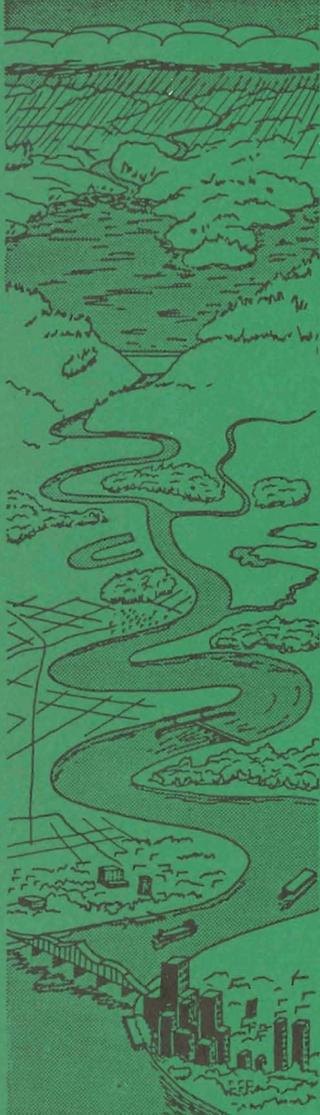




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SIZE DISTRIBUTION OF PLANKTONIC
AUTOTROPHY AND MICROHETEROTROPHY
IN DeGRAY AND WEST POINT RESERVOIRS:
A COMPARATIVE STUDY

by

Bruce L. Kimmel, Alan W. Groeger

Environmental Sciences Division
Oak Ridge National Laboratory
Oak Ridge, Tennessee 37831



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Particle size is an important determinant of food resources available to planktonic consumers and of the efficiency of energy transfer through planktonic foodwebs. Thus, the environmental factors controlling the size distributions of planktonic autotrophy (algal photosynthesis) and microheterotrophy (bacterial heterotrophic activity) are of considerable ecological interest. To examine hypotheses regarding their environmental control, the authors compared the size distributions of planktonic autotrophy and microheterotrophy within and between (Continued)		

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oligotrophic DeGray Reservoir (Arkansas) and eutrophic West Point Reservoir (Alabama-Georgia). Naturally occurring assemblages of reservoir phytoplankton and bacterioplankton were radiolabeled with sodium ^{14}C -bicarbonate and sodium ^3H -acetate and were size-fractionated by filtration through polycarbonate membrane filters.

Planktonic autotrophy in both reservoirs was dominated by microalgae, with usually >60% of the total photosynthetic carbon uptake associated with organisms in the <8.0- μm size fraction. Microheterotrophic activity in the 0.2- to 1.0- μm size fraction (indicative of small, free-living bacterioplankton rather than of large bacteria or bacteria attached to suspended particles) usually accounted for >80% of the planktonic microheterotrophy. Relative to marked uplake-to-downlake gradients in physical and chemical conditions, size distributions of autotrophy and microheterotrophy were remarkably uniform in both reservoirs. Uplake-to-downlake shifts in size distributions appear to correspond to within-reservoir transitions from riverine to lacustrine conditions; however, the specific environmental factors controlling the size distributions of planktonic autotrophy and microheterotrophy remain uncertain. Our results suggest that additional ecological factors (e.g., size-selective losses of cells by grazing and/or sinking, autotroph-microheterotroph interactions) must be considered, in addition to the availability of nutrients and suspended particles, as potential environmental controls on the size distributions of planktonic autotrophy and microheterotrophy.

PREFACE

This report was prepared by Dr. Bruce L. Kimmel and Mr. Alan W. Groeger, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tenn., for the US Army Engineer Waterways Experiment Station (WES) under Intra-Army Order No. WESRF-82-277. The study forms part of the Environmental and Water Quality Operational Studies (EWQOS) Program, Work Unit VIIA, Reservoir Field Studies. The EWQOS Program was funded by the Office, Chief of Engineers (OCE), US Army, and was assigned to the WES under the purview of the Environmental Laboratory (EL). The OCE Technical Monitors for EWQOS were Dr. John Bushman, Mr. Earl Eiker, and Mr. James L. Gottesman.

The study was conducted under the management of Dr. Robert H. Kennedy, Aquatic Processes and Effects Group (APEG), and under the general supervision of Dr. Thomas L. Hart, Chief, APEG, and Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division, EL. Dr. John Harrison was Chief, EL. Dr. Jerome Mahloch was Program Manager, EWQOS. Ms. Jessica Ruff, Publications and Graphic Arts Division, WES, was editor.

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SIZE DISTRIBUTION OF PLANKTONIC AUTOTROPHY AND MICROHETEROTROPHY
IN DeGRAY AND WEST POINT RESERVOIRS: A COMPARATIVE STUDY

PART I: INTRODUCTION

1. Ecologists' perceptions of the planktonic environment are shaped to a large extent by the methods used for collecting and examining plankton samples. For decades, views of plankton community structure and trophic interactions were restricted to organisms retained by a 64- μm pore size plankton net, i.e., the "net plankton." Smaller organisms that passed through the net (<64- μm , the "nanoplankton") were unnoticed until more process-oriented measurements revealed that these smaller organisms were responsible for much of the biomass and metabolic activity occurring in the planktonic environment (e.g., Rodhe et al. 1958, Holmes 1958, Yentsch and Ryther 1959, Pomeroy and Johannes 1968, Pomeroy 1974). More recent investigations of the size distributions of plankton biomass and metabolic activities using epifluorescence and scanning electron microscopy, radioisotopic labeling, differential filtration methods, and autoradiography have focused attention on progressively smaller organisms (e.g., see Sieburth et al. 1978, Kimmel 1983, Li et al. 1983, Platt et al. 1983, Ducklow 1983).

2. Hypotheses regarding the environmental factors controlling the size distributions of planktonic autotrophy and microheterotrophy in marine and freshwater systems focus primarily on the influence of nutrient availability (for autotrophy) and on the availability of nutrients and particle surfaces for bacterial attachment (for microheterotrophy). Because particle size is a primary determinant of metabolic rates, of food resources available to consumers, and of the efficiency of energy transfer through planktonic foodwebs (Ryther 1969; Gliwicz 1969; Parsons and Lebrasseur 1970; Kerr 1974; Sheldon et al. 1972, 1977), the environmental control of the size distributions of planktonic autotrophy and microheterotrophy is of considerable ecological interest.

3. Phytoplankton photosynthesis is the primary means of organic matter production in most planktonic systems. The contribution of nanoplankton (<64 μm) to phytoplankton production and biomass is

now well documented (e.g., Rodhe 1958, Ryther and Yentsch 1958, Holmes and Anderson 1963, Gilmartin 1964, Malone 1971, Kalff 1972, Kalff and Knoechel 1978) and recent studies have demonstrated the importance of ultrananoplankton (<8 μm) to algal community productivity in nutrient-poor planktonic environments (Munawar and Munawar 1975, Paerl 1977, Paerl and Mackenzie 1977, Ross and Duthie 1981, Li et al. 1983, Platt et al. 1983, Caron et al. 1985). The predominance of small algae in oligotrophic environments is usually attributed to high cell surface-to-volume ratios and a resulting enhanced ability to grow at low nutrient concentrations (Dugdale 1967, Eppley et al. 1969, Caperon and Meyer 1972, Parsons and Takahashi 1973, Friebele et al. 1978). The relative importance of larger algae generally increases in more productive systems (e.g., mesotrophic and eutrophic lakes, estuaries, upwelling and coastal marine environments) in which nutrient availability is higher (Kalff and Knoechel 1978, Malone 1980, Watson and Kalff 1981, Schlesinger et al. 1981).

4. Bacterial production can also be an important trophic resource for planktonic consumers (Pomeroy 1974, Sieburth 1976, Peterson et al. 1978, Porter et al. 1979, Ducklow 1983). Bacterial uptake of algal excretion products returns an otherwise unharvestable portion of the primary production to the grazer food chain (Paerl 1974, 1978; Cole 1982). In aquatic systems that receive considerable organic matter loading from their watersheds (e.g., streams, rivers, reservoirs, and riverine lakes), the microheterotrophic conversion of allochthonous dissolved organic matter (DOM) to bacterial biomass may significantly supplement ecosystem productivity (Rodina 1963, Kuznetsov 1968, Sorokin 1972, Marzolf 1984).

5. Bacterial association with suspended particles and detrital aggregates in nutrient-poor pelagic environments is believed to be mediated by adsorption of dissolved organic compounds and inorganic nutrients to particle surfaces, thus creating an enriched microenvironment for bacterial growth (e.g., Seki 1972; Jannasch and Pritchard 1972; Paerl and Goldman 1972; Paerl 1973, 1980). Fluvial inputs of suspended particles to reservoirs provide a large number of

particles and a high surface area for bacterial attachment and growth, but whether a similar enhancement of microbial activity is associated with suspended particle surfaces in higher nutrient environments, such as particle-rich reservoirs, remains uncertain (Goldman and Kimmel 1978). However, DOM adsorption and bacterial growth associated with suspended clay particles appear to be of major importance to zooplankton and fish production in Tuttle Creek Reservoir (Kansas), where phytoplankton production is limited by abiogenic turbidity (Marzolf 1980, Marzolf and Arruda 1981, Arruda et al. 1983, Adams et al. 1983).

