CONF-8310318--1

CONF-8310318--1

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SIZE DISTRIBUTION OF PLANKTONIC AUTOTROPHY AND MICROHETEROTROPHY IN DeGRAY RESERVOIR, ARKANSAS

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ABSTRACT

Naturally occurring assemblages of phytoplankton and bacterioplankton were radiolabelled with sodium ^{14}C-bicarbonate and sodium ^{3}H-acetate and size fractionated to determine the size structure of planktonic autotrophy and microheterotrophy in DeGray Reservoir, an oligotrophic impoundment of the Caddo River in south-central Arkansas. Size distributions of autotrophy and microheterotrophy were remarkably uniform seasonally, vertically within the water column, and along the longitudinal axis of the reservoir despite significant changes in environmental conditions. Planktonic autotrophy was dominated by small algal cells with usually >50% of the photosynthetic carbon uptake accounted for by organisms <8.0 μm. Microheterotrophic activity in the 0.2- to 1.0-μm size fraction, presumably associated with free-living bacterioplankton not attached to suspended particles, usually accounted for >75% of the planktonic microheterotrophy. Longitudinal patterns in autotrophic and microheterotrophic activities associated with >3-μm and >1-μm size fractions, respectively, suggest an uplake to downlake shift from riverine to lacustrine environmental influences within the reservoir.

DISCLAIMER

INTRODUCTION

The plankton ecologist's perception of the environment that he investigates is shaped to a large extent by the methods used for collecting and examining plankton samples. For years, our views of plankton community structure, metabolism, and trophic interactions were restricted to the 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 it was realized that they were responsible for much of the biomass and most of the metabolic activity occurring in the planktonic environment (e.g., Rodhe et al. 1958, Holmes 1958, Yentsch and Ryther 1959). Recent investigations of the size distributions of planktonic biomass and metabolic activities, using epifluorescence and scanning electron microscopy, radioisotopic labelling, differential filtration methods, and autoradiography, have focused attention on progressively smaller organisms. Because particle size is a primary determinant of the food resources available to consumers and the efficiency of energy transfer through foodwebs (Ryther 1969; Gliwicz 1969; Parsons and Lebrasseur 1970; Kerr 1974; Sheldon et al. 1972, 1977), the size distributions of planktonic autotrophy (algal photosynthesis) and microheterotrophy (bacterial productivity) are of considerable ecological interest.

The contribution of nanoplankton (<64 μm) to phytoplankton production and biomass is now well documented (e.g., Rodhe 1958, Ryther and Yentsch 1958, Gilmartin 1964, Malone 1971, Kalff 1972, Kalff and Knoechel 1978), and recent studies have demonstrated the importance of microplankton (<8 μm) to algal community productivity in nutrient-poor planktonic environments (Paerl 1977, Paerl and Mackenzie 1977, Ross and Duthie 1981, Munawar and Munawar 1975, Li et al. 1983, Platt et al. 1983). 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 the larger algae generally increases in more productive systems where nutrient availability is higher (e.g., mesotrophic and eutrophic lakes, estuaries, upwelling and coastal marine environments) relative to oligotrophic lakes and the open ocean (Kalff and Knoechel 1978, Malone 1980, Watson and Kalff 1981, Schlesinger et al. 1981). Net plankton can make major contributions to phytoplankton productivity by virtue of large biomass accumulations (Kalff and Knoechel 1978). However, the biomass-specific productivity of large algae is usually low (Stull et al. 1973, Kalff and Knoechel 1978), and zooplankton grazing occurs primarily on small (<30 μm) cells that are most efficiently filtered, ingested, and assimilated (Burns 1968, Gliwicz 1969, Porter 1977).

Phytoplankton photosynthesis is the primary means of organic matter production in most planktonic systems; however, bacterial production may also be an important trophic resource for planktonic consumers (Pomeroy 1974, Sieburth 1976, Sieburth et al. 1978, 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., reservoirs and riverine lakes), the microheterotrophic conversion of biologically available allochthonous dissolved organic matter (DOM) to bacterial biomass may significantly supplement ecosystem productivity (Kuznetsov 1968, Sorokin 1972) if the bacterial production is efficiently harvested by planktonic consumers. Bacteria associated with detrital particles or aggregates appear to be more efficiently harvested by macrozooplankton than are free-living bacterioplankton by virtue of their greater effective particle size (Peterson et al. 1978, Hobbie and Wright 1979, Kimmel 1983). Small (<30 μm) ciliates and heterotrophic microflagellates may provide a trophic link between the free-living bacterioplankton and macrozooplankton (Sieburth et al. 1978, Porter et al. 1979, Pace and Orcutt 1981, Beaver and Crisman 1982); however, the energetic cost of additional trophic transfers may diminish the significance of this linkage to the foodweb.

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 (Seki 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). 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 (Azam and Hodson 1977, Wiebe and Pomeroy 1972, 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). Paerl and Goldman (1972) concluded that suspended particles transported by turbid stream inflow to ultraoligotrophic Lake Tahoe stimulated planktonic microheterotrophy by serving as both a surface for microbial attachment and an enriched microenvironment for bacterial growth.

Jannasch and Pritchard (1972) reemphasized earlier suggestions (Waksman and Carey 1935a,b; Zobell and Anderson 1936) that adsorption of dissolved inorganic and organic nutrients increases concentration gradients at particle surfaces and thereby promotes microbial attachment to suspended particles in oligotrophic environments. Fluvial inputs of suspended particles to reservoirs provide a greater number of particles and a greater surface area for bacterial attachment and growth than occur in most oceanic and lacustrine environments. Whether a similar enhancement of microbial activity in association with suspended particle surfaces occurs in higher-nutrient environments, such as particle-rich reservoirs, remains uncertain (Goldman and Kimmel 1978). However, Marzolf and co-workers (Marzolf 1980, Marzolf and Arruda 1981, Arruda et al. 1983) have demonstrated that DOM adsorption

and bacterial growth associated with suspended clay particles can be of major importance to reservoir zooplankton when significant phytoplankton production is prevented by abiogenic turbidity.

