

Zooplankton grazing experiments indicated that (1) most grazing pressure occurs on 3.0–8.0 μm particles, (2) grazer limitation of the occurrence of attached bacteria and microbial-detrital aggregates is unlikely, and (3) free-living bacteria are inefficiently harvested, relative to algae, by most reservoir zooplankton. Autotrophic particulate production is generally more available to filter-feeding zooplankton than is microheterotrophic production due to (1) the smaller particle size of most free-living bacteria relative to most microalgae, and (2) the apparent sparsity of bacteria-colonized particles and microbial-detrital aggregates. Relative to autotrophy, the microheterotrophic conversion of allochthonous dissolved organic matter and algal excretion products to bacterial biomass appears unlikely to be a significant source of organic carbon for planktonic grazers in most reservoirs.

INTRODUCTION

Man-made impoundments appear to occupy an intermediate position between natural lakes and rivers in regard to trophic characteristics, as well as to some morphologic and hydrodynamic features. Lacustrine foodwebs are based mainly on autochthonous primary production and lotic foodwebs on allochthonous organic matter and heterotrophic secondary production. Soon after impoundment, most reservoirs develop planktonic communities similar to those of natural lakes, but continue to receive large quantities of inorganic nutrients, suspended particles, and organic matter from their watersheds, as do rivers. Organic matter input-output budgets for reservoirs reflect significant allochthonous

contributions to the total organic matter supply (e.g., Lind 1971, Straskrabova 1975), but cannot reveal (1) the extent of allochthonous organic carbon incorporation into reservoir foodwebs, or (2) whether such incorporation occurs primarily by planktonic or benthic pathways.

The microheterotrophic conversion of dissolved organic matter (DOM) to bacterial biomass may represent a means for the direct incorporation of allochthonous DOM into the reservoir planktonic food chain (Paerl 1978, Goldman and Kimmel 1978, Kimmel 1979), if bacterial production is efficiently harvested by planktonic grazers (Fig. 1). Whether organic particles result from autotrophic or microheterotrophic production, particle size is a critical determinant of availability to higher trophic levels. In order to examine the size distributions of autotrophic and microheterotrophic activities in reservoirs, I combined dual radioisotopic labeling and size fractionation of naturally-occurring reservoir phytoplankton-bacterioplankton assemblages in four U.S. impoundments of differing limnological characteristics and trophic status: Lake Mead (oligo-mesotrophic, Colorado River, Arizona-Nevada), Broken Bow Lake (mesotrophic, Mountain Fork River, southeastern Oklahoma), Lake Texoma (eutrophic, Red River, Oklahoma-Texas), and Normandy Lake (eutrophic, Duck River, southcentral Tennessee). Grazing experiments were conducted in Texoma and Broken Bow reservoirs to (1) assess directly the relative availability of autotrophic and microheterotrophic production to planktonic grazers, and (2) determine grazing effects on the size distribution of microheterotrophy.

METHODS

Morphometric and limnological characteristics of the reservoirs sampled are summarized in Table 1. Lake Texoma was sampled on several dates over a two-year period, while Lakes Mead, Broken Bow, and Normandy were sampled on one occasion each. Lake Mead samples were obtained from stations located along a nutrient-productivity gradient resulting from the influx of municipal wastes to Las Vegas Bay on the western (downstream) end of the reservoir (Paulson et al. 1980). Standard methodologies (Strickland and Parsons 1972) were used for physical-chemical measurements, nutrient and chlorophyll analyses, and phytoplankton productivity estimates.

Dual Labeling and Size Fractionation Measurements

Water samples were obtained with an opaque PVC Van Dorn sampler, and returned to the laboratory for incubation and size-fractionation filtration. Subsamples in 125-mL light and dark bottles were inoculated with 0.5 mL $\text{NaH}^{14}\text{CO}_3$ solution ($4.72 \mu\text{Ci mL}^{-1}$, specific activity = $59.3 \text{ mCi mmol}^{-1}$) and 0.2 mL sodium ^3H -acetate solution ($25 \mu\text{Ci mL}^{-1}$, 2 Ci mmol^{-1}) to label autotrophs and microheterotrophs, respectively, and incubated for 2-4 h at light levels of $60\text{-}75 \mu\text{Ein m}^{-2} \text{ sec}^{-1}$ and ambient lake water temperature. Subsamples poisoned with 1 mL saturated HgCl_2 solution were similarly inoculated and incubated to provide a correction for radioisotope adsorption to particles and filters. Immediately after incubation, samples were placed in an ice bath in the dark to minimize further radioisotope uptake, and 5 to 20-mL aliquots (depending on particulate matter concentrations) were