6. There is no general agreement in the literature on the relative importance of free-living and attached bacteria in planktonic environments. Numerous investigators have observed bacterial colonization of suspended particles and microbial-detrital aggregates (Rodina 1963; Seki 1972; Paerl and Goldman 1972; Paerl 1973, 1975; Bent and Goulder 1981), but others have reported most bacterioplankton to be free-living (Wiebe and Pomeroy 1972, Hobbie and Rublee 1975, Ferguson and Rublee 1976, Palumbo et al. 1984). Measurements made in coastal and open ocean systems indicate that generally 80% or more of the bacterial biomass and activity is due to free-living rather than attached bacteria (Wiebe and Pomeroy 1972, Azam and Hodson 1977, Ducklow and Kirchman 1983), and similar results have been obtained for a variety of natural lakes (Paerl 1980) and reservoirs (Kimmel 1983). However, attached bacteria have been reported to dominate microheterotrophic activity in planktonic systems having high concentrations of suspended particles; e.g., near-shore waters in large lakes and in coastal regions (Paerl 1977, 1980) and turbid rivers (Jannasch 1956) and estuaries (Hanson and Wiebe 1977, Bent and Goulder 1981). The availability of bacterial production as food for planktonic grazers depends on the size of bacterial cells and the extent of bacterial association with larger suspended particles (Peterson et al. 1978, Hobbie and Wright 1979, Kimmel 1983, Palumbo et al. 1984).

7. Kimmel (1983) surveyed several reservoirs of differing trophic status and reported that microalgae ($<8.0 \mu\text{m}$) and free-living

bacteria ($<1.0 \mu\text{m}$) were primarily responsible for planktonic autotrophy and microheterotrophy, respectively, in the impoundments examined. However, his sampling was limited spatially and temporally. Here we report the results of more thorough seasonal and spatial sampling of two limnologically dissimilar impoundments: West Point Reservoir, a eutrophic impoundment of the Chattahoochee River in southwestern Georgia, and DeGray Reservoir, an oligotrophic impoundment of the Caddo River in south-central Arkansas.

8. Previous studies of West Point and DeGray reservoirs, conducted under the auspices of the Corps of Engineers Environmental and Water Quality Operational Studies (EWQOS) Program, had shown that marked trophic and water quality differences existed between the two reservoirs and that both impoundments possessed well-defined longitudinal gradients in nutrient concentrations, water clarity, algal biomass, and phytoplankton productivity (Thornton et al. 1982, Kennedy et al. 1982, Bayne et al. 1983). Therefore, in addition to making seasonal and between-lake comparisons, this within-reservoir spatial heterogeneity allowed us to examine phytoplankton-bacterioplankton responses to gradients of those environmental factors (nutrient availability, suspended particle levels) hypothesized to control the size distributions of planktonic autotrophy and microheterotrophy. Based on the postulated relationships reviewed above, we advanced the working hypotheses listed in Table 1.

Table 1

Summary of Working Hypotheses Advanced a priori to Predict the Size Distributions of Planktonic Autotrophy and Microheterotrophy in Terms of Nutrient Availability and the Availability of Suspended Particles for Bacterial Attachment

Hypothesis 1: If the size distribution of planktonic autotrophy is controlled primarily by nutrient availability, then the relative importance of photosynthetic production by "large" ($>8 \mu\text{m}$) algae should

- a. be less in summer than in winter,
- b. be less in nutrient-poor DeGray Reservoir than in relatively nutrient-rich West Point Reservoir, and
- c. decrease from uplake to downlake along the longitudinal axes of the reservoirs.

Hypothesis 2: If the size distribution of planktonic microheterotrophy is controlled primarily by nutrient availability, then the relative importance of attached bacteria ($>1.0 \mu\text{m}$) should

- a. be greater in summer than in winter,
- b. be greater in DeGray Reservoir than in West Point Reservoir, and
- c. increase from uplake to downlake.

Hypothesis 3: Alternatively, if the primary environmental control on the size distribution of planktonic microheterotrophy is the availability of particle surfaces for bacterial attachment, the relative importance of attached bacteria ($>1.0 \mu\text{m}$) should be

- a. directly related to suspended particle concentrations (and, therefore, inversely related to Secchi depth),
 - b. be greater in particle-rich West Point Reservoir than in particle-poor DeGray Reservoir, and
 - c. decrease from uplake to downlake.
-

PART II: DESCRIPTION OF STUDY SITES

West Point Reservoir

9. West Point Reservoir (Fig. 1, Table 2), Alabama-Georgia, was formed in 1975 by impoundment of the Chattahoochee River near Lagrange, Georgia. Its drainage basin is large (8910 km²) relative to the lake surface area (drainage basin area-to-lake surface area ratio = 85) and

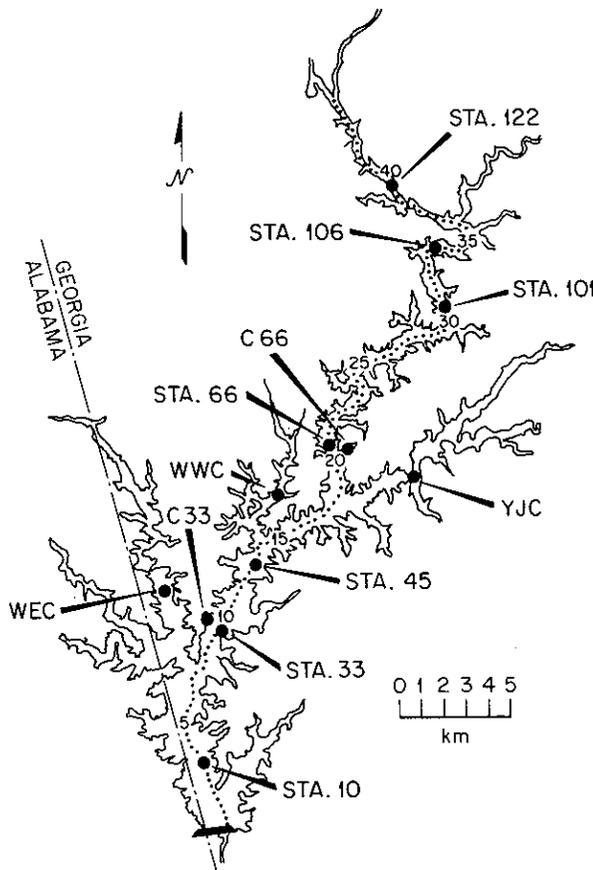


Fig. 1. West Point Reservoir, Alabama-Georgia, an impoundment of the Chattahoochee River located in southwestern Georgia. The submersed river channel (thalweg) and the distance (in kilometers) upstream from the dam are represented by the dotted line and interspersed numerals, respectively. Channel and cove sampling stations are also shown

Table 2
Morphologic, Hydrologic, and Productivity-Related Data for DeGray and
 West Point Reservoirs

<u>Characteristics</u>	<u>West Point</u>	<u>DeGray</u>
Location	Ga.-Ala.	Ark.
River impounded	Chattahoochee	Caddo
Year impounded	1975	1969
Lake surface area, ha	10,467	5,431
Watershed area-to-surface area ratio	85	22
Lake volume, m ³ x 10 ⁶	735	808
Mean depth, m	7	15
Maximum depth, m	21	59
Outlet depth, m	21	6
Mean annual water retention time, d	58	420
Mean annual water level fluctuation, m	4	6
Total reservoir length, km	53	45
Shoreline length, km	845	333
Shoreline development	23	13
Total dissolved solids, (µg l. ⁻¹)	40	55
Length of growing season, d	218	215
Mean phytoplankton productivity (µg C m ⁻² d ⁻¹)	684 ^a	199 ^b
Morphoedaphic index (MEI) ^c	5.1	3.7

a 1976-1979 ¹⁴C method estimates, Bayne et al. (1983).

b 1978-1979 ¹⁴C method estimates, R. H. Kennedy (unpublished data).

c MEI [= total dissolved solids (mg l.⁻¹)/mean depth (m)] is often used by fishery biologists as an indicator of the relative biological productivity of lakes and reservoirs.

the reservoir receives runoff from both the Blue Ridge Mountains and the Piedmont province. Both regions have relatively infertile soils, but erosion products from the Piedmont province include clays and silts that result in high abiotic turbidity in the reservoir following periods of high watershed runoff (Kennedy et al. 1982, Bayne et al. 1983). Land-use activities within the drainage basin are primarily agricultural (70%) and residential/industrial (30%). The impoundment is located 110 km downstream from Atlanta, Georgia, and receives treated domestic and industrial effluents from ~50% of the Atlanta metropolitan area in addition to runoff from nonpoint, agricultural sources (Kennedy et al. 1982, Bayne et al. 1983).

10. West Point Reservoir is highly dendritic, relatively shallow, rapidly flushed, moderately turbid, and biologically productive in comparison to DeGray Reservoir (Table 2). The dam outlet (at 21 m) allows a hypolimnetic release. Based on ^{14}C -method phytoplankton productivity measurements made during 1976-1979 (Bayne et al. 1983), West Point Reservoir falls in the mesotrophic-to-eutrophic range (Likens 1975; Wetzel 1975; Kimmel et al., in press).

DeGray Reservoir

11. DeGray Reservoir (Fig. 2, Table 2) was formed in 1969 by the impoundment of the Caddo River near Arkadelphia, Arkansas. The Caddo River above the reservoir drains a relatively small (1162 km²; drainage basin area-to-lake surface area ratio = 22), infertile, and mostly forested watershed in the Ouachita Highlands of south-central Arkansas. DeGray Reservoir is less dendritic than West Point Reservoir and is smaller on an areal basis. However, it is much deeper and its volume exceeds that of West Point. DeGray Reservoir flushes more slowly, undergoes stronger thermal stratification during the growing season, and, because of its less erodible drainage basin, the reservoir water is usually clear. The DeGray dam has a selective-withdrawal outlet structure; releases were from the metalimnion (6 m) during the period of this study.