Kimmel (1983) surveyed several reservoirs of differing trophic status and reported that microalgae (<8.0 μm) and free-living bacteria (<1.0 μm) were primarily responsible for planktonic autotrophy and microheterotrophy, respectively, in the impoundments examined. However, his sampling was limited both spatially and temporally, and did not include an oligotrophic system. Here we report the results of a more thorough sampling of DeGray Reservoir, an oligotrophic impoundment of the Caddo River in south-central Arkansas. Previous water quality studies of DeGray Reservoir have shown it to possess marked longitudinal gradients in nutrient concentrations, water clarity, algal biomass, and phytoplankton productivity (Thornton et al. 1982, Kennedy et al. 1982, J. Nix, unpublished data). This spatial heterogeneity provided us the opportunity to examine within a single system the responses of naturally occurring phytoplankton-bacterioplankton assemblages to gradients of environmental factors hypothesized to control the size distributions of planktonic autotrophy and microheterotrophy.

METHODS

DeGray Reservoir was sampled on three occasions (31 August - 2 September 1982, 1-4 February 1983, and 21-23 June 1983), representative of late-summer, mid-winter, and early-summer environmental conditions, respectively. During each sampling trip, we obtained near-surface (1 to 2 m) samples from stations located along the longitudinal axis of the reservoir and a vertical series of samples at selected stations. Water samples were collected with a submersible pump connected to a weighted opaque hose, pumped into 10-L plastic cubitainers, and then subsampled for various measurements and experiments. Water temperature, dissolved oxygen, pH, and conductance were measured with either a Hydrolab or a Martek monitoring system. Incident solar radiation was monitored with a calibrated mechanical pyrheliograph, and photosynthetically active radiation (PAR, 400-700 nm)

was measured in situ with a Li-Cor quantum meter equipped with a spherical submersible sensor. In vivo chlorophyll fluorescence (IVF) was also determined in situ (Lorenzen 1966). Dissolved nutrients, chlorophyll a concentrations, and phytoplankton productivity were estimated by standard automated methods (Stainton et al. 1974), methanol extraction (Marker et al. 1980), and ^{14}C uptake (Goldman 1963, Vollenweider 1971), respectively.

Size distributions of planktonic autotrophy and microheterotrophy were determined by isotopic labelling and differential filtration of natural phytoplankton-bacterioplankton assemblages (Kimmel 1983). Subsamples in 130-mL light and dark bottles were inoculated with 0.5 mL $NaH^{14}CO_3$ solution (56.5 mCi/mmol specific activity, 5.5 µCi/mL) and 0.1 mL sodium ^{3}H-acetate (10 Ci/mmol, 25.0 µCi/mL; 0.5 µg/L acetate enrichment over ambient concentration) to label autotrophs and microheterotrophs, respectively, and incubated in situ for 4-5 h. Vertical series samples were incubated at the depths from which they were taken. Longitudinal series samples were obtained from the mixed layer (from 1-2 m) at stations along the reservoir longitudinal axis (Fig. 1) and incubated at a single station at the depth of photosynthetically saturating light (150-300 $\mu E\ m^{-2}\ sec^{-1}$), usually at 2-3 m. In September and February, samples were double-labelled (inoculated with both ^{14}C-bicarbonate and ^{3}H-acetate); however, because of problems in detecting adequate ^{3}H activity in February samples, all June samples were inoculated separately. Selected samples were poisoned with 1 mL saturated $HgCl_2$ solution, inoculated, and incubated to provide a correction for radioisotope adsorption to particles and filters.

Immediately after incubation, 15-mL aliquots were gently vacuum filtered (<100 torr) in parallel through 47-mm Nucleopore polycarbonate filters of 0.2, 1.0, 3.0, and 8.0 µm pore diameter. Filters and retained particles were rinsed three times with deionized water and placed in plastic minivials. Six milliliters of Aquasol fluor were added to each minivial, and all samples were radioassayed using a Packard 4640 liquid scintillation spectrometer. Automatic external standardization, calibrated with quenched series of ^{14}C and ^{3}H

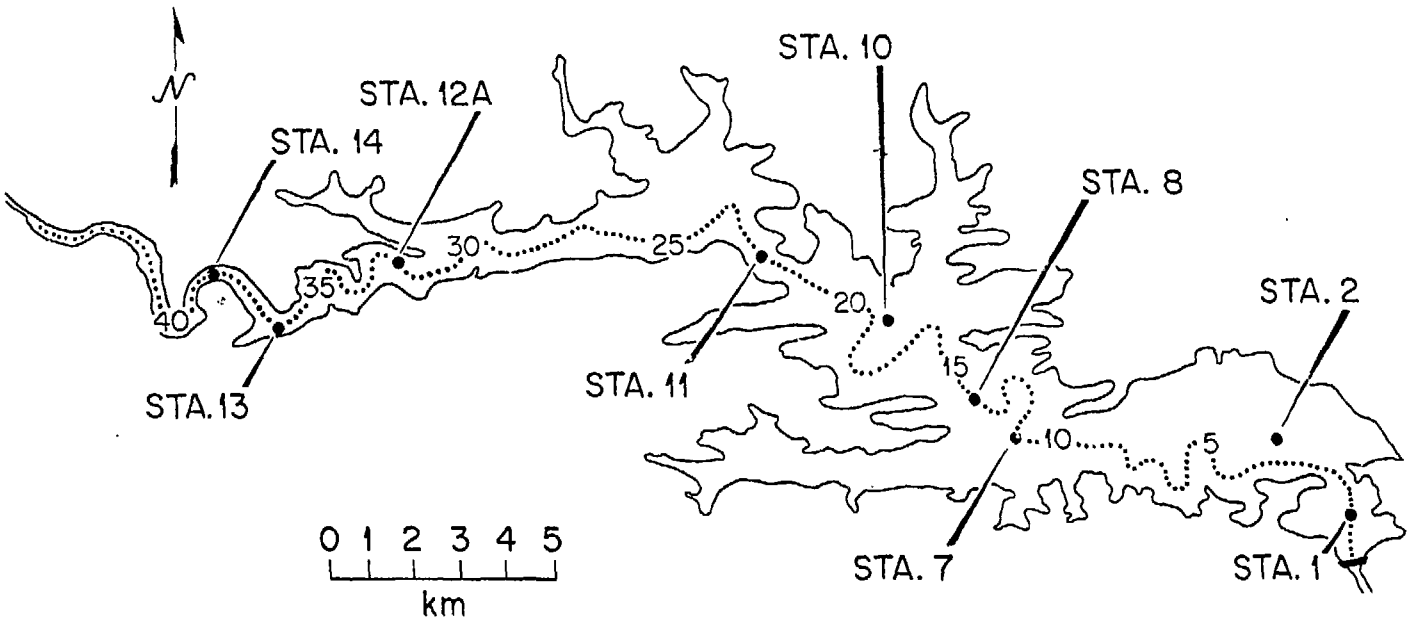

Fig. 1. Map of DeGray Reservoir, an impoundment of the Caddo River located in south-central Arkansas. The submerged river channel (thalweg) and the distance above the dam (in kilometers) are indicated by the dotted line and interspersed numerals, respectively. Sampling stations located along the longitudinal axis of the reservoir are also shown.

