IN SITU RESPIROMETRY FOR THE DETERMINATION OF AUTOTROPHIC AND HETEROTROPHIC PRODUCTION IN SOUTHEASTERN LAKES

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Abstract. Representative and accurate measurements of both autotrophic and heterotrophic production in lakes are essential parts of basic limnological research and lake monitoring, management, and restoration programs. We describe preliminary data that demonstrate the utility of a continuously recording, *in situ* respirometer for measuring diel oxygen production and consumption in lake water. The data can be used to compute P, R, P *vs.* I, P *vs.* T, P/R, P/B and other basic parameters of primary productivity and heterotrophic activity per unit volume of lake water or per unit chlorophyll. In combination with information on morphometry and water residence time, these volumetric production estimates can be used to compute integrated whole lake metabolism and production budgets.

In our preliminary studies we found that heterotrophic processes dominated the water column in Lake Oglethorpe, Georgia.

NEED FOR *IN SITU* RESPIROMETERS

Comparisons of Lake Health. The majority of "text book" paradigms for limnology are based on extensive studies of small, northern, dimictic lakes. These lakes lie above 38° N in the glaciated regions of North America and Europe. By comparison, there is little extensive, long-term, or comparative limnological information on southeastern lakes. Lakes of this region are primarily man-made, and those that stratify are monomictic. Efforts to collect long term data on southeastern lakes will allow comparisons with those from northern lakes.

One aspect of lake ecology necessary for regional comparisons is a good estimate of annual production. For all lakes, year round primary productivity measurements are rare. Indirect, and probably unrepresentative measures of autotrophic productivity are often the only information available for comparative studies (see NES, NASQUAN comparisons of Soballe and Kimmel, 1987; and northern lake comparisons of Carpenter *et al.*, 1990). Annual *in situ* measures of heterotrophic activity are even rarer (see McDonough *et al.*, 1986).

When compared, measures of autotrophic and heterotrophic production are valuable indicators of lake health. In extensive studies of acidification, eutrophication, and global climate change effects on experimental lakes in Canada, Schindler (1989; Schindler *et al.*, 1990) found that P/R remained stable over a broad range of experimental "stresses." Deviations from the expected P/R value for a given lake system indicated the ecosystem was at risk.

Southern Lakes. Our 15 year study of autotrophic and heterotrophic processes in Lake Oglethorpe, a small monomictic lake near Athens, Georgia, indicate that these systems differ in many ways from northern lakes. These differences warrant further quantification and generalization so that southern lakes can be managed and evaluated by appropriate criteria. For example, in northern lakes, phytoplankton and crustacean zooplankton predominate in the planktonic community all year round, and are especially abundant in spring and summer. In Lake Oglethorpe, however, crustaceans are generally less abundant and are common only during the mixed period (October through April) (Pace and Orcutt, 1981). Instead, the plankton is dominated by members of the "microbial loop" community. These are the bacteria, flagellates, ciliates, and rotifers, and these groups are especially common during summer stratification (Porter and Stockner, 1989; Sanders *et al.*, 1989).

Hypothesis. These differences lead us to hypothesize that, on an annual average, heterotrophic processes dominate in this and most other southeastern lakes, even in shallow water. This would be indicated by low or negative P/R ratios, especially during stratification (summer), when the microbial loop is predominant feature of the aquatic food web.

Production Rate Measurement. To test this hypothesis we needed a safe, cost-effective means of determining autotrophic and heterotrophic production rates and P/R ratios. Permit restrictions on field use of radiotracers and the prohibitive cost of their extensive use led us to look for alternative means of measuring productivity *in situ.*

Here we report the successful application of *in situ* respirometers, developed originally for the study of marine benthos (described in detail in Porter, 1980), to measure whole water oxygen production and consumption rates in Lake Oglethorpe.

We believe that this method provides representative data in a cost-effective and environmentally safe manner. This could make primary and heterotrophic production and P/R measures more common in monitoring studies, as well as contribute to our criteria for pond, reservoir, and lake management and restoration.

METHODS OF MEASURING AUTOTROPHIC AND HETEROTROPHIC PRODUCTION

Autotrophic and heterotrophic production rates in standing waters are usually measured by the "light and dark bottle" method. Oxygen flux or radiotracers are used to quantify autotrophic and heterotrophic production (Hall and Moll, 1975). Diel, free-water oxygen curves are used in flowing waters but have not been routinely applied to lakes due to problems in correcting for gas exchange at the water surface. Other measures of annual whole lake metabolism such as hypolimnetic or under-ice oxygen deficits, are crude and only suitable for broad comparisons among systems.