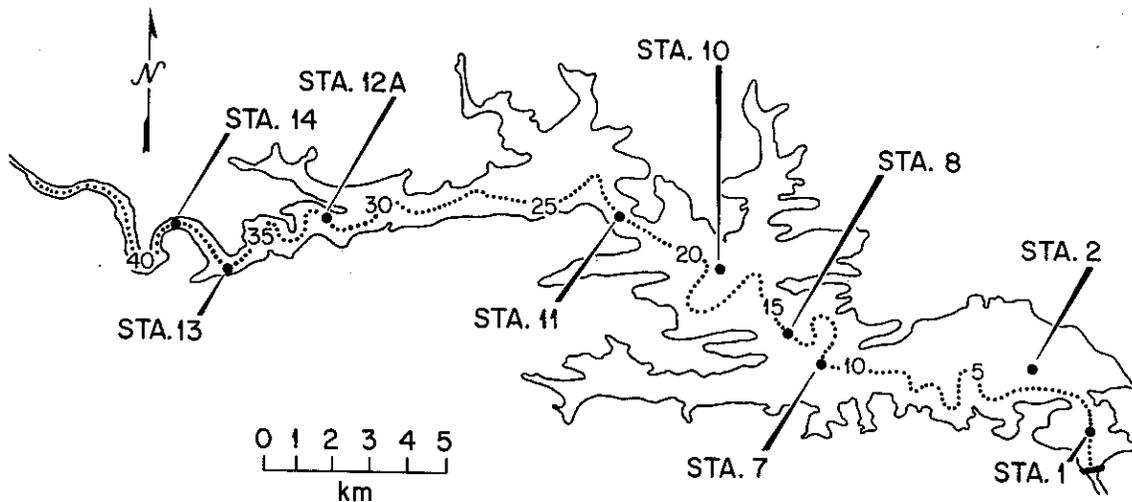


Fig. 2. DeGray Reservoir, an impoundment of the Caddo River located in south-central Arkansas. The thalweg and the distance (in kilometers) upstream from the dam are indicated by the dotted line and interspersed numerals, respectively. Sampling stations located along the longitudinal axis of the reservoir are also shown

12. In contrast to West Point Reservoir, DeGray Reservoir does not receive large point-source nutrient inputs and its phosphorus and nitrogen loading rates are relatively low ($0.22 \text{ g P m}^{-2} \text{ yr}^{-1}$ and $3.6 \text{ g N m}^{-2} \text{ yr}^{-1}$, USEPA 1978). DeGray Reservoir is considerably less productive than West Point Reservoir, falling in the oligotrophic range as indicated by ^{14}C -uptake productivity estimates during 1978-1979 (R.H. Kennedy, unpublished data; Kimmel et al., in press).

PART III: METHODS AND MATERIALS

Field Sampling and Measurements

13. West Point Reservoir was sampled in midsummer (21-22 July 1981) and in midwinter (25 February 1982). DeGray Reservoir was sampled on three occasions (31 August to 2 September 1982, 1-4 February 1983, and 21-23 June 1983) representative of late-summer, midwinter, and early summer conditions, respectively. Locations of sampling stations are shown in Figs. 1 and 2.

14. During each sampling trip, we obtained mixed-layer samples (from 1- to 2-m depths) from stations located along the reservoir longitudinal axis. We also sampled several coves in West Point Reservoir to compare cove and channel productivities and size distributions of planktonic autotrophy and microheterotrophy. Vertical series of samples were obtained at DeGray Reservoir to evaluate the variability in size distributions with depth in a well-stratified reservoir. Due to the well-mixed nature and high turbidity of West Point Reservoir, we conducted minimal vertical sampling there.

15. Water samples were collected with an opaque Van Dorn sampler in West Point Reservoir and with a submersible pump connected to a weighted opaque hose in DeGray Reservoir. Water temperature, dissolved oxygen, pH, and specific conductance were measured in situ with either a Hydrolab or a Martek monitoring system. Photosynthetically active radiation (PAR, 400-700 nm) was measured with a Li-Cor quantum meter equipped with a spherical submersible sensor. At West Point Reservoir, in vivo chlorophyll fluorescence (IVF) was determined on discrete water samples using an Aminco fluorocolorimeter. At DeGray Reservoir, IVF was measured using the pump sampling system and a Turner Designs field fluorometer equipped with a large-volume, flow-through cuvette (Lorenzen 1966). Dissolved nutrients, chlorophyll a concentrations, and phytoplankton productivity were estimated by standard automated methods using a Technicon autoanalyzer (Stainton et al. 1974), methanol extraction (Marker et al. 1980), and ^{14}C uptake (Goldman 1963, Vollenweider 1971), respectively.

Size Distribution Determinations

16. Size distributions of planktonic autotrophy and microheterotrophy were determined by isotopic labeling and differential filtration of natural phytoplankton-bacterioplankton assemblages (Kimmel 1983). Subsamples in 130-mL light and dark bottles were inoculated with 0.5 mL $\text{NaH}^{14}\text{CO}_3$ solution (56.5 mCi mmol^{-1} specific activity, $5.5 \mu\text{Ci mL}^{-1}$) and 0.1 mL sodium ^3H -acetate (10 Ci mmol^{-1} , $25.0 \mu\text{Ci mL}^{-1}$; $0.5 \mu\text{g L}^{-1}$ acetate enrichment over ambient concentration) to label autotrophs and microheterotrophs, respectively, and incubated in situ for 4-5 h.

17. Mixed-layer water samples were obtained at stations along the longitudinal axes of both reservoirs and from cove stations in West Point Reservoir (Figs. 1 and 2), as described above. These samples were incubated at a single station in each reservoir at the depth of photosynthetically saturating light ($150\text{--}300 \mu\text{E m}^{-2} \text{s}^{-1}$). Vertical profile samples from DeGray Reservoir were incubated at the depths from which they were taken. All West Point samples and the September and February DeGray samples were double-labeled (inoculated with both ^{14}C -bicarbonate and ^3H -acetate). However, because of problems in detecting adequate ^3H activity in size-fractionated February samples from DeGray Reservoir, all June samples were inoculated separately. In all cases, selected samples were poisoned with 1 mL saturated HgCl_2 solution, inoculated with $\text{NaH}^{14}\text{CO}_3$ and sodium ^3H -acetate solutions, and incubated as described above to provide a correction for abiotic adsorption of radioisotopes to filters and retained particles.

18. Immediately after incubation, 10- to 15-mL aliquots from each sample were gently vacuum-filtered ($<13 \text{ kPa} = <100 \text{ mm Hg}$ pressure difference) in parallel through 47-mm Nucleopore polycarbonate filters of 0.2-, 1.0-, 3.0-, and 8.0- μm pore diameters. Filters and retained particles were rinsed three times with deionized water and placed in plastic minivials. Aquasol scintillation fluor (6 mL) was added to each minivial, and all samples were radioassayed using a Packard 4640

liquid scintillation spectrometer. We used automatic external standardization, calibrated with quenched series of ^{14}C and ^3H standards, to correct for sample quenching.

19. Planktonic autotrophy was estimated as the difference between light- and dark-bottle ^{14}C uptake, and microheterotrophy was estimated as ^3H uptake in the dark. All samples were corrected for abiotic radioisotope adsorption. Size distributions of autotrophic and microheterotrophic activities were expressed as percentages of the activity retained by the 0.2- μm filter.

Data Analysis

20. Analysis of variance (ANOVA) was used to test for differences among data groups, and relationships between variables were tested by linear correlation analysis (Sokal and Rohlf 1969, SAS Institute 1982). We used longitudinal series, mixed-layer samples as within-lake replicates to compare seasonal and between-lake differences in physical-chemical variables, phytoplankton productivity, planktonic microheterotrophy, and size distributions of autotrophic and microheterotrophic activities. In doing so, the relatively high degree of spatial variability in these variables within each reservoir results in conservative statistical tests for significant differences between reservoirs and among sampling dates. An arcsine transformation was applied to size distribution data (expressed as the percent of the total autotrophic or microheterotrophic activity in a stated particle size fraction) prior to statistical analysis, as recommended by Sokal and Rohlf (1969) for data expressed as percentages or proportions. All references to statistical significance are for the $P < 0.05$ level, unless stated otherwise.

PART IV: RESULTS AND DISCUSSION

Vertical Patterns of Planktonic Autotrophy
and Microheterotrophy in DeGray Reservoir

Autotrophy

21. Phytoplankton productivity at the depth of maximum photosynthesis (P_{max}) was highest in February and lowest in September in DeGray Reservoir; however, integral productivity did not vary greatly on a seasonal basis (19, 23, and 25 $mg\ C \cdot m^{-2} \cdot h^{-1}$ in September, February, and June, respectively) because of a progressive increase in the depth of the euphotic zone (Fig. 3) and in the degree of algal nutrient deficiency from winter to late summer (Groeger and Kimmel, in press). In vertical profile samples, an average of 66%

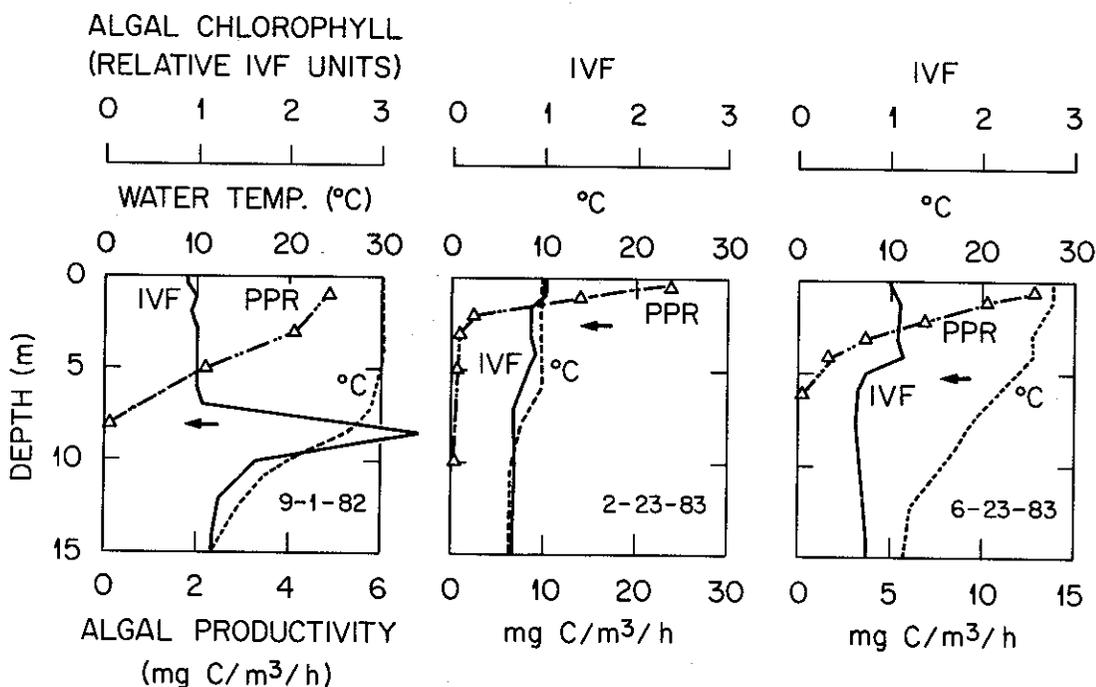


Fig. 3. Representative vertical profiles of water temperature, algal biomass [as indicated by in vivo chlorophyll fluorescence (IVF) measurements], and phytoplankton productivity (PPR, as measured by ^{14}C uptake) for September 1982, February 1983, and June 1983 sampling dates. Arrows indicate the depth of the euphotic layer (= 1% surface light penetration). Note that the PPR scales differ for each date