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

RESULTS AND DISCUSSION

Vertical Patterns

Light availability restricted significant planktonic autotrophy to the upper 5 to 6 m of the water column in DeGray Reservoir (Fig. 2). Phytoplankton productivity at the depth of maximum photosynthesis was highest in February and lowest in September (Fig. 3a); however, integral primary production did not vary greatly on a seasonal basis (19, 23, and 25 mg C m^{-2} h^{-1}) in September, February, and June, respectively) due to a progressive increase in euphotic zone depth and, probably, in algal nutrient deficiency from winter to late summer.

Vertical changes in the size distribution of autotrophy were not statistically demonstrable due to the low number of samples; however, within the euphotic zone (>1% surface light), the relative importance of the >3-µm size fraction appeared to decline with increasing depth (Fig. 3b). This apparent decrease with depth in the activity of "larger" cells (i.e., 3- to 8-µm and >8 µm) was more gradual in September and June than in February, suggesting a direct relationship to light intensity. However, at lower 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). In June, all autotrophy at 6 m was associated with >3-µm organisms, with 71% of the total in the 3- to 8-µm fraction and 29% >8 µm. Cells >8 µm appeared
to be somewhat more important during the summer months than in mid-winter, but in almost all cases, <50% of the total autotrophic activity occurred in the >8-µm size fraction.

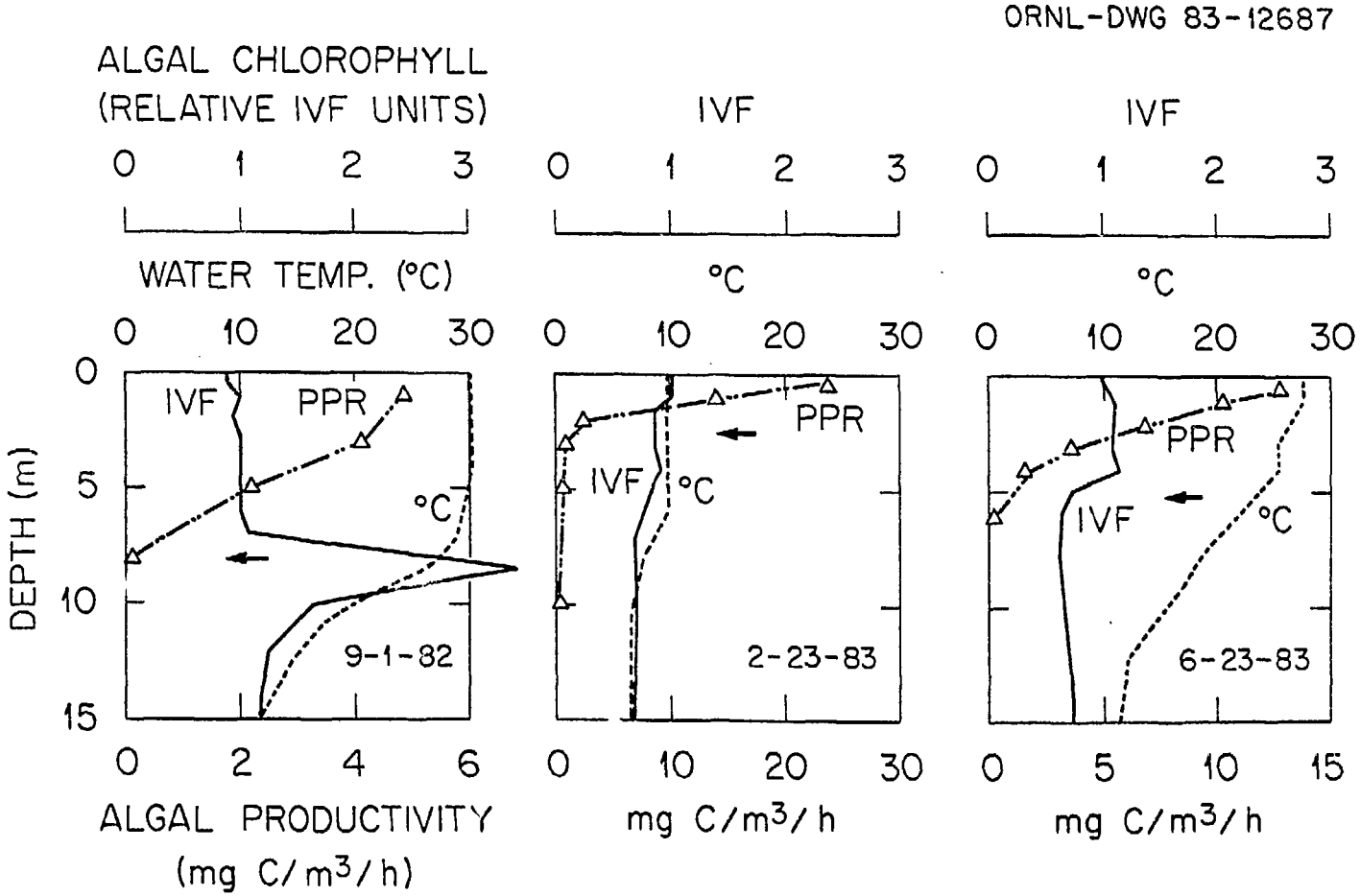

Fig. 2. Representative vertical profiles of water temperature, algal biomass [as indicated by in vivo chlorophyll fluorescence (IVF) measurements], and phytoplankton productivity (PPR) for September 1982, February 1983, and June 1983 sampling periods. Arrows indicate the depth of the euphotic layer (=1% surface light penetration). Note that the phytoplankton productivity scale differs for each date.