gently vacuum filtered (< 0.3 atmos vacuum pressure) through 47-mm Nucleopore polycarbonate filters of 0.2, 0.8, 3.0, and 8.0 μm pore diameters. Filters and retained particles were rinsed three times with deionized water and radioassayed by liquid scintillation methods using a Beckman LS-8000 spectrometer. Automatic external standardization, calibrated with quenched standards for $\text{NaH}^{14}\text{CO}_3$ and sodium ^3H -acetate, was used to correct for sample quenching.

Planktonic autotrophy was estimated as the difference of light and dark bottle ^{14}C uptake, and microheterotrophy as ^3H uptake in the dark. All samples were corrected for radioisotope adsorption, which was always < 3% of unpoisoned sample activity. Particle size distributions of autotrophic and microheterotrophic activities were expressed as percent retention of the "total" activity (that retained by the 0.2 μm filter) retained by filters of greater pore size, e.g.,

$$\% \text{ retention by } 3.0\text{-}\mu\text{m filter} = \frac{\text{dpm retained by } 3.0\text{-}\mu\text{m filter}}{\text{dpm retained by } 0.2\text{-}\mu\text{m filter}} \times 100.$$

Grazing Experiments

Grazing experiments were conducted with naturally-occurring plankton assemblages from Broken Bow and Texoma reservoirs. Water samples were filtered through 64- μm Nytex mesh to remove large zooplankton, placed in 1-L clear glass bottles (3 experimental bottles, 1 control), and returned to the laboratory. Each bottle was inoculated with 1 mL $\text{NaH}^{14}\text{CO}_3$ solution ($20 \mu\text{Ci mL}^{-1}$, $59.3 \text{ mCi mmol}^{-1}$) and incubated in the light for 2 h, then inoculated with 1 mL sodium ^3H -acetate ($25 \mu\text{Ci mL}^{-1}$, 2 Ci mmol^{-1}) and similarly incubated for an

additional hour. Zooplankton collected in a 6-L Van Dorn bottle sample were gently concentrated in a 30- μm mesh chamber, and placed in 1-L of 64- μm screened, unlabeled lake water for 1-h acclimation prior to grazing experiments. Zooplankton were then reconcentrated, subsampled with a wide-bore pipet, and added to bottles of double-labeled seston, which resulted in a 1-1.5 x concentration of zooplankton relative to lake concentrations. In each experiment, one zooplankton subsample was heat-killed in water prior to its addition to the control seston bottle. Duplicate sets of aliquots from the control bottle were size-fractionated as described above to determine the size distributions of autotrophic and microheterotrophic activities in the experimental systems. Zooplankton were permitted to graze for 20-25 min, and were then reconcentrated on 30- μm mesh, rinsed thoroughly, transferred to glass scintillation vials, dried at 80°C, solubilized with NCS, and radioassayed. ^{14}C and ^3H activities of heat-killed zooplankton were subtracted from those of experimental samples to correct for radioisotope adsorption. In Lake Texoma experiments, zooplankton in three additional bottles of double-labeled seston were transferred to unlabeled 64- μm screened lake water after the initial grazing period and permitted to graze for another hour in order to clear their guts prior to the final collection and radioassay. These samples permitted estimation of assimilated ^{14}C - and ^3H -labeled materials, in addition to that ingested. The grazer selection coefficient (S) for ^3H -labeled particles was calculated as described by Lampert (1974).