($\bar{X} \pm 95\% \text{ CI} = 66.4 \pm 11.2\%$) of the total autotrophic activity was associated with $<8\text{-}\mu\text{m}$ particles (Fig. 4). We anticipated that, during stratified conditions, planktonic autotrophy associated with $<8.0\text{-}\mu\text{m}$ particles would be more important in the nutrient-depleted DeGray Reservoir mixed layer than in more nutrient-rich euphotic portions of the metalimnion and hypolimnion. However, we were unable to test this hypothesis in DeGray Reservoir since light availability restricted significant planktonic autotrophy to the mixed layer (Fig. 3).

22. Vertical changes in the size distribution of autotrophy were not statistically demonstrable because of the low number of samples from the euphotic zone ($>1\%$ surface light); however, the relative importance of the $>3\text{-}\mu\text{m}$ size fraction appeared to decline with increasing depth in the upper portion of the euphotic zone (Fig. 4b).

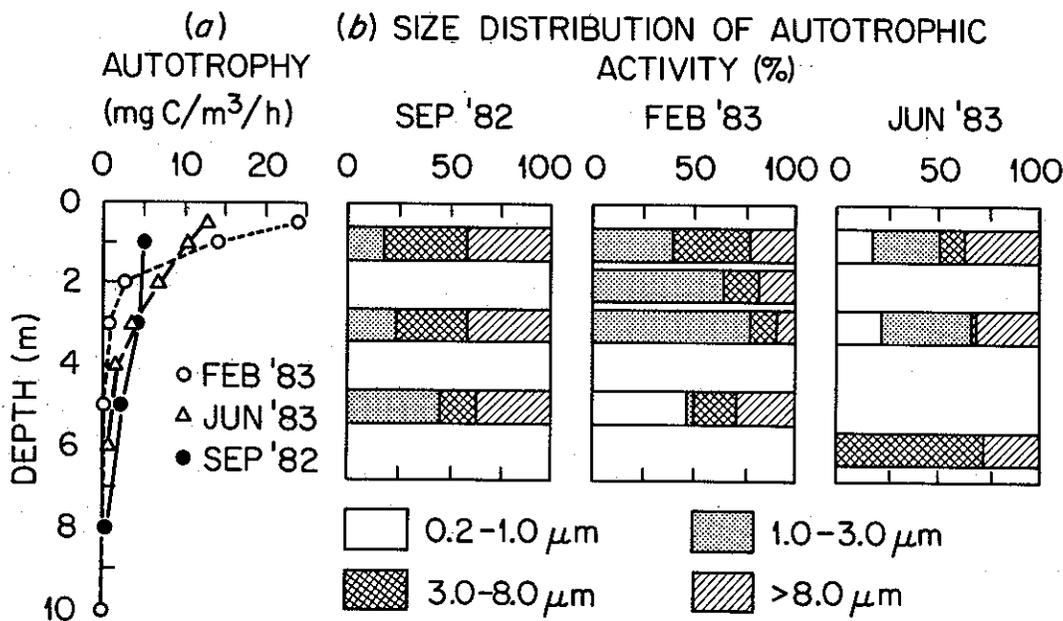


Fig. 4. (a) Vertical distributions of total planktonic autotrophy for 1 September 1982, 23 February 1983, and 23 June 1983 at lacustrine stations in DeGray Reservoir. (b) Changes in the size distribution of autotrophic activity with water column depth

At greater depths and at very low light levels (<1% surface light), the fraction of total autotrophy associated with >3- μm particles increased (at 5 m in February and at 6 m in June, Fig. 4b).

23. These results are of interest in regard to the influences of nutrient and light availability on size-dependent phytoplankton growth. Much research has indicated that small algal cells (e.g., nanoplankton) have a competitive advantage over larger cells with respect to nutrient uptake and cell growth in nutrient-poor environments. However, some algal growth models assume that both growth and respiration rates are inversely related to cell size and, therefore, predict that large cells should grow faster than small cells at low light intensity (Laws 1975, Shuter 1979, Schlesinger et al. 1981). In DeGray Reservoir, almost all of the autotrophic activity occurs in size fractions smaller than those specifically considered in algal growth models. However, the observed decrease in the relative importance of autotrophy in the >3.0- μm size fraction with depth in the euphotic zone does not support the hypothesis that the competitive advantage of small cells is reduced at low light intensities.

Microheterotrophy

24. Levels of planktonic microheterotrophy, as indicated by ^3H -acetate uptake, were significantly higher [ANOVA, $F_{(2,13)} = 29.4$, $P < 0.01$] in September 1982 than in February and June 1983 (Fig. 5a). Surprisingly, even in September when the vertical structure of water temperature, algal biomass, and phytoplankton productivity was most pronounced (Fig. 3), microheterotrophic activity did not vary significantly with depth ($r = -0.40$, 6 df, NS) (Fig. 5a).

25. Microheterotrophy was dominated (usually >75%) by the <1.0- μm size fraction in September and June samples, indicating uptake by free-living bacterioplankton rather than by bacteria associated with larger suspended particles, such as algae or detrital aggregates. The September 1982 vertical profile (Fig. 5b) shows that the importance of attached or aggregated bacteria (>1 μm) was low ($\bar{X} = 9.8\%$, range = 7.5-11.7% of the total microheterotrophic activity)

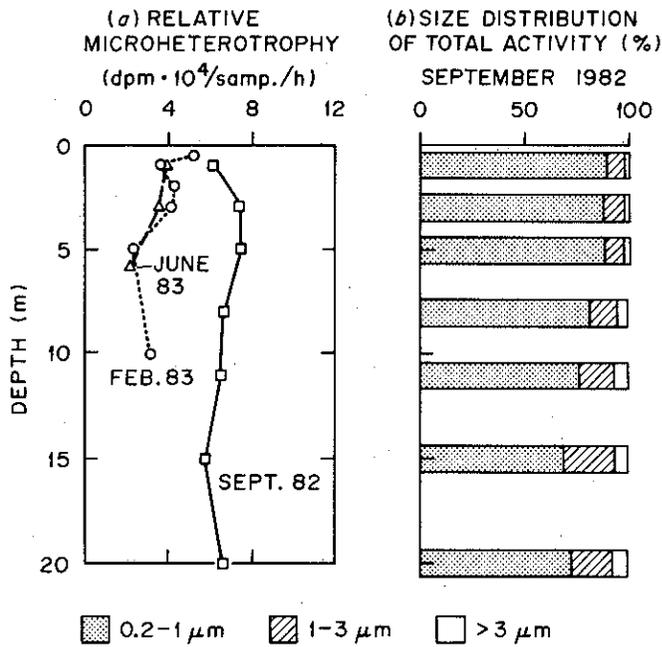


Fig. 5. (a) Vertical distribution of planktonic microheterotrophy (as indicated by ³H-acetate uptake) for 1 September 1982, 23 February 1983, and 23 June 1983 in DeGray Reservoir (dpm = disintegrations per minute). (b) Changes in the size distribution of microheterotrophic activity with water column depth for 1 September 1982

in the mixed layer (0 to 7 m), but increased significantly [ANOVA, $F_{(1,5)} = 37.6$, $P < 0.01$] in the metalimnion and hypolimnion ($\bar{X} = 24.1\%$, range = 18.6-26.4%). This shift toward larger particle sizes with depth may have resulted from decreased availability of labile dissolved organic matter (DOM) supplied by algal excretion and/or from increased concentrations of algal-derived particulate organic detritus. However, even in metalimnetic and hypolimnetic samples, microheterotrophic activity associated with particles $>3.0 \mu\text{m}$ was usually $<10\%$ ($\bar{X} = 9.1\%$, range = 6.2-10.8%) of the total.

