increase, and net productivity would decrease. But in shallow lakes or those with slower mixing rates the impact should be much less. Lake Brooker (5.2 m deep) mixed at a rapid rate (approximately $2300000 \text{ l hr}^{-1}$) and changes in light penetration and nutrient concentrations were small. The primary production rate did not change with aeration even though the algal standing crop and composition changed markedly.

The response of the phytoplankton to artificial destratification or whole lake mixing have been quite variable. Pastorok *et al.* (1980) reviewed 40 cases of complete destratification and found that the effect upon chlorophyll *a* and phytoplankton standing crop varied among lakes. These parameters either increased, decreased or remained the same subject to mixing conditions prevalent in individual lakes. Forsberg and Shapiro (1980) investigated the mechanisms underlying this variability in two Minnesota lakes and found that peak chlo-

rophyll *a* concentrations decrease as the mixed depth increases provided total phosphorus does not change, but if total phosphorus increases or decreases during mixing, peak concentrations will reflect the direction and magnitude of the change.

In shallow central Florida lakes, changes in the mixed depth are expected to be small and thus the limiting nutrient should be more predictive of changes in chlorophyll *a*. Baker *et al.* (1981) showed that in Florida there is a predominance of nitrogen-limited lakes and they recommended calculation of trophic state indices (TSI) for both total phosphorus and total nitrogen; the smaller of the two TSI's should represent the limiting nutrient for a given lake. Annual mean chlorophyll *a* concentrations in Lake Brooker did not change with aeration, possibly because the predicted reductions in nitrogen and phosphorus appear to have been confounded by point source inflow of nutrients.

Mixing can control algal blooms and phytoplankton abundance by limiting the amount of energy available for photosynthesis (Lorenzen, 1977; Lorenzen & Mitchell, 1973, 1975). Mixing also may favor non-blue-green algae by eliminating the competitive advantage of blue-green algae which are often buoyant and able to maintain themselves at optimum light levels under quiescent conditions (Lorenzen, 1977). Forsberg and Shapiro (1980) showed that changes in species composition during circulation are dependent upon the mixing rate. If mixing is slow, blue-green algae may increase in density but if mixing is fast, blue-greens decrease and green algae and diatoms often increase. In addition, they stated: 'the shift to green algae occurred only during conditions of low pH and high nutrient availability and is therefore most likely to occur when relatively deep productive lakes are mixed rapidly.' Our data on Lake Brooker show similar effects of aeration on the species composition of a shallow, acid-colored lake.

Pastorok *et al.* (1980) cite results from several aeration studies which show increases of large-bodied cladocerans during aeration. In contrast, our study showed a marked decline in crustacean zooplankton following the start of aeration. Possible causes of this rapid reduction in crustacean zooplankton abundance include: 1) increased fish predation after elimination of oxygen deficits; 2) concomitant decreases in the mean phytoplankton cell volumes; 3) changes in the sizes of the

phytoplankton; 4) rapid mixing and subsequent entrapment of organisms in the surface film; and 5) release of toxic substances from the bottom muds. Rapid mixing and changes in the phytoplankton appear more likely but additional studies will be necessary for confirmation.

Unlike the crustacean zooplankton, rotifers increased in density following the start of aeration. Brooks and Dodson (1965) suggested that the structure of freshwater zooplankton communities is controlled by size-selective predation and competition for food among zooplankton species. In the absence of size-selective predation by fish, large crustacean zooplankton (Cladocera) are expected to utilize available food more efficiently and to out-compete the smaller rotifers for these resources (see Neill, 1984). During pre-aeration this trend was apparent in Lake Brooker as population densities of crustacean zooplankton and rotifers were negatively correlated. The hypothesis concerning competition between the crustacean zooplankton and the rotifers is predicated upon the assumption that both groups consume the same sizes and types of food in nature. Early work suggested that suspension feeding rotifers were limited to small ($< 5 \mu\text{m}$) particle sizes (see Nauwerck, 1963; Gliwicz, 1969), but recent feeding experiment (e.g., Burkema *et al.*, 1978; Gilbert and Starkweather, 1978; Starkweather and Gilbert, 1978; Starkweather, 1981 and Sveda, 1984) have shown that many rotifers can utilize food sizes larger than $5 \mu\text{m}$. The rotifer community may be able to consume the same types of foods as the crustacean zooplankton; Bogdan *et al.* (1980) and Crisman *et al.* (1981) indicated that individual species of rotifers, depending on general morphology, may consume nanoplankton, nanoplankton plus bacteria, or larger phytoplankton cells. If the rotifers of Lake Brooker are capable of efficient utilization of the phytoplankton, it would be reasonable to postulate that reductions in competition for algal food with crustacean zooplankton during the first year of aeration led to increased densities of rotifers. However, the decline in rotifers during the second year of aeration and return to pre-aeration levels indicates the need for more detailed studies of zooplankton trophic dynamics during aeration studies.

Pastorok *et al.* (1980) reviewed 9 aeration/artificial circulation studies and found that responses of benthic communities have been relatively consistent, i.e., increases in the number of taxa, diversity

and biomass, especially in the profundal areas. Four of the five lakes in which *Chaoborus* formed a significant proportion of the profundal benthos before aeration displayed a decline in larval density during aeration. Chaoborids subsequently were replaced by oligochaetes, chironomids and other insect larvae which were detritivores and responded to the rich deposits of organic matter by producing large population densities (see Sikorowa, 1978). Lake Brooker showed similar trends. *Chaoborus* populations decreased, chironomids, oligochaetes and other insects increased, and numbers of taxa and diversity (H') increased with aeration. The declines in chaoborid populations in other studies usually have been attributed to destruction of anoxic refugia by aeration and to exposure of the larvae to intense fish predation. In Lake Brooker, it appears that the marked decline in crustacean zooplankton (*Chaoborus* prey items) also may have contributed to the decline.

Following the reduction of the *Chaoborus* population, densities of chironomids and oligochaetes increased in the profundal areas of Lake Brooker. However, densities of total organisms did not increase appreciably during aeration because densities for profundal areas were significantly less than those for pre-aeration. The only significant increases during aeration were at the shallow littoral stations which were no longer subject to periodic intervals of oxygen depletion. For the entire lake, the number of taxa was still increasing at the end of the study (two years after the start of aeration), but it is unlikely that significant increases in densities will occur until either all the flocculent substrate is oxidized or until different substrate conditions (particle size and/or structure) become available.

Conclusions

The multiple inversion aeration system successfully eliminated some of the undesirable features of eutrophication (e.g., oxygen depletion, noxious blue-green algal blooms and low diversity of the benthic community). But it did not decrease the trophic state index or produce significant reduction of the extensive layers of flocculent sediment (Crisman, person. comm.). Thus, aeration of hypereutrophic lakes may be necessary for multiple years to maintain desired conditions.

Acknowledgements

This research was supported by a grant from the Aquatic Plant Research and Permitting Section of the Florida Department of Natural Resources. Clean-Flo Laboratories provided the multiple inversion aeration system.

We wish to thank Susan S. Bell for constructive criticism of an earlier draft of this manuscript. We also are grateful to William E. Bros, Susan V. Diehl, H. Clark Hull, Jerilyn Jewett-Smith, Brian E. Lapointe, Amy J. Slifko and Stephan A. Watts for field and laboratory assistance.

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Received 25 March 1986; in revised form 29 July 1986; accepted 3 October 1986.