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THE FRESHWATER ASIAN CLAM Corbicula fluminea
AS A FACTOR AFFECTING NUTRIENT CYCLING
IN THE CHOWAN RIVER, N.C.

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DISCLAIMER STATEMENT

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ABSTRACT

The Asian clam Corbicula fluminea has recently invaded the Chowan River and reached stable population densities ($200 \cdot \text{m}^{-2}$) in the northern part of the river and major tributaries. Because the river experiences periodic summer blue-green algal blooms, we compared Corbicula assimilation efficiencies of blue-green (Anabaena) and green algae (Chlorella and Scenedesmus). Anabaena was assimilated with the highest efficiency (82.5 %) and Chlorella with the lowest (33 %), although Chlorella was filtered faster by the clams. Excretion rates of NH_4 and PO_4 were determined from clams freshly collected from the river seasonally in 1982, and were highest in summer. Estimates of NH_4 and PO_4 excretion, based on 1980 Corbicula biomass in the river ($357-8642 \mu \text{moles} \cdot \text{m}^{-2} \cdot \text{da}^{-1}$ for NH_4 and $161-3924 \mu \text{moles} \cdot \text{m}^{-2} \cdot \text{da}^{-1}$ for PO_4), indicate that the clams can make a significant contribution to nutrient cycling in the river, at a time when allochthonous loading is at a minimum.



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CONCLUSIONS AND RECOMMENDATIONS

1) The Asian clam Corbicula fluminea appears to have reached stable densities in the Chowan River, having invaded the upper river and tributaries between 1974-1978.

2) Feeding experiments using radiolabeled algae indicate that the clam may not suffer any negative effects of blue-green blooms in the river, although long-term feeding and survival studies are needed.

3) Corbicula is able to rapidly recycle nutrients important for phytoplankton growth (NH_4 and PO_4), and in parts of the river where it is abundant, excretion rates are significantly higher than sediment flux rates of the same nutrients.

4) Any attempts to model nutrient cycling in the river must take Corbicula abundance into consideration. Efforts are currently underway to more accurately quantify the relationships between Corbicula excretion rates and important variables such as temperature and particulate food concentrations.



INTRODUCTION

Recent nuisance blue-green algal blooms in the Chowan River, in northeastern North Carolina, have generated concern among state agencies and have prompted research efforts to describe factors controlling algal blooms in the river. This has included estimates of watershed and point-source inputs of nutrients into the river as well as determining and quantifying sources of recycled nutrients within the system (NCDEM 1982). Elsewhere, benthic invertebrates have been shown to be important factors in nutrient cycling, both indirectly, through burrowing and sediment reworking (Gallep 1979; Aller 1978), and directly, through excretion (Kuenzler 1961; Jordan and Valiela 1982). A 1980 benthic survey of the Chowan and tributaries revealed that the freshwater Asian clam Corbicula fluminea had recently invaded the watershed. Because of the relatively large biomass of the clams, they probably represent the most important source of recycled nutrients among the filter-feeding benthic invertebrates in the river. Excretion studies with saltwater mussels indicate that they can be a significant source of recycled nutrients (e.g., Jordan and Valiela 1982); our study is the first to measure excretion by Corbicula and to compare rates with other nutrient sources such as sediment-water fluxes.

Little is known of the food habits of Corbicula; a small amount of data indicates that the clam can filter a wide range of particle sizes (Wallace et al. 1977). Blue-greens are the dominant algal group in the Chowan during summer months, so it was important to first determine whether the clam was able to utilize blue-greens as a food source. Many other aquatic organisms such as filter-feeding zooplankton do not assimilate blue-greens as well as they do other kinds of algae (Schindler 1968; Arnold 1971).

This project, then, is composed of two parts: the first involved a determination of the assimilation efficiency of blue-green and green algal species by Corbicula. This has been done by labeling monocultures of different algal species with ^{14}C , feeding constant amounts of the algae to Corbicula and determining the assimilation efficiency from the amount of label taken up into tissues as well as the amount respired as $^{14}\text{CO}_2$. The second part of the project involved measuring ammonium and orthophosphate excretion by Corbicula freshly collected from the Chowan during different seasons in 1982. By utilizing data on clam distributions and biomass obtained from a 1980 benthic survey, it has been possible to calculate the volume of ammonium and orthophosphate excreted by Corbicula in summer months over most of the river and major tributaries.

LITERATURE REVIEW

Chowan River

The Chowan River is formed by the confluence of the Blackwater and Nottoway rivers near the Virginia-North Carolina border. As it flows southward it widens considerably before emptying into the Albemarle Sound at Edenton, NC (Fig. 1). A majority of the catchment lies in Virginia and drains mostly agricultural and wetlands. Point sources of nutrient input include a number of small municipal waste treatment facilities as well as several large industrial sources.

Although lunar tides seldom exceed 15 cm (Stanley and Hobbie 1977), wind tides are significant and may actually reverse the flow of the lower river (Daniel 1977). Averaged flushing times for the lower Chowan are < 10 da in winter to > 50 da in summer, and saltwater sometimes intrudes into the lower river when flows are very low. The river water is usually well mixed, but thermal stratification is sometimes observed in summer in the lower river.