Longitudinal, Seasonal, and Between-Lake Differences

26. Phytoplankton productivity was higher [$F_{(1,9)} = 5.67$, $P < 0.05$] in summer than in winter in West Point Reservoir (Fig. 6). However, seasonal changes in lake-wide phytoplankton productivity levels were not statistically different in unproductive DeGray Reservoir [ANOVA, $F_{(2,13)} = 2.81$, NS]. Seasonal differences in microheterotrophic activity in DeGray Reservoir were statistically significant [$F_{(2,13)} = 50.98$, $P < 0.01$] with levels in June 1983

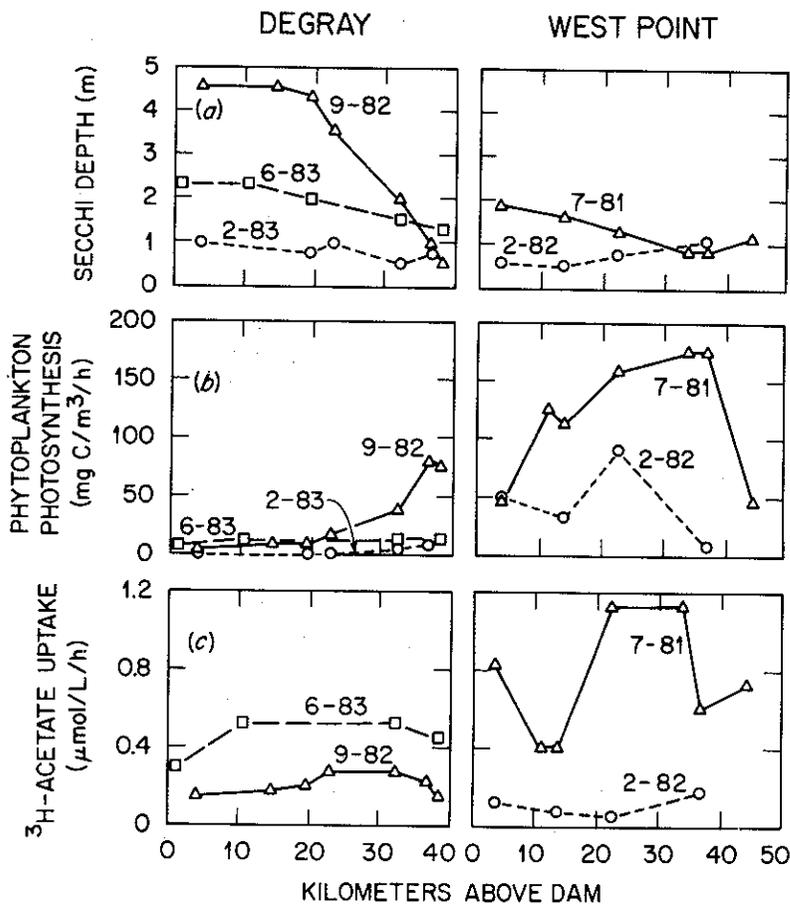


Fig. 6. Longitudinal patterns in (a) Secchi depth measurements, (b) phytoplankton productivity (autotrophy), and (c) planktonic microheterotrophy in DeGray and West Point reservoirs. Dissolved inorganic nitrogen and soluble reactive phosphorus concentrations showed similar longitudinal patterns in DeGray Reservoir but are not presented. Nutrient data are lacking for West Point Reservoir

> September 1982 > February 1983. Similarly, large seasonal differences in levels of microheterotrophy occurred in West Point Reservoir [$F_{(1,9)} = 16.21$, $P < 0.01$]. As expected, both summer PPR and microheterotrophy were much higher in eutrophic West Point Reservoir than in oligotrophic DeGray Reservoir [$F_{(2,15)} = 12.09$, $P < 0.01$ for autotrophy; $F_{(2,15)} = 12.25$, $P < 0.01$ for microheterotrophy] (Fig. 6).

27. Longitudinal gradients in mixed-layer planktonic autotrophy were most pronounced in mid-to-late summer (September 1982 in DeGray, July 1981 in West Point) in both reservoirs (Fig. 6). Phytoplankton productivity (m^{-3}) was high in the upper portion of DeGray Reservoir in September, decreased rapidly toward midlake, and then declined to <10% of the uplake level in the lower portion of the reservoir. Except for the most riverine station (station 122), where productivity was probably light-limited, planktonic autotrophy in West Point Reservoir during midsummer showed a similar, but more gradual, uplake-to-downlake decline (Fig. 6).

28. Microheterotrophic activity was relatively constant along the longitudinal axis of DeGray Reservoir, decreasing only slightly from uplake-to-downlake stations in June and September (Fig. 6). Microheterotrophy was more variable in West Point, increasing just downlake of the most riverine portion of the impoundment (at stations 106 and 66, Fig. 1) and decreasing again further downlake. In both reservoirs, winter levels for microheterotrophy were lower than summer levels, in correspondence with lower water temperature ($\sim 10^{\circ} C$) and decreased algal production.

29. On the average, both autotrophy and microheterotrophy were slightly higher at channel stations than at cove stations in West Point Reservoir in July 1981 (Table 3). However, because of variability among stations, differences in cove and channel stations were not statistically significant for either July or February samples.

30. To examine the occurrence of longitudinal gradients in environmental variables and the relationships between nutrient availability, suspended particle availability, and planktonic

Table 3

Near-Surface Planktonic Autotrophy ($\text{mg C m}^{-3} \text{ h}^{-1}$) and Microheterotrophy ($\text{mmol } ^3\text{H-Acetate Uptake L}^{-1} \text{ h}^{-1}$) at Channel and Cove Stations in West Point Reservoir on Summer and Winter Sampling Dates. [Data are Expressed as Means \pm Standard Deviations (SD), with the Number of Samples (n) in Parentheses. Differences Between Channel and Cove Stations Were Not Statistically Significant ($P > 0.05$) on Either Date.]

<u>Date</u>	<u>Sampling Stations</u>	
	<u>Channel</u>	<u>Cove</u>
21 July 1981		
Autotrophy	119.0 \pm 55.0 (7)	96.6 \pm 48.7 (5)
Microheterotrophy	0.74 \pm 0.31 (7)	0.49 \pm 0.24 (5)
23 February 1982		
Autotrophy	45.5 \pm 34.8 (4)	68.0 \pm 76.2 (2)
Microheterotrophy	0.11 \pm 0.05 (4)	0.02 \pm 0.01 (2)

autotrophy and microheterotrophy, we calculated linear correlation coefficients for relationships between physical, chemical, and biological variables during summer sampling periods (September 1982 and June 1983) in DeGray Reservoir (Table 4). Total autotrophy, soluble reactive phosphorus (SRP) and $\text{NO}_3 + \text{NO}_2\text{-N}$ concentrations, chlorophyll a, total algal cells, and Cyanobacterial dominance of the algal assemblage were all significantly ($P < 0.05$) and positively correlated with station distance upstream from the dam; water transparency (as Secchi depth) was inversely related to station distance above the dam and to total autotrophy. SRP and total algal

Table 4

Linear Correlation Coefficients (r) for Variables Associated with Total Planktonic Autotrophy and Microheterotrophy in DeGray Reservoir, September 1982 and June 1983. [The Number in Parentheses Indicates the Number of Observations (n).]

	<u>Distance Above Dam</u>	<u>Total Autotrophy</u>	<u>Total Microhet.</u>
Distance above dam	1.0	0.65(11) ^b	0.13(11)
Total autotrophy	0.65(11) ^b	1.0	-0.31(11)
Total microheterotrophy	0.13(11)	-0.31(11)	1.0
SRP	0.42(12)	0.70(11) ^b	0.09(11)
NH ₄ -N	-0.15(12)	-0.39(11)	0.80(11) ^b
NO ₃ + NO ₂ -N	0.73(12) ^c	-0.48(11)	0.09(11)
Dissolved organic carbon (DOC)	-0.81(5) ^a	-0.56(4)	-0.15(4)
Secchi depth	-0.67(12) ^b	-0.67(11) ^b	-0.39(11)
Chlorophyll a	0.95(5) ^b	0.70(4)	0.37(4)
Total algal cells	0.69(11) ^b	0.70(10) ^b	-0.03(10)
% Cyanobacteria	0.83(10) ^c	0.40(9)	-0.03(9)

a p < 0.10.

b p < 0.05.

c p < 0.01.

cells were positively related to total autotrophy; however, only the NH₄-N concentration was significantly correlated with total microheterotrophy.

Size Distributions of Planktonic Autotrophy and Microheterotrophy

Seasonal patterns

31. Particle size distributions of planktonic autotrophy and microheterotrophy for longitudinal stations in DeGray Reservoir (Fig. 7) and for channel and cove stations in West Point Reservoir (Fig. 8) showed a remarkable degree of uniformity within and between reservoirs except for the February 1982 West Point samples (Fig. 8b). The winter West Point data represent an exception to the general size distribution patterns and, therefore, are discussed separately below.

32. Otherwise, differences between channel and cove stations in West Point Reservoir (Fig. 8) were not statistically significant for autotrophy or microheterotrophy. Although there were no significant differences among individual sampling dates for DeGray Reservoir, autotrophy in the >3- and >8- μm size fractions was more important ($P < 0.05$) in summer (September and June samples) than in winter (February samples) (Table 5). Surprisingly, >8- μm autotrophic activity was significantly higher in DeGray than in West Point samples during the summer. In general, the planktonic autotrophy was about equally distributed among the 1.0- to 3.0- μm , 3.0- to 8.0- μm , and >8.0- μm particle size fractions, with about 30% of the total autotrophic activity in each (Table 5, pooled data). Usually little if any autotrophic activity (<5% of the total) was detected in the <1.0- μm fraction (however, see size distributions for West Point cove stations WWC, YJC, and WEC, July 1981; Fig. 8a).

33. The size distribution of planktonic microheterotrophy was also uniform seasonally, within, and between reservoirs (Figs. 7 and 8). With the exception of the February 1982 West Point samples, usually >80% ($\bar{X} \pm \text{SD} = 86.1 \pm 0.84\%$, $n = 24$) of the total microheterotrophic activity was associated with the <1.0- μm size

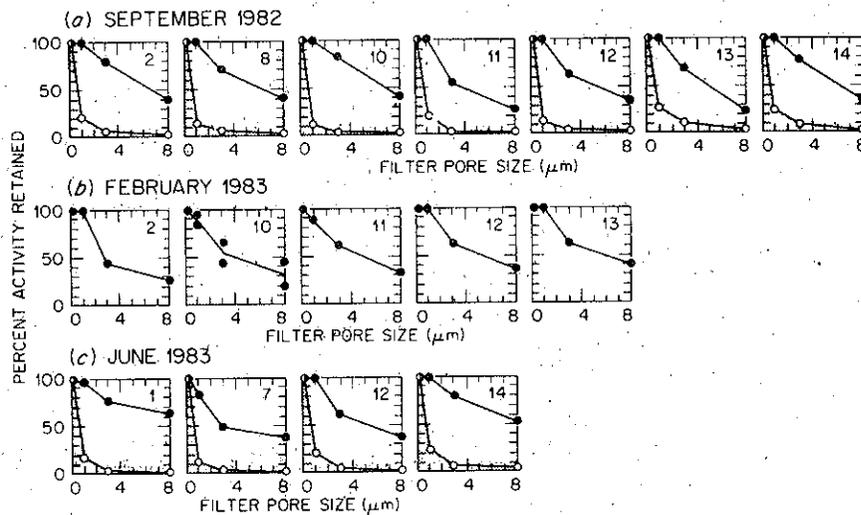


Fig. 7. Size distributions of planktonic autotrophy and microheterotrophy in near-surface (1- to 2-m) samples from selected stations along the longitudinal axis of DeGray Reservoir on (a) 2 September 1982, (b) 25 February 1983, and (c) 21 June 1983.