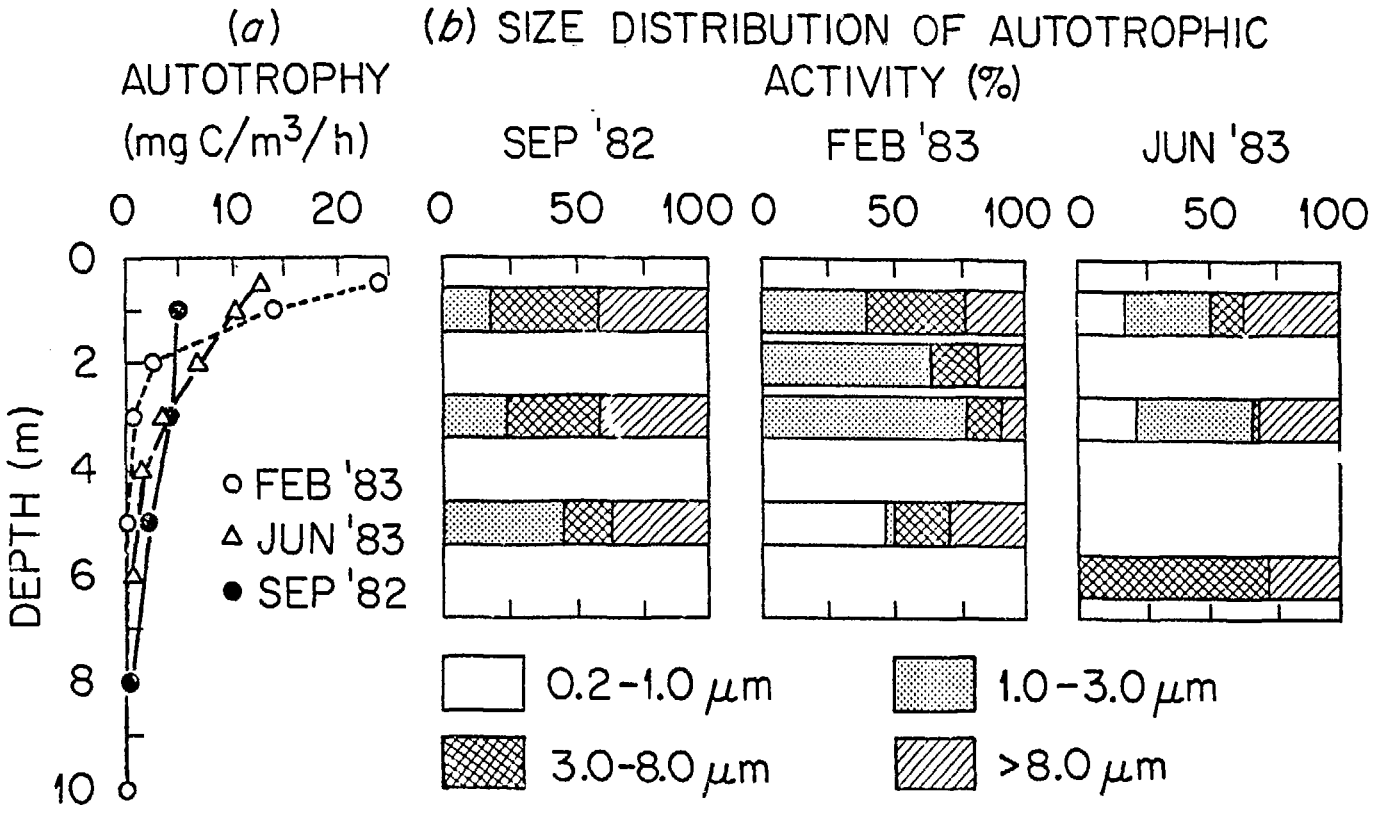

Fig. 3. (a) Vertical distributions of total planktonic autotrophy for 1 September 1982, 23 February 1983, and 23 June 1983 at lacustrine stations in DeGray Reservoir. (b) Changes in the size distribution of autotrophic activity with water column depth.

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, the models of Laws (1975) and Shuter (1979) 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. In DeGray Reservoir, most of the autotrophic activity occurs in smaller size fractions than those specificially considered in algal growth models. However, the observed vertical patterns in the size distribution of autotrophy appear to support the hypothesis that the competitive advantage of small cells in nutrient-poor environments is reduced at low light intensities (Schlesinger et al. 1981).

Comparisons of microheterotrophic activity are problematic because of the numerous organic substrates potentially available for microbial uptake in natural waters and our lack of knowledge of the identities, concentrations, and relative availabilities of these substrates. We used ^{3}H-acetate as an analog of low molecular weight, dissolved organic compounds that should be readily available for bacterial uptake. Levels of planktonic microheterotrophy, as indicated by ^{3}H-acetate uptake, were significantly higher (ANOVA, $F_{[2,13]} = 29.4$, $P < 0.01$) in September 1982 than in February and June 1983 (Fig. 4a). Average turnover times of the ^{3}H-labelled acetate pool for the depths sampled were 9.6, 16.9, and 20.3 h for September, February, and June vertical profiles, respectively. Microheterotrophic activity did not vary significantly with depth ($r = -0.40$, 6 df, NS) even in September when the vertical structure of water temperature, algal biomass, and phytoplankton productivity was pronounced (Fig. 2).

We were unable to determine the size distribution of microheterotrophy in February due to a misjudgement of the proportion of ^{14}C and ^{3}H activities added to the samples. As a result of our error, ^{3}H activity in the larger size fractions was undetectable relative to the ^{14}C activity present. However, in September and