The C^{14} and tritiated thymidine radiotracer methods used to measure autotrophic and heterotrophic production, respectively, are expensive, labor intensive, require special precautions, and may not represent actual water column production (McDonough *et al.*, 1986; Bower *et al.*, 1987). Oxygen production and consumption techniques have the advantages that they cost less, are easier and safer to use, and provide more information about whole system metabolism. Autotrophic production and heterotrophic activity are measured simultaneously by oxygen flux methods, allowing the balance of metabolism (P/R) to be assessed.

We selected *in situ* respirometry as a practical method for O_2 flux determinations. To test the applicability of this method, we chose to conduct experiments on two dates that we believed would provide examples of major differences in P/R. These were August 3-5, 1992, at the end of summer stratification, and October 21-23, 1992, during fall turnover.

LAKE OGLETHORPE

Lake Oglethorpe is a small, monomictic lake (30 ha, Z_{max} = 8.5 m, z = 3 m) located 20 km southeast of Athens, in the Georgia Piedmont (33°52'01"N, 83°13'58"W). Lake Oglethorpe is eutrophic in terms of nutrient chemistry (total phosphorus ranges from 16 to 1078 μg/L) and bacterial densities (total counts range from 1.5 to 32.0 x 10^6 cells mL^{-1}), but primary production rates are more typical of mesoeutrophic lakes (100-200 g C $m^{-2}yr^{-1}$) (Likens, 1975). This modest productivity is attributed to seasonally high levels of turbidity (Secchi depths as low as 0.2 m) caused by suspended clays from watershed runoff and vertical mixing (see Pace and Orcutt, 1981).

EXPERIMENTS

Physical and Chemical Profiles. Our ongoing Lake Oglethorpe monitoring program includes measures of temperature and dissolved oxygen (YSI Meter), irradiance (LiCor Quantum Sensor and Secchi disk depth), and algal, bacterial and zooplankton populations and biomass. In the August 3-5 experimental period reported in this paper, warm (28 °C), well-oxygenated waters of the epilimnion interface at the 3 m thermocline with cold (12-14 °C), deoxygenated waters of the meta- and hypolimnion (Figure 1). The extent of stratification observed at this time is typical of summer conditions at Lake Oglethorpe.

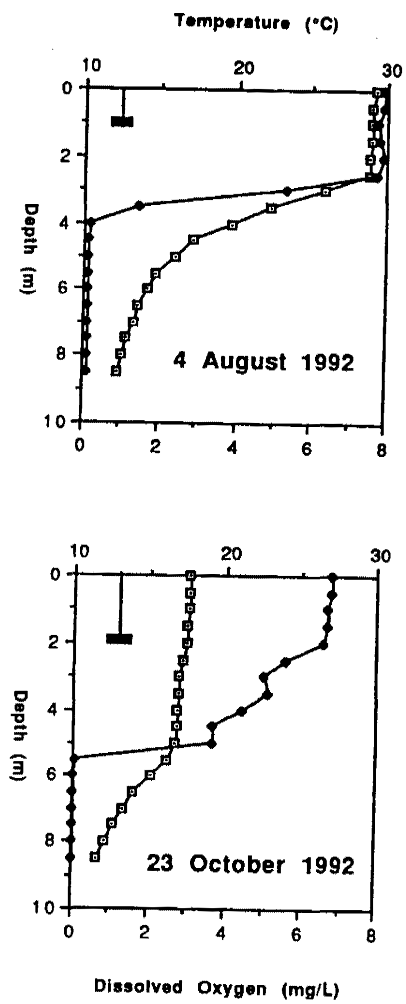

Figure 1. Secchi disk depth, temperature (open squares), and dissolved oxygen (closed squares) at half-meter intervals during the stratifed period (August 4, 1992) and the onset of mixis (October 23, 1992) in Lake Oglethorpe, Georgia.