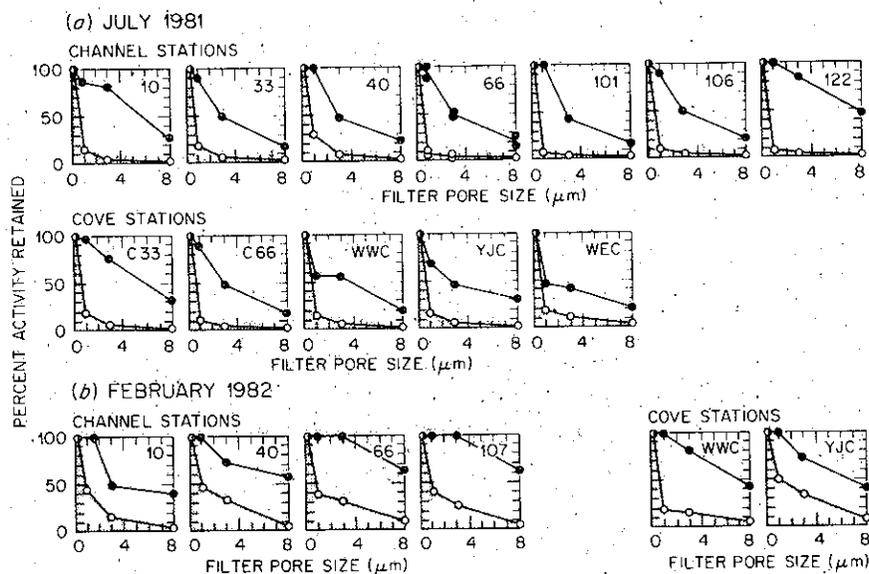


Fig. 8. Size distributions of planktonic autotrophy and microheterotrophy in near-surface (1-m) samples from channel and cove sampling stations in West Point Reservoir on (a) 21-22 July 1981 and (b) 23 February 1982.

Table 5
Percentages of the Total Planktonic Autotrophy Associated with Specific Particle Size Fractions in DeGray and West Point Reservoirs. [Data are Expressed As Means + 95% CI for Near-Surface Samples (n = Number of Samples). Locations of Sampling Stations Are Shown in Figs. 1 and 2.]

<u>Lake/Season</u>	<u>n</u>	<u>Particle Size Fractions (μm)</u>			
		<u>0.2-1.0</u>	<u>1.0-3.0</u>	<u>3.0-8.0</u>	<u>>8.0</u>
<u>DeGray</u>					
Summer	11	0.31 \pm 0.34	28.79 \pm 0.19	28.80 \pm 0.30	39.25 \pm 0.26
Winter	5	1.63 \pm 0.90	37.53 \pm 0.55	25.14 \pm 0.16	32.21 \pm 0.31
<u>West Point</u>					
Summer	13	10.99 \pm 1.28	26.64 \pm 1.12	30.99 \pm 0.17	22.66 \pm 0.16
Winter	6	0.05 \pm 0.30	14.89 \pm 10.97	26.69 \pm 2.72	50.67 \pm 1.38
<u>Lakes Pooled</u>					
Summer	24	4.28 \pm 0.60	27.62 \pm 0.36	29.98 \pm 0.11	29.95 \pm 0.17
Winter	11	0.62 \pm 1.20	26.25 \pm 4.34	25.85 \pm 0.83	40.58 \pm 1.23
Winter	5	[-----[As above for DeGray - Winter-----]]			
<u>Lakes and Seasons Pooled^a</u>	29	3.58 \pm 0.41	29.78 \pm 0.25	28.86 \pm 0.08	30.45 \pm 0.11

^a Excludes West Point February 1982 data.

fraction, indicative of small, free-living bacteria. Of the microheterotrophy due to bacteria associated with $>1\text{-}\mu\text{m}$ particles, most was in the 1.0- to $3.0\text{-}\mu\text{m}$ size fraction ($\bar{X} \pm \text{SD} = 9.9 \pm 0.8\%$, $n = 24$) with usually $<5\%$ ($\bar{X} \pm \text{SD} = 3.8 \pm 0.3\%$, $n = 24$) of the total activity associated with particles $>3 \mu\text{m}$ (Table 6).

February data from West Point Reservoir

34. Size distributions of planktonic autotrophy and microheterotrophy in West Point Reservoir during February 1982 are markedly shifted toward larger particle size fractions ($>8 \mu\text{m}$ for autotrophy, $>3 \mu\text{m}$ for microheterotrophy) and are significantly

Table 6
Percentages of the Total Planktonic Microheterotrophy Associated with Specific Particle Size Fractions in DeGray and West Point Reservoirs. [Data Are Expressed As Means Plus 95% CI for Near-Surface Samples (n = Number of Samples). Locations of Sampling Stations Are Shown in Figs. 1 and 2.]

Lake/Season	n	Particle Size Fractions (μm)			
		0.2-1.0	1.0-3.0	3.0-8.0	>8.0
DeGray					
Summer	11	83.33 \pm 0.09	12.82 \pm 0.06	2.51 \pm 0.06	1.06 \pm 0.02
Winter	0				
West Point					
Summer	13	88.31 \pm 0.15	7.62 \pm 0.13	2.88 \pm 0.03	0.75 \pm 0.01
Winter	6	61.69 \pm 1.66	12.40 \pm 2.20	19.24 \pm 1.01	5.07 \pm 0.37
Lakes Pooled					
Summer	24	86.12 \pm 0.07	9.86 \pm 0.06	2.71 \pm 0.02	1.00 \pm 0.01
Winter	6	[---As above for West Point - Winter---]			
Lakes and Seasons Pooled ^a	24	[---As above for Lakes Pooled - Summer---]			

^a Excludes West Point February 1982 data.

different (ANOVA, $P < 0.01$) from those for West Point July 1981 samples and from all DeGray Reservoir samples (Figs. 7 and 8, Tables 5 and 6). Our winter sampling of West Point Reservoir followed a prolonged period of precipitation and high watershed inflow that resulted in very turbid conditions within the reservoir. Abiogenic turbidity caused by suspended silts and clays was quite high (vertical extinction coefficient, n'' , $\bar{X} \pm \text{SD} = 3.16 \pm 0.57$, $n = 5$; Secchi depth $\bar{X} \pm \text{SD} = 0.64 \pm 0.15$ m, $n = 5$) within coves and the main body of the impoundment relative to that in the reservoir headwaters ($n'' = 1.55$, Secchi depth = 1.3 m at station 107), where clearer water was entering the reservoir. The concurrence of high abiogenic turbidity (reflecting elevated concentrations of suspended silt and clay particles in the water column) and significant shifts in the size distributions of autotrophy and microheterotrophy toward larger particle sizes strongly suggests an interaction between suspended silts and clays and planktonic algae and bacteria.

35. Our previous experimental results (Kimmel 1981) and the results of others (Aynimelech et al. 1982) indicate that, in high concentrations, suspended clays introduced to aquatic systems in watershed runoff can cause coflocculation and sedimentation of planktonic microorganisms. Microorganism-particle interactions are better known from investigations of soils than from aquatic systems (Bitton and Marshall 1980). However, it is recognized that in the aquatic phase of soils or sediments, bacteria may be reversibly or irreversibly sorbed at solid surfaces, enveloped in colloidal material, and coflocculated with particulates of comparable size (Marshall 1980a,b). Our February 1982 West Point results appear to provide further support for the occurrence of clay-microorganism coflocculation in aquatic systems that receive episodic inflows of turbid water.

36. DeGray Reservoir was relatively turbid (Secchi depth $\bar{X} + SD = 0.84 \pm 0.17$ m, $n = 5$), as compared to its normally high water transparency, when sampled in February 1983 (Fig. 6); however, similar shifts in the size distributions of planktonic autotrophy and microheterotrophy were not observed. In addition to a lower level of turbidity in DeGray than in West Point during February 1982, the turbid inflow to DeGray had occurred much less recently (in early December 1982), and much of the turbidity remaining in DeGray in February 1983 was a result of the continued suspension of very small, colloidal clays that flocculate less readily than larger particles. Indeed, considerable fine clay turbidity persisted in the DeGray Lake water column through the winter and spring of 1983 and was still present during our June 1983 sampling trip.

Longitudinal patterns

37. Within-reservoir patterns in the size distributions of planktonic autotrophy and microheterotrophy suggest that their environmental controls may change along the longitudinal axes of reservoirs. In general, autotrophy $>3.0 \mu\text{m}$ decreased from uplake

to midlake and then increased again further downlake in both reservoirs during the growing season (Figs. 9 and 10). In DeGray Reservoir, the uplake-to-midlake decline in the relative importance of autotrophy associated with $>3\text{-}\mu\text{m}$ particles extended further downlake in June 1983 than in September 1982, indicating that longitudinal shifts in size distributions may be flow related. During the winter, autotrophy $>3\ \mu\text{m}$ remained at a relatively constant level from uplake to midlake and then declined downlake in both reservoirs, a pattern also consistent with the longitudinal expansion of riverine conditions downlake during the winter. However, we found no clear relationships between the size distributions of autotrophy and microheterotrophy and nutrient levels or levels of suspended particles (Table 7).