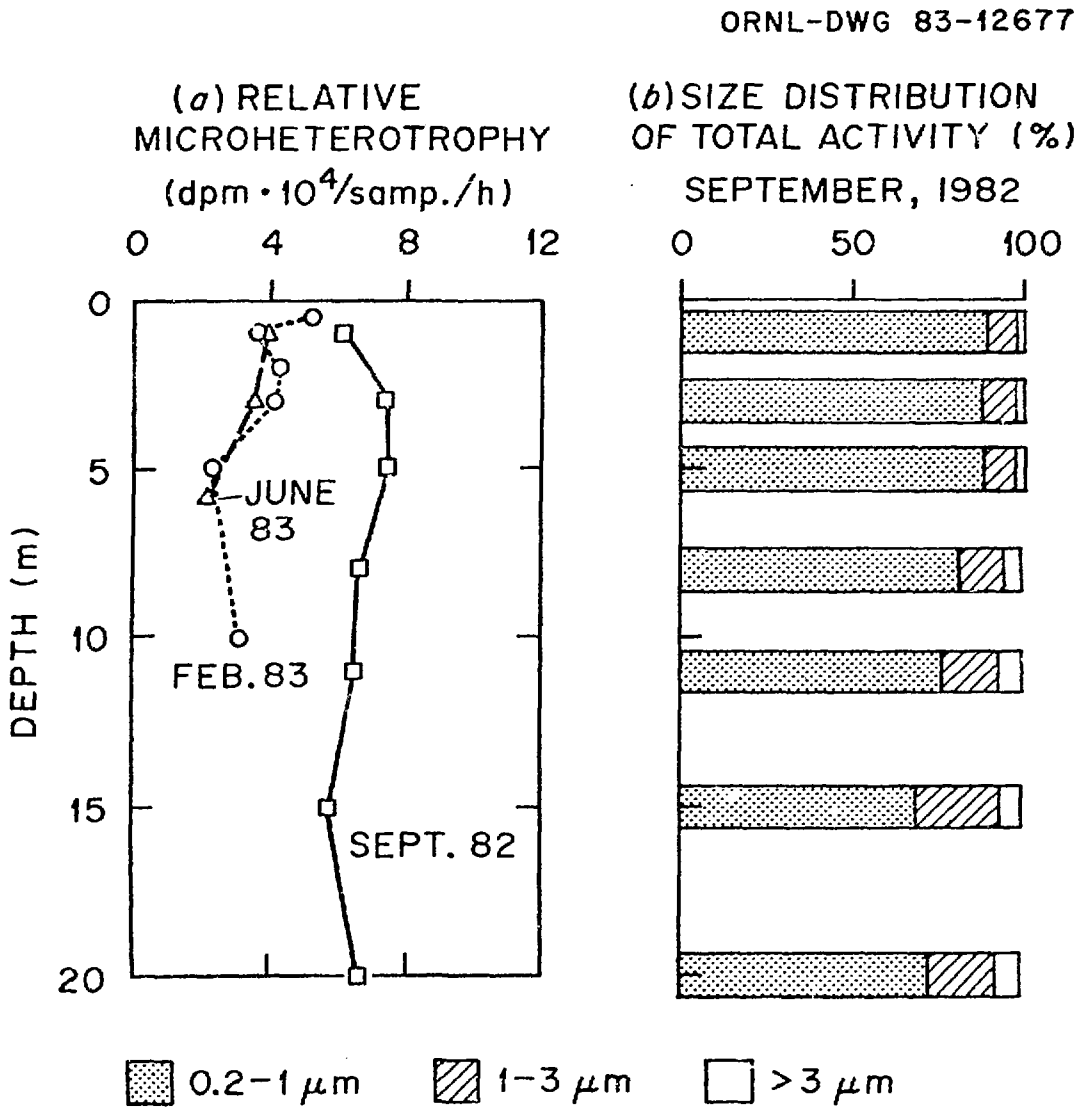

Fig. 4. (a) Vertical distributions of planktonic microheterotrophy (as indicated by ^{3}H-acetate uptake) for 1 September 1982, 23 February 1983, and 23 June 1983 at lacustrine stations in DeGray Reservoir. (b) Changes in the size distribution of microheterotrophic activity with water column depth for 1 September 1982.

June samples, microheterotrophy was dominated (usually >75%) by the <1.0-μm size fraction, indicating uptake by free-living bacterioplankton. The September 1982 vertical profile (Fig. 4b) shows that the importance of attached bacteria (>1 μm) was low ($\bar{X}$ = 9.8%, range = 7.5-11.7% of the total microheterotrophic activity) 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 was likely a result of decreased availability of labile DOM supplied by algal excretion and increased concentrations of algal-derived particulate organic detritus. However, even in metalimnetic and hypolimnetic samples, microheterotrophic activity associated with particles >3.0 μm was usually <10% ($\bar{X}$ = 9.1%, range = 6.2-10.8%) of the total.

Longitudinal Patterns

Longitudinal changes in the magnitudes of near-surface planktonic autotrophy and microheterotrophy were most apparent in September 1982, although uplake to downlake reductions in both were observed on all three sampling dates (Fig. 5). Phytoplankton productivity was high in the upper portion of the impoundment (stations 14 and 13) in September 1982, decreased rapidly toward midlake (stations 12A and 11), and then declined to <10% of the uplake level in the lower portion of the reservoir (stations 10, 7, and 2). Microheterotrophy showed a similar, but less marked, longitudinal pattern. Except for a two-fold reduction between stations 14 and 13 in September, microheterotrophic activity was relatively constant along the longitudinal axis of the reservoir, decreasing only slightly from uplake to downlake stations.

Longitudinal trends in the size distributions of planktonic autotrophy and microheterotrophy were less apparent than changes in the magnitudes of the total autotrophic and microheterotrophic activities within DeGray Reservoir (Fig. 6, Table 1). As in vertical profiles, much (X = 54%, range = 32-77%) of the total autotrophic activity was associated with the 1.0- to 8.0-μm size fraction; however, autotrophy in the >8-μm size fraction was quite important and comprised most of the remaining activity (X = 40%, range = 23-65%). Usually, there was