Grazing Effects on the Size Distribution of Microheterotrophy

Zooplankton grazing effects on the size distribution of microheterotrophic activity were tested by size fractionation of subsamples from grazed and ungrazed Lake Texoma water samples. Two 19-L translucent polyethylene carboys were filled with water collected from a 2-m depth with a 6-L Van Dorn sampler. Zooplankton were removed from the "ungrazed" system by passing the water through 64- μm mesh as the carboy was filled, while the "grazed" sample was not screened. Both carboys were floated at the water surface in the University of Oklahoma Biological Station boat harbor throughout the 3-day experiment to maintain ambient temperature and particle suspension. Triplicate subsamples were siphoned from each carboy on successive days, placed in 125-mL dark bottles, inoculated with 1 ml sodium ^{14}C -acetate ($2 \mu\text{Ci mL}^{-1}$, 58 mCi mmol^{-1}), and incubated at lake water temperature for 4-5 h. One subsample set from each carboy was HgCl_2 -poisoned, prior to inoculation and incubation, to provide an adsorption correction. Size-fractionation and radioassay procedures were conducted as described above. The contents of each carboy were filtered through 30- μm mesh at the end of the experiment, and the zooplankton present in "grazed" and "ungrazed" treatments were enumerated.

RESULTS AND DISCUSSION

Size Distribution of Autotrophy and Microheterotrophy

Major fractions of autotrophic activity (33-96% in Lake Texoma, 83-97% in Lake Mead, 80-87% in Normandy Lake) and usually > 95% of microheterotrophic activity occurred in the < 8.0- μm size fraction

(Fig. 2, Table 2). Although variable, most microheterotrophy was associated with $< 0.8 \mu\text{m}$ particles (13-95%, $x = 62\%$ in Texoma; 23-30% in Broken Bow; 96-98% in Mead; and 47-63% in Normandy) indicating a usual predominance of free-living, rather than attached, bacteria in reservoir plankton. Microautoradiographic analyses of Texoma and Broken Bow samples showed algal uptake of ^3H -acetate to be negligible relative to bacterial uptake and confirmed that association of metabolically-active bacteria with larger particles was infrequent (White 1981).

The fraction of microheterotrophy associated with $> 3.0\text{-}\mu\text{m}$ particles was slightly greater at uplake than at downlake stations (Table 2) and in hypolimnetic than in epilimnetic samples (Fig. 3, Table 2). Microheterotrophy attributable to free-living bacteria was less (53 -vs- 84% $< 0.8 \mu\text{m}$) within a surface turbidity plume than in an adjacent non-turbid water mass (Lake Texoma, V-20-80, Table 2), indicating that bacteria do associate with suspended silt and clay particles as in turbid inflowing water. Size fractionations of microheterotrophy conducted during simulated watershed runoff experiments (Kimmel 1981) support this interpretation, but whether the observed shift in size distribution is due to active bacterial attachment to suspended particles or to coflocculation of bacterioplankton by settling silt or clay particle aggregates (e.g., Marshall 1980a, b) is uncertain.

The Lake Mead nutrient-productivity gradient provided, within one system, conditions representative of eutrophy, mesotrophy, and oligotrophy at inner Las Vegas Bay, outer Las Vegas Bay and Boulder

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Basin, and Virgin Basin stations, respectively (Fig. 4). Despite such marked differences among stations, greater than 95% of the total microheterotrophic activity was associated with free-living bacteria (< 0.8 μm) at all stations (Fig. 5). Both the predominance of free-living bacteria and the uniformity of size distributions of microheterotrophy at Lake Mead stations are noteworthy relative to previous reports that in nutrient-poor planktonic systems (1) adsorption of DOM and inorganic nutrients at suspended particle surfaces promotes microbial colonization and particle aggregation (e.g., Seki 1972, Paerl 1973, 1974), and (2) bacterial metabolic activity occurs primarily in association with detrital particles (e.g., Zobell 1943, Marshall 1980a). If organic and inorganic nutrient levels control the extent of bacterial association with suspended particles in Lake Mead, one would expect (1) large differences in the size distribution of microheterotrophy in inner Las Vegas Bay relative to the other sampling stations, and (2) more bacterial attachment at more nutrient-deficient stations. My data do not support this view. Less than 5% of total microheterotrophy was associated with particles > 0.8 μm at all Lake Mead stations, and bacterial attachment to larger particles was most important in nutrient-rich, inner Las Vegas Bay (Fig. 5), probably due to the greater concentration of particles there. Azam and Hodson (1977) reported a similar uniformity in the size distribution of microheterotrophy in a comparison of productive and unproductive coastal waters off Northwest Africa.