38. A combination of size-dependent gain and loss factors is probably responsible for the observed decreases in the relative importance of $>3\text{-}$ and $>8\text{-}\mu\text{m}$ autotrophy in the upper portions of DeGray and West Point reservoirs (Fig. 9). For example, settling losses of larger, heavier cells with decreasing advective flow and turbulent mixing of the water column, grazing losses of the larger nanoplankton (i.e., 10- to 30- μm size range), and reduced cell size in response to decreasing nutrient availability downlake could account for the observed patterns. Alternatively, reduced cell size could result from a size-dependent growth response to the transition from a relatively fluctuating advective nutrient supply in the riverine portions of the impoundments to a lower, but more constant, level of available nutrients supplied by internal recycling further downlake. Midlake-to-downlake increases in autotrophy in the $>3\text{-}\mu\text{m}$ size fraction are more difficult to explain. However, marked uplake-to-downlake transitions from phytoplankton community dominance by Cyanobacteria to dominance by green algae and Cryptomonads (Fig. 11) probably influence the size distributions of both autotrophy and microheterotrophy. It appears likely that we are viewing the net

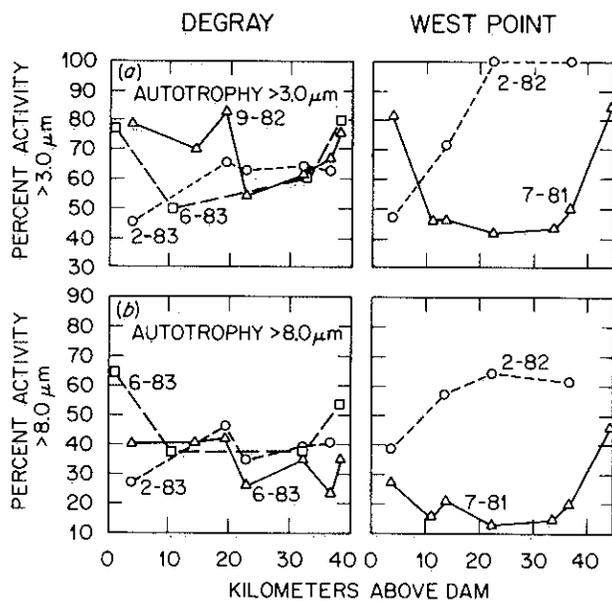


Fig. 9. Longitudinal gradients in planktonic autotrophy associated with (a) $>3.0\text{-}\mu\text{m}$ and (b) $>8.0\text{-}\mu\text{m}$ particle size fractions in DeGray and West Point reservoirs

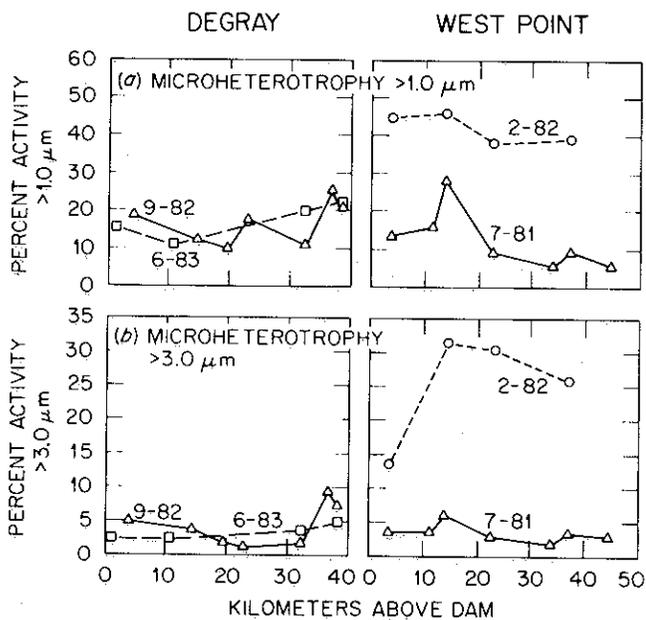


Fig. 10. Longitudinal gradients in planktonic microheterotrophy associated with (a) $>1.0\text{-}\mu\text{m}$ and (b) $>3.0\text{-}\mu\text{m}$ particle size fractions in DeGray and West Point reservoirs

Table 7

Correlation Matrix for Environmental Variables Associated with the Size Distribution of Planktonic Autotrophy and Microheterotrophy in DeGray Reservoir, September 1982 and June 1983. [The First Number Represents the Correlation Coefficient (r) and the Second Number Shows the Number of Observations (n).]

	Autotrophy >3 μm	Autotrophy >8 μm	Microhet. >1 μm	Microhet. >3 μm
Distance above dam	-0.03(11)	-0.43(11)	0.53(11) ^a	0.47(11)
Total autotrophy	-0.04(11)	-0.55(11) ^a	0.54(11) ^a	0.74(11) ^c
Total microheterotrophy	-0.50(11)	0.19(11)	-0.02(11)	-0.27(11)
SRP	-0.31(11)	-0.40(11)	0.19(11)	0.34(11)
NH ₄ -N	-0.09(11)	0.63(11) ^b	0.07(11)	-0.18(11)
NO ₃ + NO ₂ -N	0.21(11)	-0.05(11)	0.58(11) ^a	0.50(11)
DOC	-0.59(4)	-0.10(4)	-0.81(4)	-0.98(4) ^b
Secchi depth	0.14(11)	0.07(11)	-0.56(11) ^a	-0.52(11)
Chlorophyll a	0.39(4)	-0.17(4)	0.92(4) ^a	0.96(4) ^b
Total algal cells	-0.12(10)	-0.40(10)	0.26(10)	0.31(10)
% Cyanobacteria	0.19(9)	-0.30(9)	0.63(9) ^a	0.27(9)

^a $p < 0.10$.

^b $p < 0.05$.

^c $p < 0.01$.

result of both size-dependent and species-specific algal growth responses to a changing combination of environmental controls along reservoir longitudinal axes.

39. Similar, but less marked, longitudinal patterns in planktonic microheterotrophy associated with >1.0- μm and >3.0- μm particles (Fig. 10) also suggest the operation of different environmental controls in the upper and lower portions of reservoirs. In September 1982 and June 1983, attached bacteria (>1 μm) accounted for 19-24% of the total microheterotrophic activity in the relatively nutrient- and particle-rich upper portion of DeGray Reservoir, but decreased in

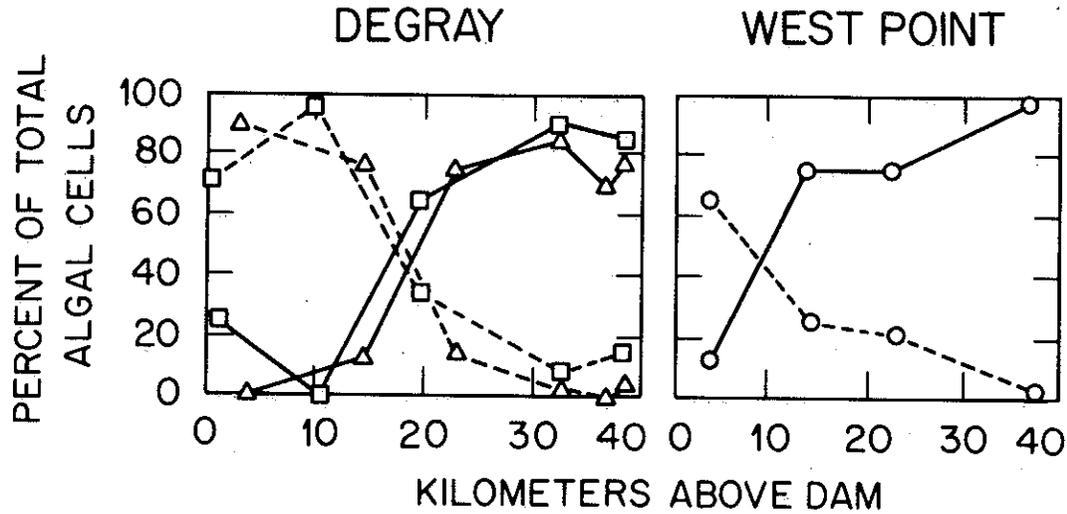


Fig. 11. Longitudinal gradients in phytoplankton community composition for September 1982 (triangles) and June 1983 (squares) in DeGray Reservoir and for February 1982 (circles) in West Point Reservoir. Data are expressed as the percentage of the total number of algal cells present accounted for by Cyanobacteria (blue-green algae) [solid lines] and by green algae (Chlorophyta) and Cryptomonads [dashed lines]

importance toward midlake as suspended particle levels (as reflected by increasing Secchi depth) decreased (Figs. 6 and 10). Microheterotrophy in the >1.0- and >3.0- μm size fractions increased again in the lower portion of the reservoir as nutrient levels declined and, presumably, as microenvironments associated with particle surfaces became more important for bacterial growth (e.g., Jannasch and Pritchard 1972, Paerl and Goldman 1972).

40. Our DeGray Reservoir data are consistent with a shift from control of the size distribution of planktonic microheterotrophy by suspended particle availability uplake to control by nutrient availability downlake; however, the relationships between these variables are not strong statistically (Table 7). In West Point Reservoir, which is a much more productive environment having higher concentrations of nutrients and particles throughout its basin (Bayne et al. 1983) than occur in DeGray Reservoir, planktonic microheterotrophy associated with attached bacteria (>1- μm

particles) generally increased from uplake to downlake (Fig. 10), probably in response to decreasing dissolved nutrient levels (Bayne et al. 1983).

41. Size distribution measurements made in relatively productive environments have suggested that the availability of suspended particles for bacterial attachment may be of greater influence than nutrient availability or trophic state (Paerl 1980, Bent and Goulder 1981, Kimmel 1983). Our measurements, made in oligotrophic DeGray Reservoir and in eutrophic West Point Reservoir, indicate that both mechanisms operate simultaneously within a broad range of environmental conditions, as exemplified by the superimposed gradients of nutrient availability and suspended particle concentrations that occur along the reservoir longitudinal axes.