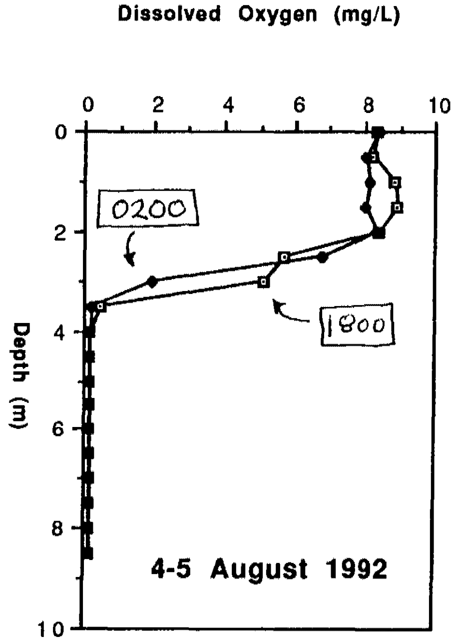

Figure 2. Biological activity as indicated by oxygen increases at 1 to 3 meters during the day (1800 hr), and oxygen depletion at night (0200 hr).

The thermal discontinuity at 3 meters is a region of high algal and microbial abundance and activity (McDonough *et al.*, 1986), similar to the metalimnetic plate found in other lakes or the midwater chlorophyll layer in marine systems. On August 4-5, diel oxygen profiles showed the greatest difference in oxygen concentrations at 3 meters, a drop of 3.2 mg/l between 1800 on August 4 and 0200 on August 5 (Figure 2).

The October 21-23 experimental period was during the period of fall mixis when cooling upper waters, ranging from 17 to 18 °C, had eroded the thermocline to 5 meters and mixed oxygen into these previously anoxic depths. However, the cold (11-16°C), unmixed waters below 5 m remained anoxic during the period of our second experiment. Secchi disc depth (SDD), a common measure of water clarity, indicated a decrease in suspended particulates between August (SDD = 1.1 m) and October (SDD = 1.9 m) (Figure 1).

Chlorophyll. Chlorophyll *a* concentrations were used to convert volumetric respirometry rates to biomass related units. Chlorophyll *a* profiles for August 4 and October 23, 1992, were determined using whole water samples collected at 1/2-meter or 1-meter intervals with a 1.2-liter Kemmerer bottle. Final concentrations were calculated using the monochromatic, pheophytin-subtraction method (Wetzel and Likens, 1991).

Chlorophyll *a* concentrations were higher (1-9X) throughout the water column in August, compared to October. Highest chlorophyll concentrations were consistently found throughout depths just below the top of the metalimnetic density discontinuity (2 to 9X increase in August at depths below 3m; 5 to 6X increase in October at depths below 5m). Differences in depth distribution of chlorophyll *a* between August and October closely reflected differences in sedimentation patterns determined by thermal discontinuities. Epilimnetic chlorophyll *a* concentrations were relatively constant among depths for both dates (August= 21.5 to 58.1 μg/L; October= 13.3 to 17.5 μg/L).

High concentrations of chlorophyll *a* in the hypolimnion may be attributed to an accumulation of settled cells, or to pigment-rich, prokaryotic algae such as *Prochlorothrix* sp. that are capable of functioning heterotrophically in this anoxic zone. In addition, green sulphur bacteria may be active at the aerobic/anaerobic boundary in the metalimnion.

Respirometry. Oxygen flux characteristics of whole lake water were determined during stratified (August) and unstratified (October) periods in Lake Oglethorpe, Georgia, using two *in situ* respirometers. Measurements were made over two consecutive 24 hour periods at two depths that span the euphotic zone (1 m and 3 m). Each respirometer consisted of three 2-liter, quartz topped, plexiglass chambers that were flushed with ambient water at designated time intervals (at 2 hrs) (Porter, 1980). Changes in O_2 inside the chambers were recorded at 4 minute intervals with Clarke polarographic oxygen electrodes (YSI). Data were stored on digital data loggers (Omnidata). At the same time, the ambient PAR flux light level was measured with an attached spherical quantum sensor (LiCor). Temperature, oxygen, irradiance, phytoplankton, bacteria, and chlorophyll *a* profiles were also determined in the water column, and an integrated metazoan sample was obtained. Changes in oxygen concentration within the chambers were converted to flux rates and normalized with chlorophyll *a*, algal biovolume, and cell count data with an IBM compatible customized software package. Gross production was calculated from these measurements of community net production and nighttime respiration. Indicators of whole-system metabolism, such as production *versus* irradiance curves (P:I), production *versus* time curves (P:T), and production / respiration ratios (P/R), were also computed. We calculated P/R ratios based on gross production, assuming cloudless-day conditions (Porter *et al.*, 1984), and using an integrated 24 h respiration rate, which is based on the average hourly nocturnal respiration rate. We are aware that the nocturnal respiration rates may slightly underestimate diurnal respiration rates.