Except that large fractions of total autotrophic activity were associated with algae < 8.0 μm , the size distribution of autotrophy

Fig. 4

Fig. 5

did not show consistent patterns relative to spatial distribution or trophic status in the reservoirs sampled. Algae $> 8.0 \mu\text{m}$ accounted for larger fractions of autotrophy in well mixed, eutrophic Lake Texoma than in less productive systems (Fig. 2); however, this pattern did not hold among Lake Mead transect stations (Fig. 5, Table 2). Autotrophy associated with > 3.0 and $> 8.0 \mu\text{m}$ particles was usually greater at uplake than at downlake stations in Lake Texoma, but the opposite pattern occurred in Normandy Lake. Normandy Lake flushes more rapidly than Lake Texoma, receives more continual watershed inflow, and has less abiotic turbidity. More rapid nutrient uptake and cell growth could explain ultraphytoplankton predominance in rapidly-flushed systems in which algae are continuously displaced downlake by advection. While greater bacterial association with suspended particles at uplake stations can be attributed to higher concentrations of biotic and abiotic particulate detritus in the water column, the size distribution of autotrophy in reservoirs is likely influenced by a complex of factors including nutrient and light availability, frequency of nutrient inflow pulses, hydraulic residence time, vertical mixing rates and cell settling velocities, nutrient uptake kinetics and cell growth rate, and selective grazing pressure.

Availability of Autotrophic and Microheterotrophic Production to Planktonic Grazers

Many zooplankton are capable of collecting, ingesting and assimilating free-living bacteria (e.g., Gliwicz 1969, Pilarska 1977, Peterson et al. 1978, Friedman 1980, Starkweather 1980). However, the collection efficiency for such small particles (usually $0.5-1.0 \mu\text{m}$)

is usually considerably lower than for larger particles, e.g., nanoplankton, bacterial clumps, microbial-detrital aggregates (Gliwicz 1969, Peterson et al. 1978). Grazing experiments conducted with naturally-occurring assemblages of bacterio-, phyto- and zooplankton from Texoma and Broken Bow reservoirs indicated that for particles $> 3.0 \mu\text{m}$ there was no consistent grazer selection of either ^{14}C -labeled (algal) or ^3H -labeled (bacterial) particles (Table 3). However, about 70% of the microheterotrophic activity in Broken Bow Lake samples (Table 2: VIII-14-78) and 80-90% in Lake Texoma (Table 2: VIII-19, 23-78) were associated with $< 3.0\text{-}\mu\text{m}$ particles. Grazer selection coefficients based on ^{14}C and ^3H activities of all particles $> 0.8 \mu\text{m}$ undoubtedly reflect grazer inefficiency at collecting unattached bacteria (ca. $1 \mu\text{m}$) rather than active selection for algae.

Table 3

If zooplankton assemblages graze bacteria associated with larger particles more efficiently than free-living bacteria, grazing pressure could limit the occurrence of bacteria-colonized particles (e.g., Sieburth 1976, Azam and Hodson 1977). In a 3-day experiment designed to test grazing effects on the size distribution of microheterotrophy (Fig. 6), microheterotrophic activity associated with $3.0\text{-}8.0 \mu\text{m}$ particles was reduced significantly in the presence of grazers ($P < 0.005$, paired t-test) but was relatively unaffected in other size fractions ($P > 0.05$). Although most zooplankton grazing occurred on $3.0\text{-}8.0 \mu\text{m}$ particles, microheterotrophic activity associated with $> 3.0\text{-}\mu\text{m}$ particles never exceeded 8% of total microheterotrophy in the ungrazed enclosure, and therefore, grazer

Fig. 6

limitation of the occurrence of bacteria-colonized suspended particles and microbial-detrital aggregates seems unlikely.