The river water is highly colored because of high humic and fulvic acid content and, at times, appreciable algal biomass (Paerl 1982). Blue-green algal blooms, consisting primarily of Anabaena and Microcystis (Witherspoon et al. 1979) have plagued the river in recent

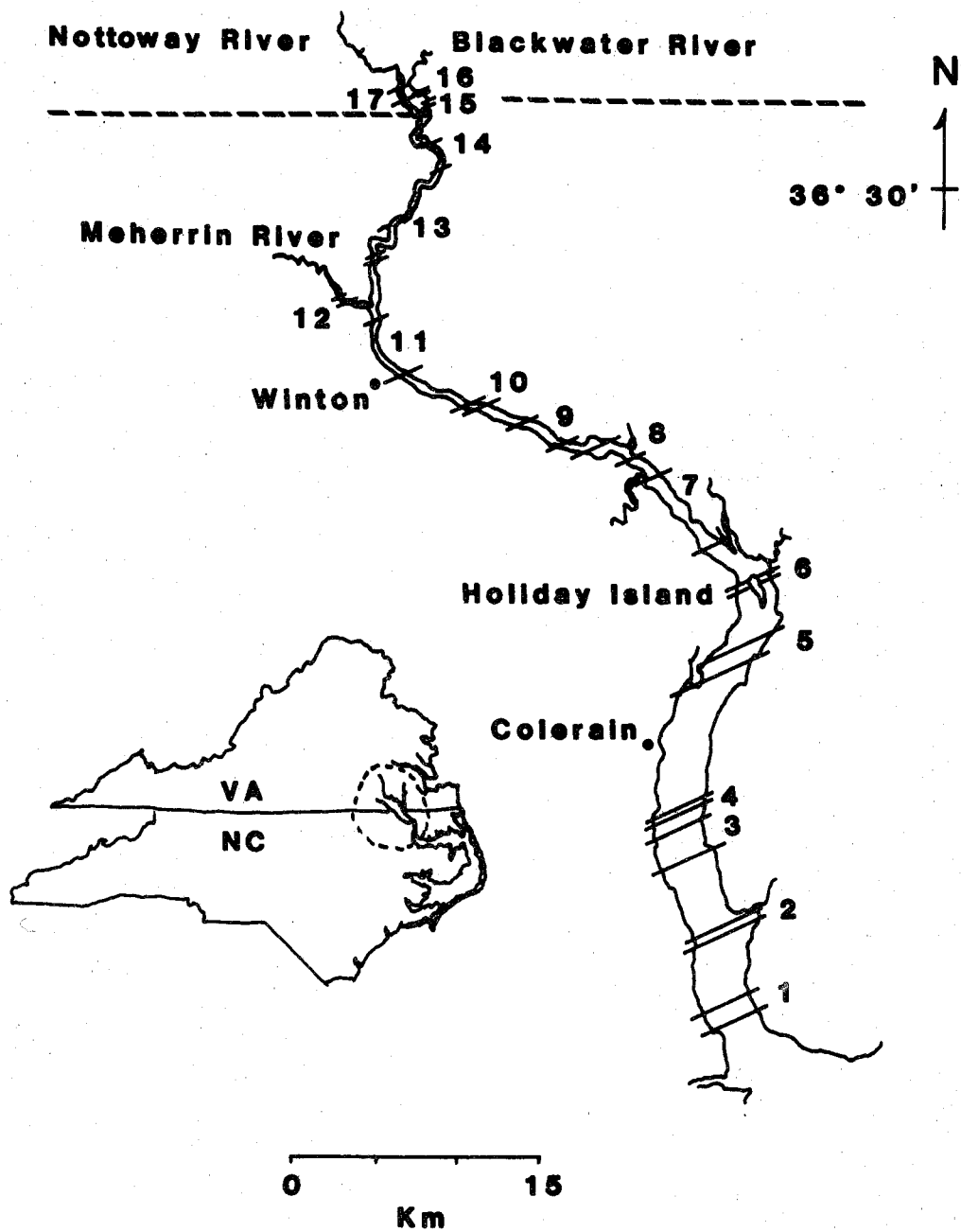


Figure 1. Chowan River and major tributaries, showing strata and transects for 1980 benthic sampling. Corbicula for 1982 excretion studies were collected from stratum 11.

years causing fish kills, foul tastes, odors and toxicity problems (NCDEM 1982). Efforts are now underway to control nonpoint as well as point sources of nutrients into the river, coordinating management efforts in North Carolina with the appropriate agencies in Virginia.

Corbicula

The freshwater Asian clam Corbicula fluminea was introduced into the West Coast of the United States in the late 1930's. Spreading rapidly throughout the region, it soon became very abundant ($>10^4$ clams $\cdot m^2$) in man-made canals and water supply systems in central and southern California (Eng 1979). Corbicula has spread across the continent since its introduction, and was first reported from the Atlantic drainage basin in the Altamaha River, Georgia, in 1970 (Sinclair 1971). The clam has reached pest proportions in some areas because of its ability to reproduce rapidly and disperse quickly. Unlike the larger freshwater mussels, which are dependent upon fish hosts to disperse their glochidial larvae, Corbicula produces veliger larvae which become planktonic and are transported with water currents. In southern North America Corbicula usually reproduces in spring and fall, depending on temperature conditions. Young clams are able to attach to solid substrates with a byssus thread and have created fouling problems in cooling water intakes and water supply

systems (Sinclair 1964; McMahon 1977).

Freshwater bivalves are suspension feeders, filtering algae, detritus and other organic material from the water they pump through their gills. Unsuitable food material is ejected as pseudofeces, while wastes generated from digestion are released as feces and dissolved excretory products such as ammonium. In the only reported study of the potential effects of bivalve filter feeding in a natural freshwater system, Stanczykowska et al. (1976) estimated that the mussel Dreissena polymorpha filtered out 8 % of the primary production in a small eutrophic lake during a single growing season. The production of fecal pellets constituted about 13 % of yearly sedimentation in the pelagic zone of the lake. Significant fluctuations were found in filtration, consumption and assimilation rates of the mussels with changes in season, leading them to conclude that variations were dependant upon changes in water temperature and seston concentrations (Stanczykowska et al. 1976). Other researchers have calculated the impact of Corbicula feeding by following changes in concentrations of nutrients as they are taken up by phytoplankton and then removed as the clams filter the suspended plankton (Habel 1970; Greer and Ziebell 1972). A Japanese species of Corbicula (C. japonica) was able to remove an estimated one-seventh of the available particulate phosphorus from

suspension in a poikilohaline lagoon in which it was abundant (Fuji 1979).