RESULTS AND DISCUSSION

Chlorophyll *a* concentrations (μg/L) decreased from August to October and increased with depth on both dates (Figure 3). At 1 m in October, Chl *a* was almost half the value from the same depth in August (29.0 μg/L in August

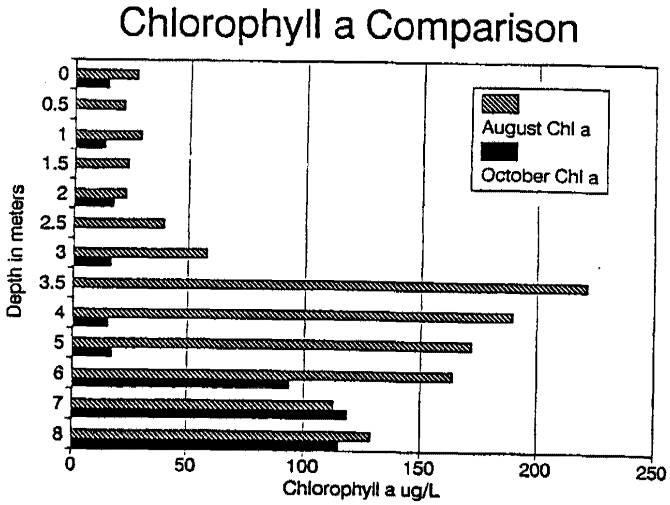

Figure 3. Chlorophyll a in μg/ml *versus* depth in meters. Hatched bars are the chlorophyll data from August 4, 1992; solid bars are the chlorophyll data from October 23, 1992.

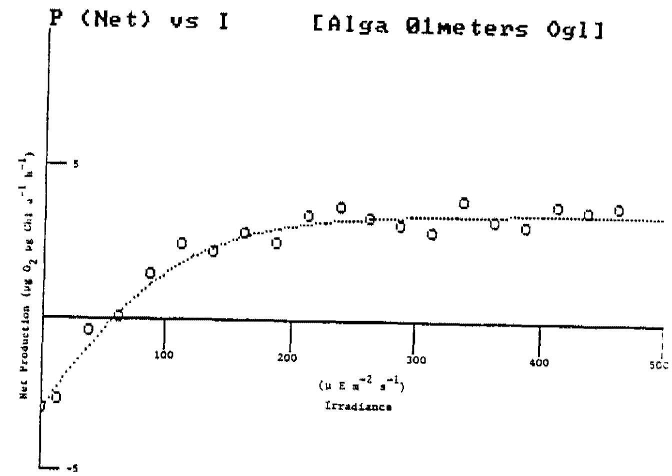

Figure 4. Production *versus* irradiance curve for the Lake Oglethorpe, Georgia, plankton community at 1 m depth for August 4-5, 1992.

versus 13.3 μg/L in October). The between-date differences were even greater at 3 m, with October values being almost one third lower (58.1 μg/L in August *versus* 16.3 μg/L in October). In both months, chl *a* concentrations were higher at 3 meters than 1 meter, but the magnitude of this difference varied (2X higher in August *versus* 1.2X higher in October).

Photosynthesis *versus* irradiance (P *vs.* I) curves (Figure 4) were used to calculate net photosynthesis and nocturnal respiration for the plankton community at each depth (Table 1). Photosynthesis *versus* 24 hour time-of-day curves were used to calculate environmentally realistic curves of oxygen flux in the chambers (Figure 5). Model comparisons between days with similar irradiances were used to calculate integrated P/R ratios (Table 1).

We were unable to calculate oxygen flux in the respirometer for the August experiments at 3 meters, due to anomolous positive readings. During the day, the water at 3 m is under-saturated (3 ppm rather than 7-8 ppm). At night, unrealistic positive O_2 fluxes were recorded. These were likely artifacts of H_2S poisoning of the electrodes. These problems did not occur at 3 m in October because the water column was then mixed down to 5 m (Table 1).