Grazer assemblages in these experiments included cladocerans, copepods, and rotifers (Table 4). Protozooplankton [small (< 30 μm) ciliated Protozoa and heterotrophic microflagellates] were probably excluded by the concentration procedures used. Ciliates have been suggested to form trophic links between free-living bacteria and larger zooplankton in marine and freshwater planktonic systems (Sieburth 1976, Sieburth et al. 1978, Porter et al. 1979); however, they are normally restricted to relatively bacteria-rich environments and are usually not particularly numerous in open waters (Fenchel 1980). Ciliated protozoans and unpigmented microflagellates were rarely observed during microscopic examination of whole water plankton samples from Texoma and Broken Bow reservoirs (M. M. White, pers. commun.). However, protozooplankton are probably inefficiently sampled by methods employed for phytoplankton and zooplankton, and therefore may be routinely underestimated or overlooked entirely in most limnological investigations. The importance of the bacterivorous protozooplankton to organic carbon flow in planktonic foodwebs requires direct evaluation in a variety of systems.

The Contribution of Allochthonous DOC and Microheterotrophy to Reservoir Planktonic Food Chains

Particle size is a primary determinant of food resources available to consumers and the efficiency of energy transfer through planktonic food chains (Ryther 1969). Although bacterial and phytoplankton production rates appear to be of the same order of magnitude in natural

Table 4

lakes and reservoirs (Kuznetsov 1968, Tilzer 1972, Monheimer 1974, Jassby 1975, Jordan and Likens 1980), the magnitude of bacterial productivity may be misleading, from a foodchain perspective, if much of the production is unavailable to planktonic grazers. More extensive data are required and my conclusions must be viewed as preliminary, but these results for four limnologically-dissimilar reservoirs indicate that small nano- and ultraphytoplankton ($< 8.0 \mu\text{m}$) and free-living bacteria ($< 3.0 \mu\text{m}$) are primarily responsible for planktonic autotrophy and microheterotrophy, respectively, even in eutrophic systems. Results of grazing experiments in Texoma and Broken Bow reservoirs indicate that autotrophic particle production is generally more available to planktonic grazers than is microheterotrophic production due to (1) the much smaller particle size of free-living bacteria relative to most phytoplankton, and (2) the sparsity of bacteria-colonized particles and microbial-detrital aggregates in the water column.

It is possible that sample collection and filtration procedures cause the disassociation of attached bacteria from particles or the dispersal of particle aggregates (e.g., Jannasch 1973). However, considering that bacterial association with larger particles has been observed relatively frequently (e.g., Kuznetsov 1968; Seki 1972; Hanson and Wiebe 1977; Paerl 1973, 1975, 1980), methodological artifact is an unsatisfactory explanation. Sieburth et al. (1978) have suggested that two groups of bacteria may exist in marine plankton: (1) very small, free-living planktobacteria which use labile dissolved organic compounds and account for most of the planktonic microheterotrophic activity, and (2) epibacteria which are metabolically inactive as free

cells but utilize polysaccharides associated with seston particles when attached. Such a view can at least partially explain conflicting observations of attached vs unattached bacteria in terms of variable suspended particle quantity and quality. In the absence of high grazing pressure, more rapid settling of bacteria-colonized particles and microbial-detrital aggregates, relative to free-living bacteria, could account for the low percentage of total microheterotrophic activity associated with larger particles. If so, bacterial colonization and production associated with sestonic detritus may be more important as a link between planktonic and benthic systems than as a carbon flow pathway within the planktonic food chain.

Relative to phytoplankton particulate production, the microheterotrophic conversion of allochthonous DOM and algal excretion products to bacterial biomass appears unlikely to be a major source of organic particles available to most reservoir zooplankton. Indeed, unless the protozooplankton prove to be quantitatively important consumers of free-living bacteria, microheterotrophic particle production may constitute a major organic carbon sink, via bacterial respiration, rather than an important organic carbon pathway to higher trophic levels in planktonic systems (Fig. 1). However, allochthonous organic matter and microheterotrophic production are likely of major importance to reservoir zooplankton at times when significant phytoplankton production is prevented (e.g., during conditions of extreme turbidity or very rapid flushing). Although such conditions are characteristic of certain reservoirs (e.g., Marzolf and Osborne 1971; Marzolf, In press; Marzolf and Arruda, In press) and occur periodically within many others, allochthonous organic carbon

contributions to reservoir foodwebs probably occur primarily through detritivore rather than grazer pathways, and via sedimentation, through benthic rather than planktonic food chains.

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Table 1. Morphometric and limnological characteristics of Lake Texoma (Okla.-Tex.), Broken Bow Lake (Okla.), Lake Mead (Ariz.-Nev.), and Normandy Lake (Tenn.). All are multiple-purpose impoundments. Values listed are for conservation pool level.