Excretion by aquatic invertebrates has only been studied in a few, mostly marine, invertebrates. Because they live in an aqueous environment, animals do not need to process or concentrate nitrogenous excretory products to reduce water loss, and excrete primarily ammonium (NH_4). Excretion studies with marine bivalves show that a significant amount of nitrogen (primarily ammonium) may be released (e.g., Bayne and Scullard 1977). Jordan and Valiela (1982) concluded that populations of a saltwater mussel released more ammonium into the water of a New England marsh than any other plant or animal population in the marsh.

MATERIALS AND METHODS

Excretion Studies

Collections of Corbicula and river water were made in May, September and December 1982 near Winton, North Carolina (Fig. 1), then immediately transported to the UNC Institute of Marine Sciences labs in Morehead City. Clams were scrubbed and sorted into size classes, with the range of sizes (shell length) and dry flesh weights of clams being used in every experiment indicated in Appendix 1. Physical and chemical data collected at Winton by N.C. Department of Environmental Management for these sampling periods is given in Appendix 2. Five clams of the same shell length were placed into 1-l beakers with 750 ml of filtered (Whatman GF/C) river water and sealed with aluminum foil to prevent contamination from the air. Two beakers containing only filtered river water were used as controls in each experiment. The rate of excretion for each treatment was determined as the difference in nutrient concentration over time between beakers with clams and the controls without clams. The May and September experiments were conducted at room temperature (about 20 ° C) while the December experiment was run at 6 ° C. Fifty ml samples were taken from each beaker after 5, 14, and 21 hr and were placed in acid-washed poly bottles. These samples were refrigerated and nutrient analysis was completed

within 24 hr of collection. At the end of the experiments the water in each beaker was filtered through a 4.25 Whatman GF/C glass fiber filter. These filters were then frozen for later analysis of total Kjeldahl nitrogen.

Ammonium concentrations were determined by the phenol-hypochlorite method of Solorzano (1969), modified for use with 10 ml samples. Samples were read on a Bausch and Lomb Spectronic 710 spectrophotometer, and a calibration solution of NH_4Cl was used as a standard.

The molybdate blue method (Murphy and Riley 1962) was used for orthophosphate (soluble reactive phosphorus) analysis. These samples were also read on a B and L Spectronic 710, subtracting turbidity and water color blanks from absorbance values for samples and standards. A calibration solution of KH_2PO_4 was used as a standard.

Clams removed from the beakers were frozen and later dried in an oven at $60-70^\circ\text{C}$ for 5-7 days. Shell length (longest dimension) and dry flesh weight were determined for each individual clam.

Assimilation of ^{14}C -Labeled Algae

Algal species used in feeding experiments were maintained in continuous culture at 20°C , with constant light provided by cool white fluorescent lamps. Cultures were gently agitated with a stirring bar and plate and were bubbled with air to maintain a constant pH. Algal

growth media and glassware were autoclaved before use, and efforts were made to keep bacterial contamination at a minimum. The green algae Scenedesmus quadricauda and Chlorella vulgaris were grown with a modified ASM media (Paerl 1983; Appendix 3), while the nitrogen-fixing blue-green Anabaena flos-aquae was grown with a modification of Chu-10 media (Chu 1942) containing no nitrogen.

Aliquots of each algal species were inoculated with 2.5 μ Ci of ^{14}C sodium bicarbonate (New England Nuclear, Boston, Mass.) 6-18 hr before feeding experiments and placed in cool white light. After light incubation, green algal cultures were then centrifuged and algal cells resuspended in filtered lake water. Because the blue-green filaments clumped up with centrifugation, ^{14}C -inoculated Anabaena cultures were allowed to settle so that growth media could be siphoned off. Cell volume and density of resuspended cultures were determined with a Coulter Counter Model T_{AI}I, and a hemocytometer was used to count the number of algal cells $\cdot\text{ml}^{-1}$ visually.

Collections of live Corbicula were made in Lake Waccamaw (Columbus Co., N.C.) and the Chowan River near Winton, N.C. The clams were maintained in aerated aquaria at 20 $^{\circ}$ C for at least a week prior to feeding experiments and during holding were fed mixed algal cultures of Anabaena, Ankistrodesmus, Scenedesmus, and Chlamydomonas.

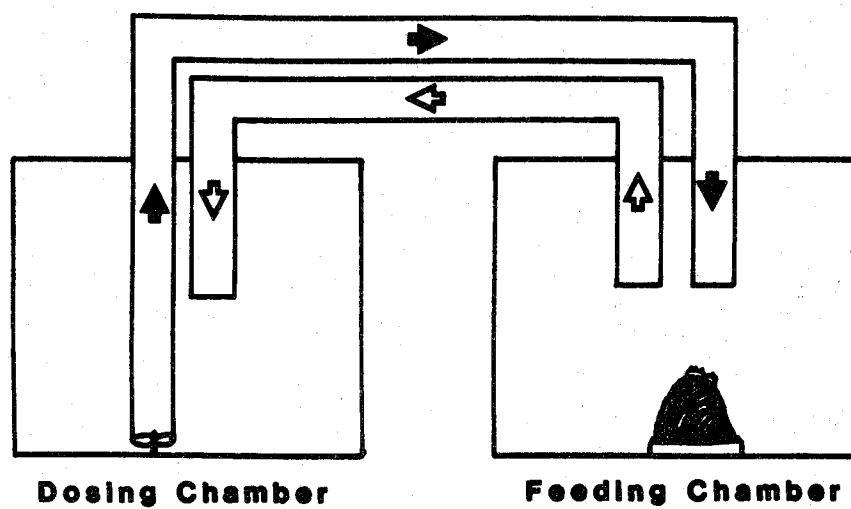


Figure 2. Schematic of continuous-flow system for feeding experiments. Algae are added to dosing chamber, then circulate to the feeding chamber, where the clam filters out the algae.