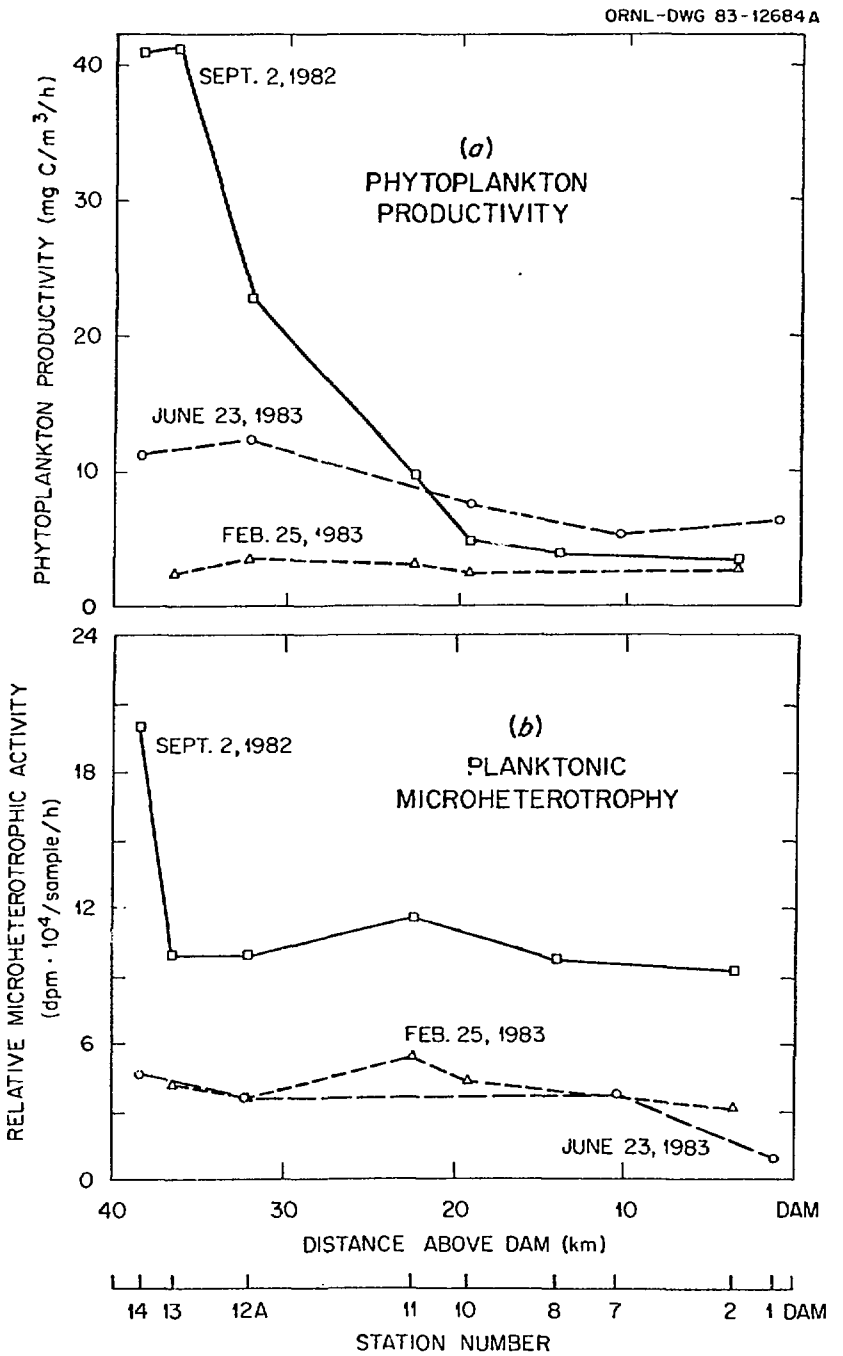

Fig. 5. Longitudinal patterns in the magnitudes of (a) phytoplankton productivity (autotrophy) and (b) planktonic microheterotrophy in DeGray Reservoir.

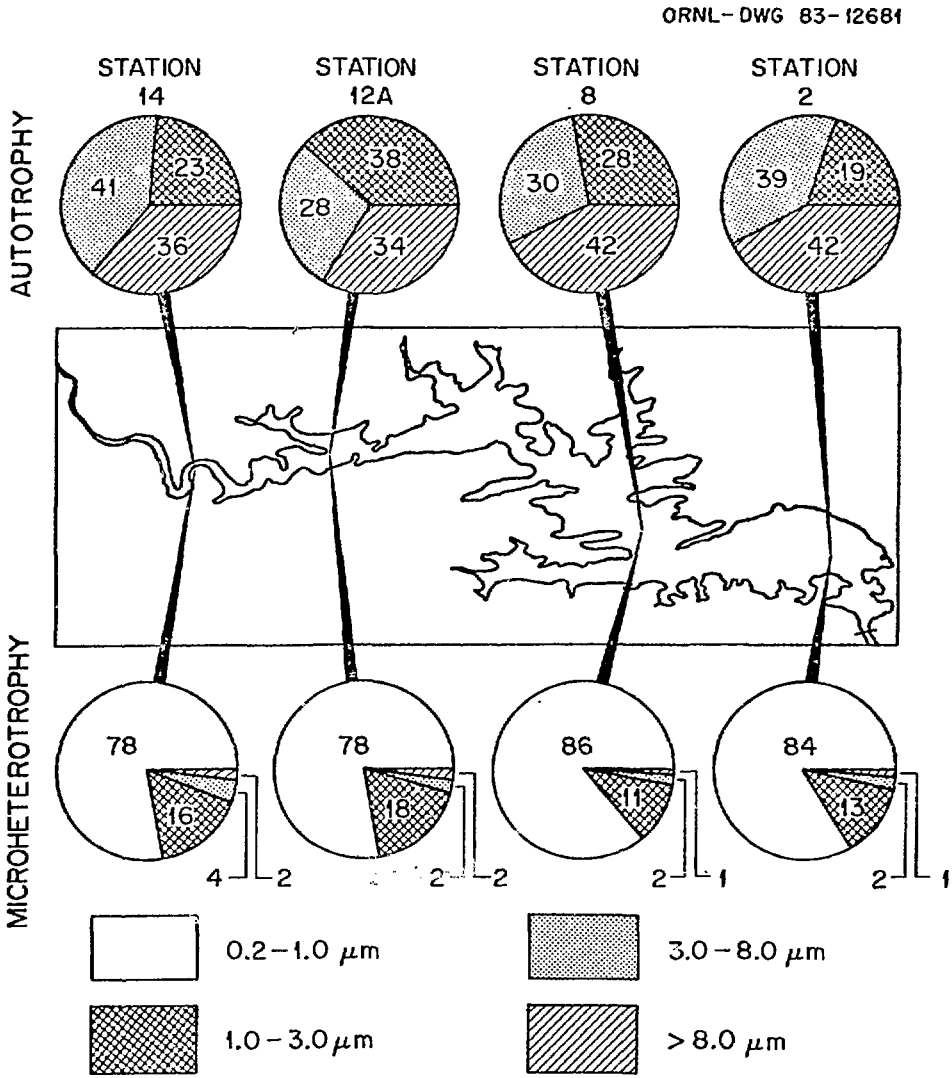

Fig. 6. Size distributions of planktonic autotrophy and microheterotrophy in near-surface (1 to 2 m) samples from selected stations along the longitudinal axis of DeGray Reservoir, 2 September 1982. Results expressed as percentages of the total activity.

Table 1. Size distributions of planktonic autotrophy and microheterotrophy in near-surface samples along the longitudinal axis of DeGray Reservoir. Station numbers increase with increasing distance from the dam; see Fig. 1 for station locations. Total autotrophic and microheterotrophic activities are defined as ^{14}C and ^{3}H activities, respectively, in particulate matter retained by a 0.2-µm pore diameter Nucleopore filter.