PART V: SUMMARY AND CONCLUSIONS

42. Discussions regarding the environmental factors controlling size distributions of planktonic autotrophy and microheterotrophy in marine and freshwater pelagic systems have been focused on (a) nutrient availability for autotrophy and on (b) the availability of nutrients and particle surfaces for bacterial attachment for microheterotrophy. Based on these ideas (reviewed in Part I of this report), we advanced the working hypotheses listed in Table 1.

43. Autotrophy associated with $>8\text{-}\mu\text{m}$ particles (hypothesis 1a) and microheterotrophy associated with $>1\text{-}\mu\text{m}$ particles (hypothesis 2a) were significantly more important in winter than in summer West Point samples. However, these differences were the result of high abiogenic turbidity (and subsequent coflocculation of planktonic algae and bacteria with suspended clay particles) caused by a winter stormflow event rather than the result of higher winter nutrient concentrations. Contrary to hypothesis 1a, autotrophic activity in the $>8\text{-}\mu\text{m}$ size fraction was significantly more important in summer samples than in winter samples from DeGray Reservoir (Table 4). Also contrary to working hypothesis (1b), $>8\text{-}\mu\text{m}$ autotrophy was significantly greater in DeGray Reservoir than in West Point Reservoir during the growing season. In general, the relative importance of autotrophic activity in the $>8\text{-}\mu\text{m}$ and $>3\text{-}\mu\text{m}$ size fractions decreased from uplake to midlake (supporting hypothesis 1c), but then increased again further downlake (Fig. 9).

44. We were unable to examine seasonal influences on the size distribution of planktonic microheterotrophy (hypothesis 2a) because of the winter stormflow event at West Point Reservoir and the lack of winter data for DeGray Reservoir. Size distributions of microheterotrophy were statistically different between reservoirs for summer samples, with the relative importance of microheterotrophic activity in the $>1\text{-}\mu\text{m}$ size fraction significantly greater in DeGray Reservoir (Table 5), supporting hypothesis 2b rather than hypothesis 3b. Although this result supports the idea that bacterial

attachment to other suspended particles increases in nutrient-poor environments, our data also show that the magnitude of the increase is small; 17% of the total microheterotrophic activity was associated with $>1\text{-}\mu\text{m}$ particles in the oligotrophic reservoir versus 12% in the mesoeutrophic system (Table 6).

45. Microheterotrophy associated with $>1.0\text{-}$ and $>3.0\text{-}\mu\text{m}$ size fractions was negatively correlated with Secchi depth (hypothesis 2d); however, the relationships were not statistically significant at the $P < 0.05$ level (Table 7; $P = 0.07$ for $>1.0\text{-}\mu\text{m}$ activity, $P = 0.11$ for $>3.0\text{-}\mu\text{m}$ activity). In DeGray Reservoir, the relative importance of microheterotrophy in $>1\text{-}$ and $>3\text{-}\mu\text{m}$ size fractions decreased from uplake to midlake and then increased from midlake to downlake, a longitudinal pattern similar to that for autotrophy $>3\text{ }\mu\text{m}$ and suggestive of a transition from environmental control by particle availability uplake (working hypothesis 3c) to nutrient availability downlake (2c). However, in West Point Reservoir, microheterotrophy $>3\text{ }\mu\text{m}$ increased from uplake to downlake in July ($r = 0.67$, $DF = 6$, $0.05 < P < 0.10$), suggesting primary control by nutrient availability (2c) in the more particle-rich impoundment.

46. Superimposed gradients of flow velocity, suspended particle levels, light availability, and nutrient concentrations along reservoir longitudinal axes reflect within-reservoir transitions from a riverine to a lacustrine environment and provide a basis for interpreting the spatial and temporal dynamics of reservoir ecosystems (Thornton et al. 1982; Kennedy et al. 1982; Kimmel and Groeger 1984; Kimmel et al., in press). Although the occurrence of longitudinal gradients in physical and chemical factors and in water quality appears to be a common feature of river-reservoir systems (see Thornton et al. 1981, Kennedy et al. 1982), ecological responses to these environmental gradients are not well documented. In this study, longitudinal gradients in physical-chemical factors, phytoplankton community composition, and planktonic autotrophy and microheterotrophy were often apparent in DeGray and West Point reservoirs. However, size distributions of planktonic autotrophy and microheterotrophy in oligotrophic DeGray

Reservoir and mesoeutrophic West Point Reservoir were remarkably uniform spatially, temporally (with the exception of West Point Reservoir in February 1982), and between impoundments (Figs. 7-10). Longitudinal patterns in the size distributions of planktonic autotrophy and microheterotrophy suggest that their environmental controls may shift along the longitudinal axes of reservoirs.

47. The relationships between physical-chemical factors and the size distributions of autotrophy and microheterotrophy are not clear; therefore, potential explanations for the observed longitudinal patterns are necessarily speculative. Indeed, the observed uniformity in size distributions relative to physical-chemical differences occurring within and between reservoirs indicates that environmental controls on the size distributions of planktonic autotrophy and microheterotrophy are more complex than previously realized. Our results suggest that ecological factors (e.g., size-selective losses of autotrophs and microheterotrophs by grazing and/or sinking, autotroph-microheterotroph interactions) must be considered, in addition to the availability of nutrients and suspended particles, as potential environmental controls on the size distributions of planktonic autotrophy and microheterotrophy.

48. As previously observed in oceanic and coastal systems (Azam and Hodson 1977) and in unproductive lakes (Munawar and Munawar 1975, Paerl 1977, Ross and Duthie 1981), planktonic autotrophy in DeGray and West Point reservoirs was dominated by ultrananoplankton, with more than 60% of the total photosynthetic carbon uptake accounted for by the $<8\text{-}\mu\text{m}$ size fraction. Similarly, free-living bacterioplankton ($<1.0\ \mu\text{m}$) were responsible for 80 to 90% of the planktonic microheterotrophy. Spatial and seasonal size distributions of planktonic autotrophy and microheterotrophy in DeGray and West Point reservoirs correspond well to previously reported results of more limited sampling of several impoundments (Kimmel 1983) (Fig. 12). Taken together, these data show that, over a broad range of environmental conditions and trophic states, the predominant fractions of planktonic autotrophy and microheterotrophy in reservoirs are

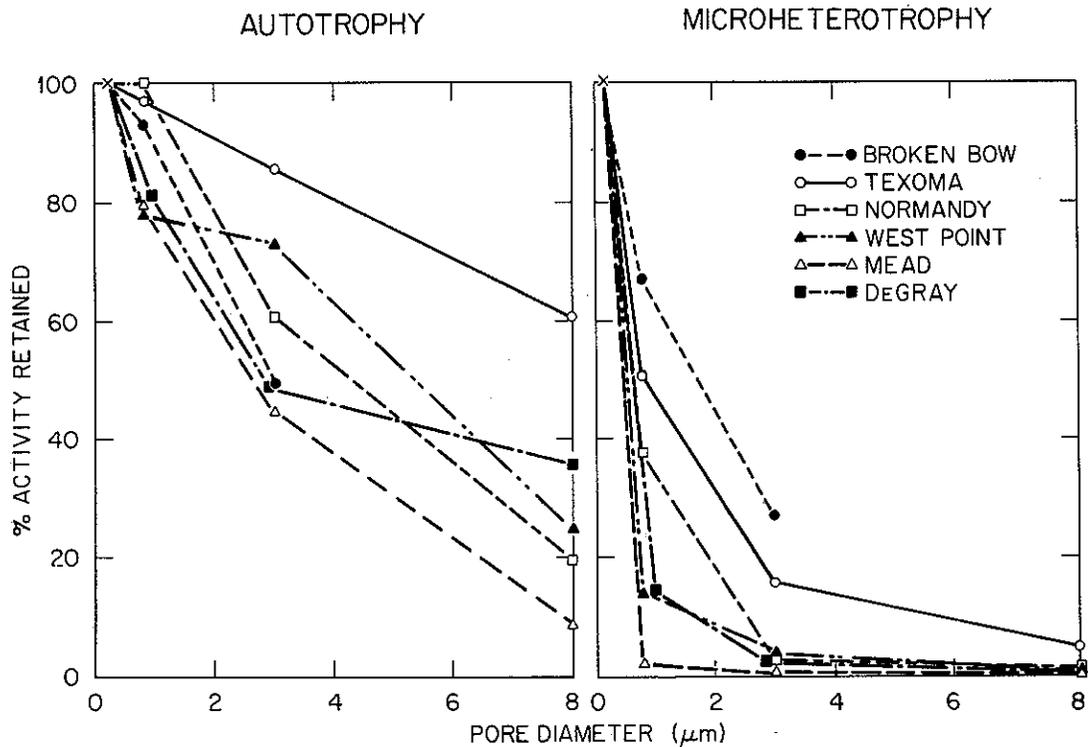


Fig. 12. Particle size distributions of planktonic autotrophy and microheterotrophy in near-surface samples from six limnologically dissimilar reservoirs representative of a broad range of environmental conditions and trophic states: Broken Bow Lake, Oklahoma (mesotrophic); Lake Texoma, Oklahoma-Texas (eutrophic); Normandy Lake, Tennessee (eutrophic); West Point Lake, Alabama-Georgia (mesoeutrophic); Lake Mead, Arizona-Nevada (oligotrophic); and DeGray Lake, Arkansas (oligotrophic). Modified from Kimmel (1983)

consistently associated with $<8\text{-}\mu\text{m}$ algae and $<1\text{-}\mu\text{m}$ bacteria, respectively.

49. Our results support the view that pelagic ecosystem metabolism is dominated by very small organisms (Pomeroy 1974, Sieburth et al. 1978, Williams 1981, Ducklow 1983) and demonstrate that such a view applies not only to oligotrophic open ocean, coastal, and lacustrine environments, but also to relatively productive lakes and reservoirs.

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