Twenty-four hours before the start of feeding experiments clams of similar sizes were isolated in beakers of filtered lake water to empty their guts.

Individual clams were placed in feeding chambers with 1.5 l of circulating, filtered lake water one hour before dosing with labeled algae to allow them to acclimate. A schematic of a feeding chamber is illustrated in Fig. 2; they were a modification of a design by Peirson (in press) and Riisgard and Mohlenberg (1979). Specific volumes (usually 2 mm³) of labeled algae were added to the dosing reservoirs of the chambers, and the clams were allowed to feed for 4 hr. At the end of the experiments any pseudofeces produced were collected separately with a pipette. The contents of the feeding chambers were filtered through 4.25 Whatman GF/C filters and radioassayed.

Clams removed from the feeding chambers were placed in aerated 1-l filter flasks with 500 ml of filtered lake water. Flask sidearms were connected to impinger traps containing 25 ml of a 2:1 mixture of ethylene glycol monomethyl ether and ethanolamine to trap ¹⁴CO₂ (Peirson in press). Feces were collected daily onto Whatman GF/C filters and radioassayed separately. After three days, the clams were removed from the flasks and frozen. The water in the filter flasks was acidified with 1 ml of

concentrated HCl, then aerated for 30 min with the impinger traps still attached to drive off any remaining $^{14}\text{CO}_2$. Aliquots of the flask water were assayed to determine the amount of ^{14}C in soluble form. One ml of methanol was added to aliquots of the mixture in the CO_2 traps before radioassay to facilitate mixing of this liquid with the scintillation cocktail.

Clam tissue was removed from the shells and placed in scintillation vials, to which a mixture of 3 ml of Scintigest and 1 ml water were added. Tissues were then digested 12-24 hr in a 50°C water bath. One-half ml of Scintigest tissue solubilizer was added to fecal samples before addition of scintillation cocktail.

Ten ml of Scintiverse scintillation cocktail was added to all filters, liquid and tissue samples before counting on a Beckman LS-200B liquid scintillation counter. A toluene ^{14}C standard (New England Nuclear) was used to determine counting efficiencies for each kind of sample counted.

In radiotracer experiments, assimilation is determined by adding the radioactivity retained in the animal (without gut contents) to the complete metabolic losses (respiration) of tracer during the experimental period. Animals were held in respiration chambers for a 3-day period after feeding experiments so that unassimilated

material would be voided while at the same time measuring $^{14}\text{CO}_2$ evolved. Because the clams did not filter out all of the labeled algal cells even after 4 hours in the feeding chambers, assimilation was determined from the percentage of tracer ingested.

Filtration Rate Calculations

The following equation was used to determine filtration rate for individual clams (Coughlan 1969):

$$\text{filtration rate} = \frac{\text{volume (ml)}}{\text{time (hr)}} \log_e \frac{\text{initial conc}}{\text{final conc}}$$

The concentration ratio was determined as the total amount of algal radioactivity dosed divided by the algal radioactivity that remained in the chamber at the end of the feeding period. Because the water in the feeding chambers was continuously circulating, algal settling was assumed to be negligible.

To determine if the volume (or density) of algae fed affected filtration rate (the amount of algae ingested), experiments were run adding cultured Chlorella to reach final densities of 1.33, 2.67, and 4 $\text{mm}^3 \cdot \text{l}^{-1}$. Since filtration rates were significantly different (Kruskal-Wallis test, $p < .05$; Fig. 3), the lowest density (1.33 $\text{mm}^3 \cdot \text{ml}^{-1}$) was used in subsequent feeding experiments with Anabaena and Scenedesmus to determine assimilation efficiencies.