Date and Station	% Autotrophic Activity Retained				% Microheterotrophic Activity Retained			
	0.2–1.0	1.0–3.0	3.0–8.0	>8.0 µm	0.2–1.0	1.0–3.0	3.0–8.0	>8.0 µm
Sept. 2, 1982								
Sta. 14	0	23.1	41.4	35.7	78.2	15.8	4.5	1.5
13	0	32.9	43.8	23.3	75.8	16.0	6.2	2.0
12A	0	37.8	27.7	34.5	78.4	17.6	2.1	1.9
11	0	45.1	27.2	27.7	88.7	9.7	1.0	1.0
8	0	28.1	30.3	41.5	86.8	10.7	1.8	1.0
2	0	19.0	38.7	42.3	83.9	12.9	2.5	1.0
Feb. 25, 1983								
Sta. 13	0	36.8	22.6	40.6	—	—	—	—
12A	0	36.2	25.8	37.9	—	—	—	—
11	11.6	26.2	28.4	33.8	—	—	—	—
10	15.3	18.5	20.4	45.7	—	—	—	—
2	0	54.8	17.7	27.5	—	—	—	—
June 23, 1983								
Sta. 14	0	19.5	27.1	53.3	81.1	14.7	1.9	2.3
12A	0	38.8	23.7	37.5	75.9	20.3	2.2	1.5
7	18.0	32.4	12.2	37.4	83.6	13.5	1.4	1.4
1	2.9	20.6	11.6	64.8	72.5	21.8	2.4	3.3

little if any autotrophic activity detected in the <1.0-µm fraction (Table 1). The size distribution of planktonic microheterotrophy was even more uniform. Generally, >75% ($\bar{X}$ = 80%, range = 72-89%) of the total microheterotrophic activity was associated with the <1.0-µm size fraction, indicative of free-living rather than attached bacteria. Of the microheterotrophy apparently due to bacteria associated with suspended particles, most was in the 1.0- to 3.0-µm size fraction, with usually <5% ($\bar{X}$ = 4.3%, range = 2.0-6.2%) of the total activity associated with particles >3 µm.

If autotrophy >3.0 µm and microheterotrophy >1.0 µm (those size fractions likely to be most available to planktonic macroconsumers) are examined, longitudinal patterns are discernible that suggest changes in controlling mechanisms along the longitudinal axis of the reservoir (Fig. 7). In September 1982, autotrophy >3.0 µm decreased gradually from station 14 to 11, then increased again further downlake. In June 1983, the decrease in the relative importance of >3-µm autotrophy extended further downlake to station 7 before increasing again at station 1. In contrast, autotrophy >3 µm remained at a lower, but relatively constant, level from uplake to midlake and then declined downlake in February 1983. This different pattern likely resulted from the extension of riverine conditions throughout the reservoir during the 1982-83 winter following a record flood in December (J. Nix, personal communication).

Settling and/or grazing losses of larger cells, reduced cell size in response to decreasing nutrient availability downlake, or a size-dependent growth response to a shift from a relatively fluctuating advective nutrient supply in the most riverine portion of the impoundment to a lower, but more constant, level of available nutrients supplied by internal recycling further downlake could account for the June and September declines in the relative importance of >3-µm autotrophy in the upper portion of DeGray Reservoir. The experimental results of Turpin and Harrison (1979) suggest that the growth of larger cells may be favored by the temporal patchiness of a limiting nutrient. The subsequent increases in autotrophy associated with the >3-µm size fraction downlake are more difficult to explain. However,