	TEXOMA	BR. BOW	MEAD	NORMANDY
Date Impounded	1944	1968	1935	1976
River Impounded	Red	Mtn. Fork	Colorado	Duck
Surface Elevation (m) ^a	188	183	374	267
Lake Surface Area (ha)	36,000	5,750	66,000	1,308
Lake Volume (m ³ 10 ⁶)	3,359	1,134	36,000	93
Mean Depth (m)	9	20	55	7
Maximum Depth (m)	35	55	180	23
Discharge Depth (m)	29	21	83	20
Retention Time (yr)	0.8	1.0	3.9	0.2
Shoreline Length (km)	993	290	885	117
Shoreline Development	13.9	10.8	9.7	9.1
Summer Thermal Stratification	Weak	Strong	Strong	Strong
Approx. Summer Secchi Depth (m)	1-2	3-4	5-20	0.5-1.5
Trophic Status ^b	E	M	0-M	E

^ameters above mean sea level

^b0 = oligotrophic, M = mesotrophic, E - eutrophic.

Table 2. Particle size distributions of planktonic autotrophic and microheterotrophic activities observed in Texoma, Broken Bow, Mead and Normandy reservoirs. Naturally-occurring phytoplankton and bacterioplankton assemblages were double-labeled with ^{14}C -bicarbonate and ^3H -acetate, and size-fractionated by filtration through 0.2, 0.8, 3.0, and 8.0- μm pore diameter Nucleopore filters. Total autotrophy and microheterotrophy defined as ^{14}C and ^3H activities, respectively, in particulate matter retained by the 0.2- μm filter.

Reservoir, Trophic Status, and Date	Sample	% Autotrophic Activity Retained				% Microheterotrophic activity retained			
		0.2-0.8	0.8-3.0	3.0-8.0	> 8.0 μm	0.2-0.8	0.8-3.0	3.0-8.0	> 8.0 μm
Lake Texoma (eutrophic)									
VIII-19-78	2m	7	23	70 ^a	-	56	33	11 ^a	-
VIII-23-78	2m	8	6	85 ^a	-	59	23	18 ^a	-
VIII-31-78	2m	3	11	25	61	50	34	11	5
	5m	7	22	34	45	63	28	7	2
	10m	6	9	3 ^a	52	70	20	6	4
	20m	8	32	24	36	13	66	11	10
III-13-79	2m	-	-	-	-	52	39	7	2
VI-24-79	Up lake - 2m	-	27 ^b	6	67	-	94 ^b	3	3
	Dn lake - 2m	-	35 ^b	8	53	-	96 ^b	2	2
V 6-80	Up lake - 2m	0	52	17	31	90	9	1	0
	Dn lake - 2m	10	80	6	4	95	5	0	0
V-20-80	In plume - 2m	0	5	63	32	53	43	3	1
	Not in plume - 2m	0	31	47	22	84	14	2	0
Broken Bow Lake (mesotrophic)									
VIII-14-78	3m	7	44	49 ^a	-	23	40	27 ^a	-
	7m	7	18	75 ^a	-	30	38	32 ^a	-
Lake Mead (oligo-mesotrophic)									
III-27-80	Sta A - 3m	27	35	29	9	96	2	2	0
	Sta B - 3m	23	19	40	17	98	1	1	0
	Sta C - 3m	21	34	36	9	98	1	1	0
	Sta D - 3m	10	62	25	3	97	3	0	0
	Sta E - 3m	22	29	39	10	97	2	1	0
Normandy Lake (eutrophic)									
IX-15-80	Up lake - 1m	8	58	20	13	61	33	4	2
	Dn lake - 1m	0	3 ^a	41	20	63	35	1	1
	Dn lake - 14m	-	-	-	-	47	47	5	1

^a Activity in > 3.0 - μm size fraction.

^b Activity in 0.2-3.0 μm size fraction.

Table 3. Results of zooplankton feeding on seston double-labeled with $\text{NaH}^{14}\text{CO}_3$ (autotrophy) and sodium ^3H -acetate (micro-heterotrophy). Calculations based on activity of seston retained by 0.8 and 3.0 μm Nucleopore filters. Data expressed as $x \pm 1 \text{ SD}$, $n = 3$.