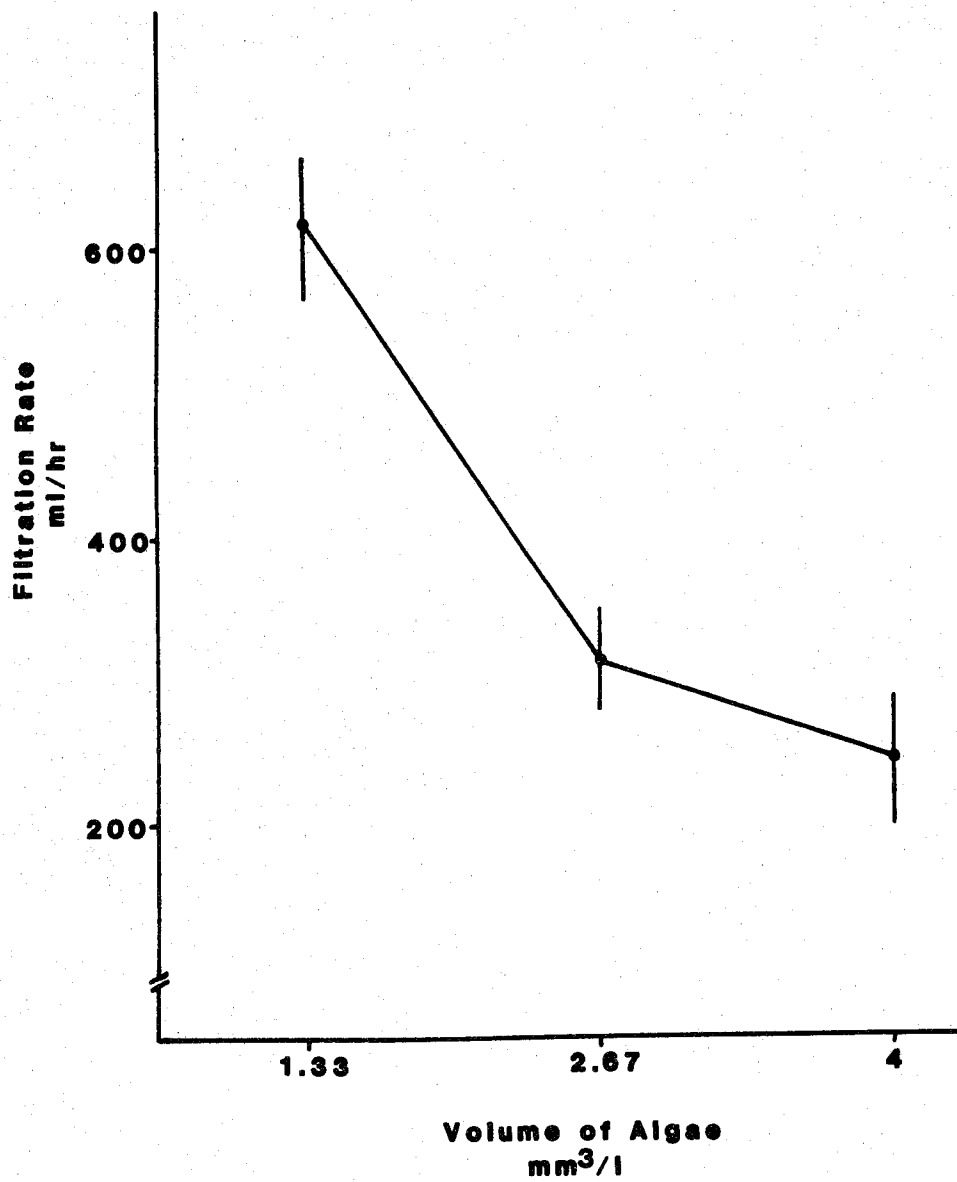


Figure 3. Mean individual filtration rates ($\text{ml}\cdot\text{hr}^{-1} \pm 1 \text{ S.E.}$) for different volumes ($\text{mm}^3\cdot\text{l}^{-1}$) of Chlorella by Corbicula ($n = 6, 6, 4$ clams).

1980 Chowan River Benthic Surveys

Surveys undertaken in March-April and in July 1980 provided data on density, age distributions and biomass of Corbicula in the Chowan River. A stratified random sampling design was devised to compare with N.C. Div. of Environmental Management stations and provide unbiased population estimates (Fig. 1; Table 1). The seventeen strata sampled included the entire Chowan River and the lower ends of its three major tributaries: the Meherrin (12), the Nottoway (17), and the Blackwater (15-16). Each stratum was composed of two transects, each with 6 sample sites. Transect positions were chosen at random within each stratum. The starting point was also selected at random within the first 1/6 river width on each transect. The five remaining sites on each transect were then spaced 1/6 river width apart. Sites were plotted in advance on a navigational chart and located along a compass line by using navigational markers and landmarks. Time and weather constraints limited winter (March-April) sampling to strata 1,2,5-7,9,10,15-17.

Benthic samples were taken with a Ponar grab (487 cm²), washed through a sieve with 4 mm mesh widths, and then preserved in 10 % buffered formalin. Shell size (the longest dimension) of each clam collected was measured with vernier calipers. Shell length-dry flesh weight (log-log)

Table 1. Comparison of 1980 Benthos Survey strata with N. C. Division of Environmental Management monitoring stations.

<u>Benthos</u>	<u>N.C.D.E.M.</u>	<u>Approx. River Mile</u>
1	C-16	2
2	C-15	5
3	none	
4	C-13	13
5	C-12	16
6	C-11	20
7	C-7A	24
8	C-6	27
9	C-5	31
10	C-4	33
11	C-3	34
12	C2D	(Meherrin) 40M
13	C2C	41
14	C2B1	46
15	C2	(Blackwater) 50.5B
16	C1B	" 51B
17	C1	(Nottoway) 51N

regressions were calculated for samples of Corbicula collected from both the winter and summer surveys (Fig. 4). These regressions were used to obtain estimates of Corbicula dry flesh weight (biomass) on a m^2 basis in each stratum of the river.