There was substantially more light at 1 m in October than in August because the water was clearer during fall (Figure 1). In August, for instance, maximum irradiance was 475 μE $m^{-2}s^{-1}$, and in October 775 μE $m^{-2}s^{-1}$. For the

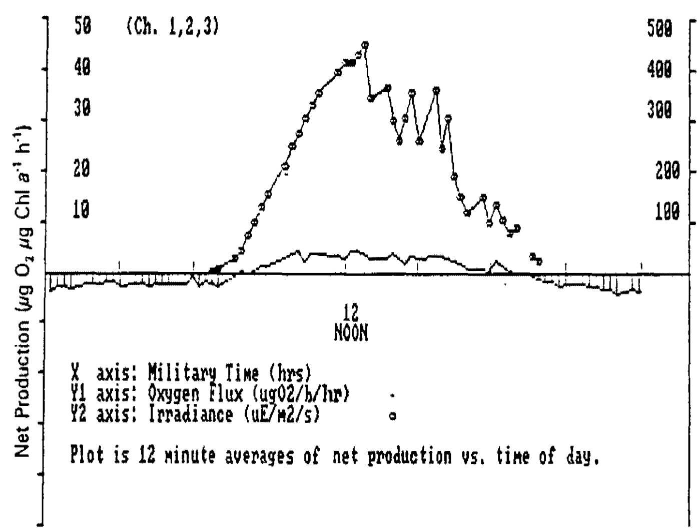

Figure 5. Net production *versus* time for the Lake Oglethorpe, Georgia, plankton community at 1 m depth for August 4-5, 1992. Net oxygen flux (closed dots) is plotted as the average of 3 consecutive 4-minute readings (μgO_2 $\mu gChla^{-1}$ hr^{-1}). Irradiance (open dots) is plotted as instantaneous light readings (μE m^{-2} s^{-1}).

August experiments, idealized (cloudless day), integrated irradiance was 6.1 E $m^{-2}d^{-1}$ at 1 m; values for the October experiments were 12.9 and 9.7 E $m^{-2}d^{-1}$ at 1 and 3 m, respectively.

Calculated net photosynthesis per unit chlorophyll *a* was the same at 1 m during both August and October experiments (3.50 $\pm$0.55 and 4.40 $\pm$0.67 μg O_2 μg Chl a^{-1} hr^{-1}, respectively). Net photosynthesis at 3 m depth in October was significantly less than at 1 m on either date (1.20 $\pm$0.57) (Table 1). There was some tendency for higher instantaneous net photosynthesis values at the higher irradiances in October *vs.* August, with peak net production at 1 m in October of 5.99 $\pm$0.37 *vs.* 3.94 $\pm$0.48 in August (same units).

Respiration is significantly higher at 1 m in August (-2.95 μg O_2 μg Chl a^{-1} hr^{-1}) than at the same depth in October (-1.42 μg O_2 μg Chl a^{-1} hr^{-1}) (Table 1). It is interesting to note that respiration at 3 m depth in October is not significantly different from respiration at 1 m August (Table 1). We could not calculate the respiration of 3 m lake water in August, probably due to the presence of hydrogen sulfide at that depth. The elevated respiration rate of the lake community at 1 m in August is logical, given the higher concentration of material in the water during that season.

Despite the high chlorophyll *a* values in shallow water in August, and intense surface irradiance, the lake is significantly heterotrophic in August (Table 1). Even during ideal weather conditions (cloudless sky), the gross P/R ratio is only 0.85, suggesting that there must be an allochthanous input of 15% of the organic carbon necessary to balance respiratory demands of the shallow water

Table 1. Net Photosynthesis and Respiration, and P/R Ratio, for the Lake Oglethorpe Planktonic Community, with P and R in units of μgO_2 per μgChl*a* per hour.

Depth (m)	August (08/04/92)	October (10/22/92)
Community P_{net} Max		
1 meters	3.50 ± 0.55	4.40 ± 0.67
3 meters	---	1.20 ± 0.57*
Community Respiration		
1 meters	-2.95 ± 0.09	-1.42 ± 0.06*
3 meters	---	-2.33 ± 0.23
Community P/R Ratio *		
1 meters	0.85	1.58*
3 meters	---	0.5

Notes: Mean values ± standard error; N = 3 chambers.
Significant difference ($P \leq 0.05$; N = 3).
* Ratio of Gross Photosynthesis to 24 h Respiration, for idealized irradiance (cloudless day): (P_c gross 24 h / R_c total 24 h).

community. In October, the lake community is highly photo-autotrophic in shallow water, with a Gross P/Total R ratio of 1.58 (Table 1). As would be expected, P/R is low at 3 m depth (0.55) in October, where high community respiration and low irradiance combine to keep the P/R ratio low.

It remains to be seen whether the lake is autotrophic or heterotrophic over an annual cycle. We hypothesize that it will be heterotrophic, unlike many northern lakes and some fast-flowing streams.