Experiment	Selection coefficient ^a	
	> 0.8 μm	> 3.0 μm
Broken Bow, VIII-14-78		
3m, Ingestion	0.70 + 0.18	1.18 + 0.30
7M, Ingestion	0.30 + 0.04 ^b	1.46 + 0.20
Texoma, VIII-19-78		
2m, Ingestion	0.11 + 0.03 ^b	1.04 + 0.25
2m, Assimilation	0.05 \pm 0.04 ^b	0.43 + 0.42
Texoma, VIII-23-78		
2m, Ingestion	0.04 + 0.01 ^b	0.50 + 0.08 ^b
2m, Assimilation	0.11 + 0.06 ^b	1.20 + 0.66

^a Selection coefficient (S) calculated as:

$$S = \frac{{}^{14}\text{C}_{\text{seston}} \times {}^3\text{H}_{\text{zoopl.}}}{{}^3\text{H}_{\text{seston}} \times {}^{14}\text{C}_{\text{zoopl.}}}$$

A coefficient of 1.0 indicates non-selective feeding, > 1.0 means selection for ^3H -labeled material, and < 1.0 means selection for ^{14}C -labeled particles.

^b Significantly different from 1 at $\alpha = 0.05$ by t -test.

Table 4. Zooplankton assemblages present in grazer selectivity experiments in Broken Bow Lake (VIII-14-78) and Lake Texoma (VIII-19-78 and VIII-23-78) and in the experiment conducted to assess grazer effects on the size distribution of microheterotrophic activity (Lake Texoma: III-13-16-79). Zooplankton densities are in organisms per liter.

Genus	Broken Bow		Texoma		Texoma: III-13-16-79		
	VIII-14-78		VIII-19-78	VIII-23-78	Initial grazer density III-13	Grazers present III-16	Grazers absent III-16
	3m	7m	2m	2m			
Bosmina	8	52	0	0	4	8	0
Daphnia	0	2	0	2	24	16	1
Diaphanosoma	0	11	3	5	0	0	0
Holopedium	0	10	0	0	0	0	0
Diaptomus copepodids	3	6	23	20	49	29	10
Diaptomus nauplii	31	7	21	21	33	42	7
Brachionus and other small rotifers	20	5	3	6	172	655	178
Polyarthra	10	4	0	0	46	124	68
Asplanchna	0	1	0	0	21	16	9

FIGURE LEGENDS

- Fig. 1. Hypothesized carbon flow in a reservoir planktonic food chain. Conversion of allochthonous dissolved organic matter to bacterial biomass can comprise a major organic carbon pathway to planktonic grazers only if bacterial production is harvested efficiently.
- Fig. 2. Representative particle size distributions of planktonic autotrophy and microheterotrophy in four limnologically-dissimilar reservoirs: Lake Texoma (31 August 1978, 2m), Broken Bow Lake (14 August 1978, 3m), Lake Mead (27 March 1980, 3m, station C), and Normandy Lake (15 September 1980, 1 m, downlake station). Data expressed as percent autotrophic activity (reflected by ^{14}C -bicarbonate uptake) and percent microheterotrophic activity (reflected by ^3H -acetate uptake) associated with particulate matter retained by 0.2, 0.8, 3.0 and 8.0- μm pore diameter Nucleopore filters.
- Fig. 3. Vertical distribution of planktonic autotrophy and microheterotrophy by particle size; Lake Texoma, 31 August 1978.
- Fig. 4. Chemical and biological data on mixed-layer (3 m) samples taken along a west-east transect from inner Las Vegas Bay to the Virgin Basin, Lake Mead (Arizona-Nevada), 27 March 1980.
- Fig. 5. Size distributions of planktonic autotrophy and microheterotrophy in mixed-layer (3 m) samples taken along a nutrient-productivity gradient in Lake Mead, 27 March 1980. Phytoplankton productivity and nutrient availability decreased along the transection from station A to station E.

Fig. 6 Grazing effects on the size distribution of microheterotrophic activity. Experiment conducted in grazed and ungrazed enclosures, Lake Texoma, 13-16 March 1979. Plotted points represent means of duplicate determinations, vertical bars indicate the range.