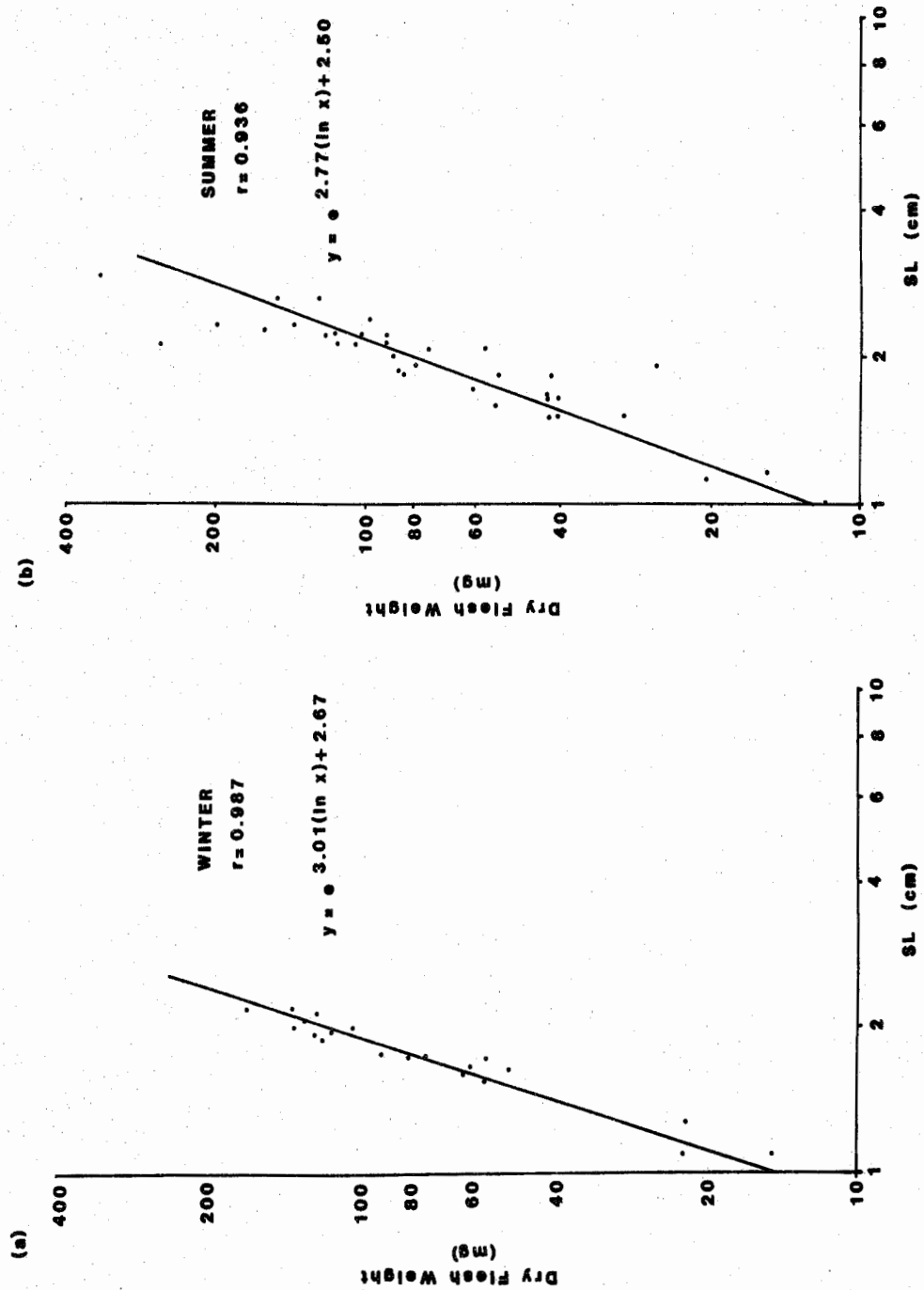


Figure 4. Shell length versus dry flesh weight (logarithmic scales) for *Corbicula* from Chowan River benthic surveys in "winter" (a, March-April) and summer (b, July), 1980.

RESULTS

Feeding Experiments

The rates at which Corbicula filtered Anabaena and Scenedesmus were variable, ranging from 278-607 ml·hr⁻¹ (Fig. 5), and as a result comparisons of rates between the different algal species were not significantly different (Kruskal-Wallis test, $p > .1$). There was no obvious correlation between flesh wet weight of Corbicula and filtration rate within the size range of clams tested (1.7-2.3 cm shell length). Anabaena was the only alga that was observed to induce pseudofecal production by the clams as they were feeding (strands formed near the exhalant siphons and could be collected with a pipette), which indicated that some of the material was rejected as they were feeding.

Assimilation efficiencies of the different algal species by Corbicula were significantly different (Kruskal-Wallis test, $p < 0.001$). The blue-green alga Anabaena was assimilated with the greatest efficiency (mean = 82.5 %) and Chlorella with the least (mean = 33 %; Fig. 6). Table 2 shows that the high efficiency with Anabaena as a food source is a result not only of higher uptake of label into clam tissues, but relatively high respiration (of ¹⁴CO₂) as well. However, since no efforts were made to distinguish