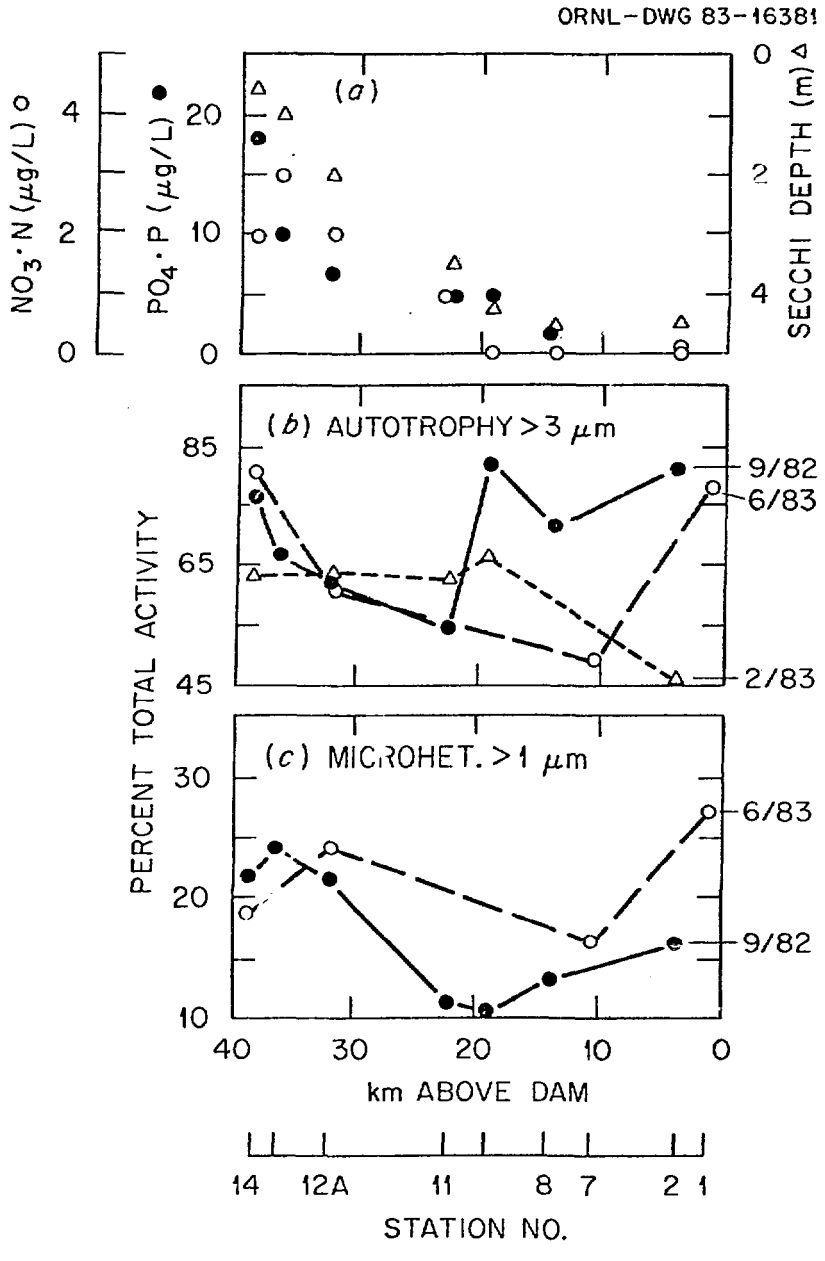

Fig. 7. Longitudinal patterns in dissolved nutrient concentrations, water transparency (as reflected by Secchi disc readings), and in the size fractions of planktonic autotrophy and microheterotrophy (>3 μm and >1 μm, respectively) most available to macrozooplankton. Nutrient and water transparency data are for the September 1982 sampling period.

an uplake to downlake shift from diatoms and blue-greens to dominance by green algae is indicated by preliminary examination of phytoplankton analyses (Kimmel, unpublished data). Therefore, it appears likely that we may be viewing the result of both size-dependent and species-specific algal growth responses to a changing combination of environmental controls along the reservoir longitudinal axis.

We observed similar longitudinal patterns in microheterotrophy associated with >1.0-μm particles (Fig. 7), also suggesting the operation of different environmental controls in the upper and lower portions of DeGray Reservoir. 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, 1978). However, size distribution measurements made in less oligotrophic 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 of the size distribution of planktonic microheterotrophy in DeGray 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 along the reservoir longitudinal axis. In September 1982 and June 1983, attached bacteria (>1 μm) accounted for 19-24% of the total microheterotrophic activity in the relatively nutrient-rich and particle-rich upper portion of the reservoir, but decreased in importance toward midlake as suspended particle levels (as reflected by increasing Secchi depth) decreased (Fig. 7). Microheterotrophy in the >1.0-μm size fraction increased again in the lower portion of the reservoir as nutrient levels declined and, presumably, as enriched microenvironments at particle surfaces became more important for bacterial growth. Therefore, our 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. Similar patterns have been observed along longitudinal transects of riverine estuaries (A. V. Palumbo, unpublished data). These results should help resolve numerous, apparently contradictory, observations regarding the relative importance of free-living versus attached bacteria in various planktonic environments.

SUMMARY AND CONCLUSIONS

The size distributions of planktonic autotrophy and microheterotrophy in oligotrophic DeGray Reservoir were remarkably uniform, both spatially and temporally (Figs. 3, 4, 6; Table 1). As previously observed in oceanic and coastal systems (Azam and Hodson 1977) and in unproductive freshwater lakes (Paerl 1977, Ross and Duthie 1981, Munawar and Munawar 1975), planktonic autotrophy was dominated by small algae with usually >50% of the total carbon uptake accounted for by the <8-μm size fraction. Similarly, free-living bacterioplankton (<1.0 μm) were responsible for 75-90% of the planktonic microheterotrophy.

Longitudinal changes in planktonic autotrophy and microheterotrophy associated with particles >3 μm and particles >1 μm, respectively, suggest that the environmental controls on the size distributions of algal and bacterial activities may shift along the longitudinal axis of the reservoir (Fig. 7). Potential explanations for the observed longitudinal patterns are necessarily speculative and, inevitably, produce more questions than answers. However, these results are significant from at least three viewpoints:

(1) These data (and those presented in the following companion paper in this volume) demonstrate that the spatial heterogeneity characteristic of reservoir ecosystems can be used to an advantage by limnologists as an experimental tool. Superimposed gradients of flow velocity, suspended particle levels, nutrient concentrations, and light availability along reservoir longitudinal axes provide research opportunities for relating the responses of biotic communities to a wide range of environmental conditions within a single aquatic system.

(2) The observed longitudinal trends in both the magnitudes and the size distributions of planktonic autotrophy and microheterotrophy are interpretable from a conceptual view of reservoirs as "river-lake hybrids" or transitional environments. Reservoirs appear to combine numerous features of river and lake environments and, to at least some degree, a shift from more riverine to more lacustrine conditions occurs within individual impoundments (Thornton et al. 1982; Kimmel et al., in press; Kimmel and Groeger, in press). The river-lake hybrid analogy has been used in a qualitative sense by numerous authors over the years, but is now receiving more serious attention as a potentially useful framework for explaining the spatial and temporal heterogeneity, diversity, and ecological structure of reservoirs as a class of aquatic ecosystems (see papers in Thornton, in press).

(3) Although the occurrence of longitudinal gradients in physical and chemical factors and in water quality within reservoirs is now becoming relatively well documented (Thornton et al. 1982, Kennedy et al. 1982, Kennedy, this volume), biological and ecological responses to such environmental gradients are not well known.

Size distributions of planktonic autotrophy and microheterotrophy in DeGray Reservoir correspond well to values previously reported for several more productive impoundments (Kimmel 1983). Together, these data show that, over a broad range of environmental conditions, the predominant fractions of planktonic autotrophy and microheterotrophy are associated with <8-μm algae and <1-μm bacteria, respectively. Furthermore, these 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 unproductive open ocean, coastal, and lacustrine environments, but also extends to other more productive lakes and reservoirs.

ACKNOWLEDGEMENTS

This research was supported by funding provided by the U.S. Army Corps of Engineers (USCE) and by the U.S. Department of Energy (DOE), Office of Health and Environmental Research. A. W. Groeger was supported by a DOE Laboratory Research Participation predoctoral fellowship administered by Oak Ridge Associated Universities. We thank R. H. Kennedy of the USCE Waterways Experiment Station, Vicksburg, Mississippi, for the opportunity to participate in EWQOS-related studies on DeGray Lake. We also thank J. Nix and co-workers for the generous assistance, courtesy, and hospitality provided to us during our vists to DeGray Lake, Ouachita Baptist University, and Arkadelphia. P. J. Mulholland, A. V. Palumbo, and W. Van Winkle contributed helpful criticism and comments on the manuscript.

Oak Ridge National Laboratory (ORNL) is operated by Union Carbide Corporation under contract W-7405-eng-26 with the U.S. Department of Energy. Publication No. ____, Environmental Sciences Division, ORNL.

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