CONCLUSIONS

Representative and accurate measurements of both autotrophic and heterotrophic production in lakes are essential parts of basic limnological research and lake monitoring, management, and restoration programs. We describe preliminary data that demonstrate the utility of a continuously recording, *in situ* respirometer for measuring diel oxygen production and consumption in lake water. The data can be used to compute P, R, P *vs.* I, P *vs.* T, P/R, P/B and other basic parameters of primary productivity and heterotrophic activity per unit volume of lake water or per unit chlorophyll. In combination with information on morphometry and water residence time, these volumetric production estimates can be used to compute integrated whole lake metabolism and production budgets.

We find that the *in situ* respirometer described above could be used to provide useful information on primary production and heterotrophic consumption at specific depths in a lake. Preliminary studies of P/R at 1 and 3 meter stations that span the euphotic zone in Lake Oglethorpe during stratification in August and after partial mixing in October indicated that the balance of metabolic processes shifts between these two experimental periods. The lake was heterotrophic (P/R< 1) throughout the water column in August, but autotrophic (P/R> 1) at the surface during turnover. Samples at the 3-meter station were heterotrophic during both experimental periods, indicating that a budget for the entire water column would result in an negative P/R even if surface production were temporarily high. Clearly, heterotrophic processes dominate the water column at these two times of the year. An annual cycle of P/R measurements will be made to determine P/R on an annual basis.

LITERATURE CITED

Bower, P.M., C.A. Kelley, E.J. Fee, J.A. Shearer, D. R. DeClerq, and D.W. Schindler. 1987. Simultaneous measurement of primary production by whole-lake and bottle radiocarbon additions. *Limnol. Oceanogr.* 32:299--312.

Carpenter, S.R., T.M. Frost, J.F. Kitchell, T.K. Kratz, D.W. Schindler, J. Shearer, W.G. Sprules, M.J. Vanni, and A.P. Zimmerman. 1991. Patterns of primary productivity and herbivory in 25 North American lake ecosystems. In: J. Cole, G. Lovett, and S. Findlay (eds.), *Comparative Analyses of Ecosystems*. Springer-Verlag, New York, NY.

Hall, C.A.S., and R. Moll. 1975. Methods of assessing aquatic primary productivity. In: H. Lieth and R. H. Whittaker (eds.), *Primary Productivity of the Biosphere.* Springer-Verlag, New York, NY.

Likens, G. 1975. Primary productivity of inland aquatic ecosystems. In: H. Lieth and R.H. Whittaker (eds.), *Primary Productivity of the Biosphere*, Springer-Verlag, New York, NY.

McDonough, R., R.W. Sanders, K. Porter, and D. Kirch man. 1986. Depth distribution of bacterial production in a stratified lake with an anoxic hypolimnion. *Appl. Environ. Microbiol.* 52:992-1000.

Pace, M., and J. Orcutt. 1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. *Limnol. Oceanogr.* 26:822-830.

Porter, J.W. 1980. Primary productivity in the sea: Reef corals *in situ*. pp. 403-410, In: P.G. Falkowski (ed.), *Primary Productivity in the Sea.* Plenum Press, New York, NY.

Porter, J.W., L. Muscatine, Z. Dubinsky, and P.G. Falkowski. 1984. Primary production and photoadaptation in light- and shade-adapted colonies of the symbiotic coral, *Stylophora pistillata*. *Proc. Roy. Soc. Lond., B* 222:161-180.

Porter, K.G. and J. Stockner. 1988. Microbial food webs in freshwater planktonic ecosystems. In: S.R. Carpenter (ed.), *Complex Interactions in Lake Communities*, Springer-Verlag, New York, NY.

Sanders, R.W., K.G. Porter, S.J. Bennett, and A.E. DeBiase. 1989. Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. *Limnol. Oceanogr.* 34: 673-687.

Schindler, D.W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *OIKOS* 57:25-41.

Schindler, D.W., K.G. Beaty, E.J. Fee, D.R. Cruikshank, E.R. DeBruyn, D.L. Findlay, G.A. Lindsaey, J.A. Shearer, M.P. Stainton, and M.A. Turner. 1990. Effects of climatic warming on lakes of the central oreal Forest. *Science* 250: 967-970.

Soballe, D.M. and B.L. Kimmel. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. *Ecology* 68: 1943-1950.

Wetzel, R.G., and G.E. Likens. 1991. *Limnological Analyses.* Springer-Verlag, New York, NY. 391 pp.