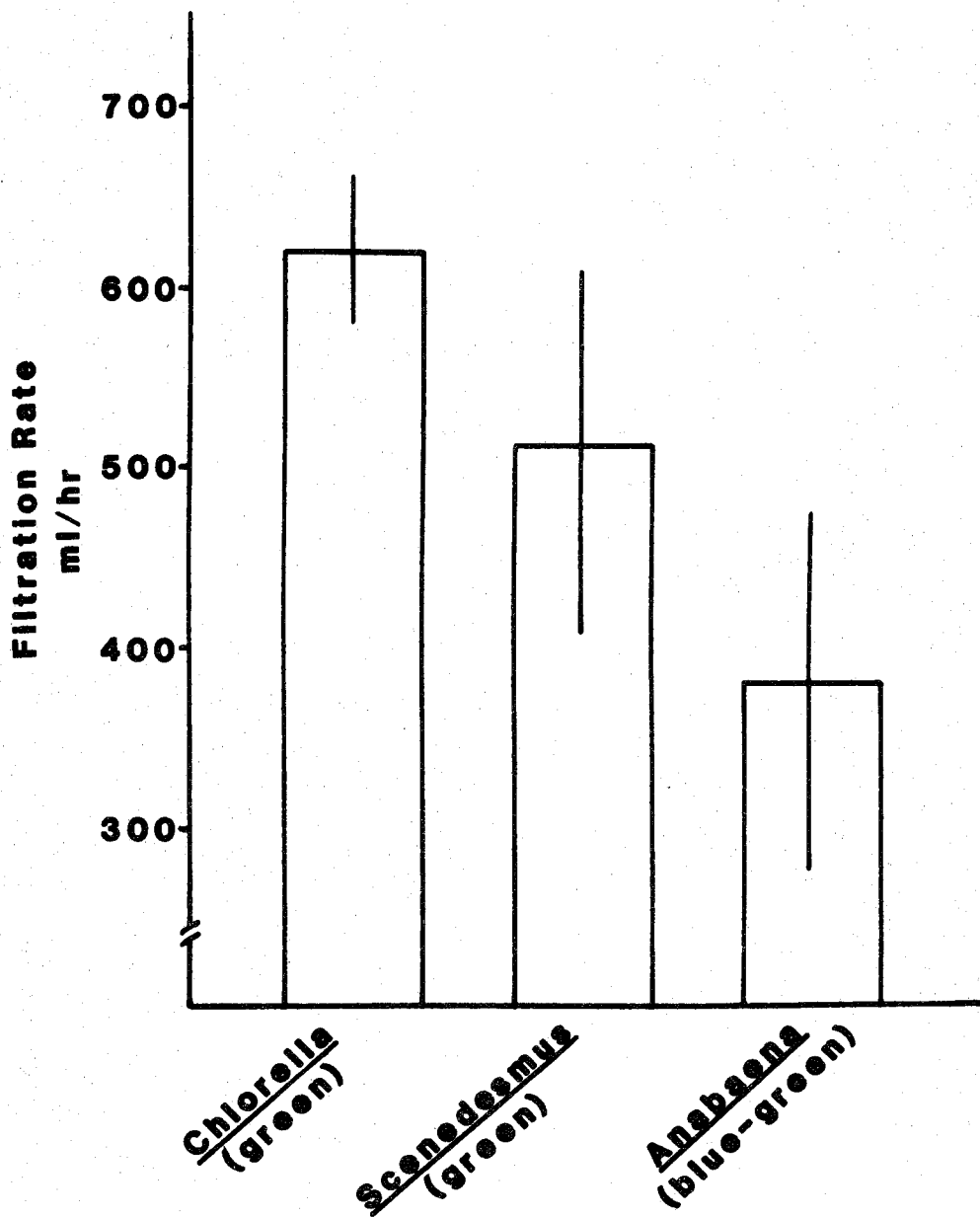


Figure 5. Mean individual filtration rates ($\text{ml}\cdot\text{hr}^{-1} \pm 1 \text{ S.E.}$) for three algal taxa (volume conc. = $1.33 \text{ mm}^3\cdot\text{l}^{-1}$) by *Corbicula* ($n = 6, 9, 9$).

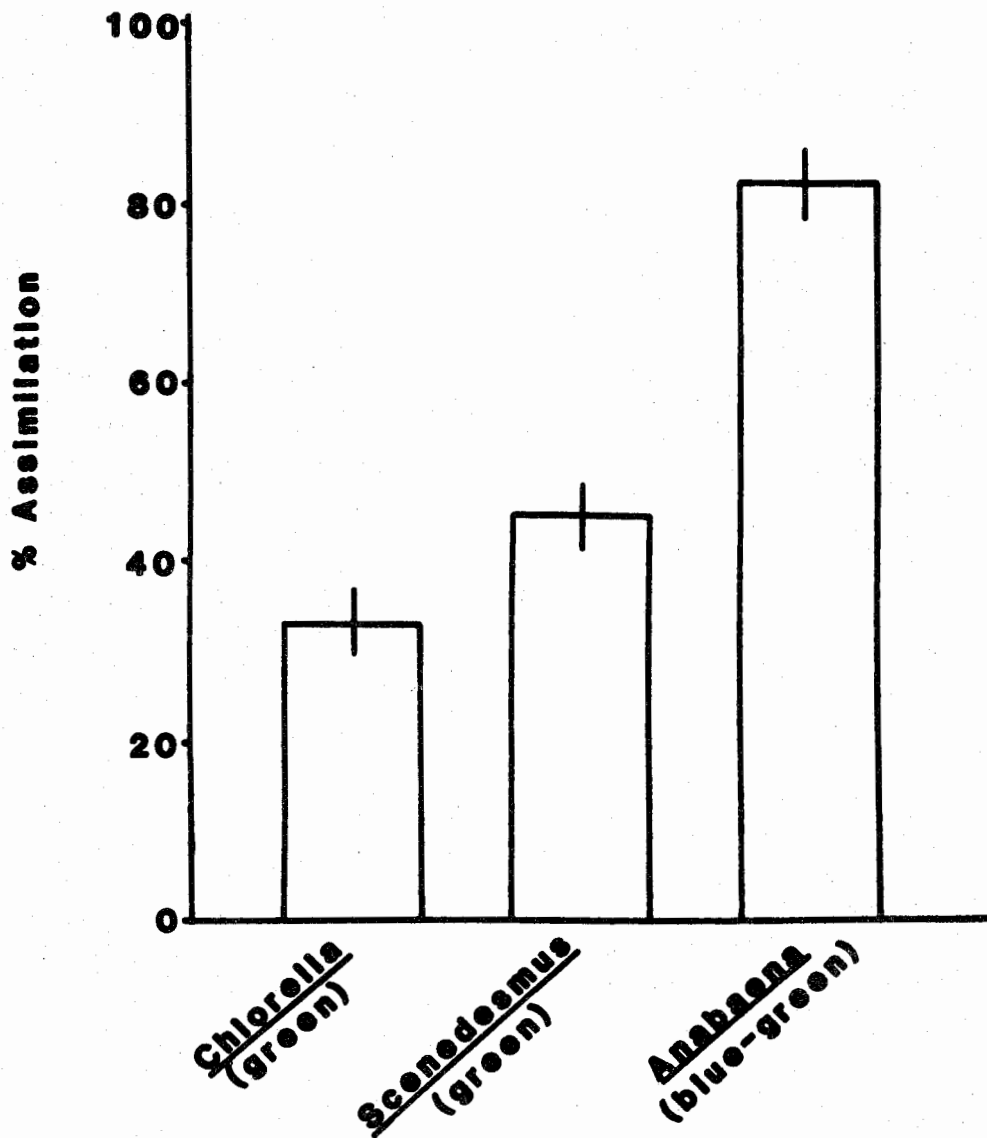


Figure 6. Corbicula mean assimilation efficiencies (% ± 1 S.E.) for three algal taxa (n = 6, 9, 9).

Table 2. Percentage of ingested radioactivity recovered in each type of sample. Respiration was determined from CO₂ impinger traps; dissolved wastes were determined from filtered water samples of respiration chambers. Feces were collected daily for three days; tissues were determined from the entire flesh of each clam.

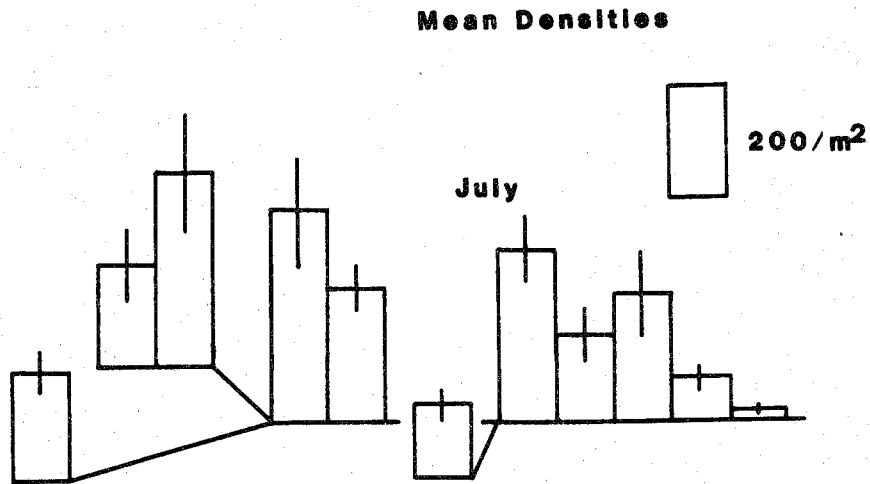
ALGAL SPECIES	% OF INGESTED RADIOACTIVITY						
	Respired	Dissolved Wastes	Feces			Tissues	
			Day 1	Day 2	Day 3		
<u>Chlorella</u>	2.78	35.02	30.06	4.91	3.88	23.36	
	9.75	31.17	36.17	4.82	4.37	13.73	
	0.85	0.32	63.36	3.52	0.52	31.43	
	1.02	0.96	66.20	2.94	1.93	26.94	
	17.99	0.42	49.44	3.64	0.98	26.89	
	8.08	1.29	49.44	4.14	1.04	35.40	
	\bar{x}	6.74	11.53	49.11	3.99	2.12	26.29
	SE	2.71	6.84	5.85	0.32	0.66	3.04
	<u>Scenedesmus</u>	9.77	24.52	8.95	8.47	5.23	43.05
		4.21	29.58	9.14	5.96	9.47	41.65
16.44		42.4	3.08	2.78	2.22	33.06	
26.30		42.19	5.08	4.00	4.02	18.39	
20.32		42.42	7.37	3.52	1.93	24.44	
25.74		40.36	5.38	5.52	2.63	20.36	
29.99		13.99	29.78	3.44	1.48	21.37	
31.67		8.98	31.66	3.26	1.44	22.99	
8.43		15.63	49.52	2.90	1.77	21.75	
\bar{x}		19.21	28.90	16.66	4.43	3.35	27.45
SE	3.34	9.60	5.43	0.63	0.87	3.13	
<u>Anabaena</u>	36.14	6.52	3.90	0.95	0.66	51.66	
	38.67	6.45	1.91	3.52	0.73	48.84	
	22.27	5.48	1.46	2.35	0.69	67.63	
	20.32	14.64	2.68	1.87	1.58	58.92	
	33.42	25.48	3.15	3.00	2.13	32.82	
	33.64	26.96	3.68	2.81	2.03	30.88	
	23.83	7.63	4.41	3.99	2.96	57.19	
	29.9	5.60	0.94	0.49	0.79	62.27	
	19.51	4.99	0.63	0.16	0.71	73.99	
	\bar{x}	28.63	11.53	2.53	2.13	1.36	53.80
SE	2.42	2.94	0.45	0.45	0.28	4.86	

microbial respiration from clam respiration, these values must be considered as maximum rates. In contrast, although the clams were filtering Chlorella at a faster rate, almost half of the radioactivity they ingested was released within the first day after feeding. Although feces and pseudofeces could be distinguished visually, they could not be separated for radioassay because the feces could not be collected with a pipette. The pseudofeces do not pass through the gut to be digested, so that the material looked amorphous and very green, while the feces were brown strands of processed wastes.

Corbicula Distributions

Mean density for strata 7-17 was $205 \cdot m^{-2}$ and for strata in the Chowan proper (7-11,13-14), $200 \cdot m^{-2}$. Strata 1-6 had densities less than $10 \cdot m^{-2}$ while stratum 14 gave the highest mean density, about $400 \cdot m^{-2}$ in July (Fig. 7). Mean biomass was $12.2 \text{ g} \cdot m^{-2}$ for strata in the Chowan proper. Mean length calculated from mean individual dry flesh weight and the length-weight relationship, ranged from 14.1 mm in stratum 13 to 20.7 mm in stratum 10. Since clams smaller than 4 mm were not quantitatively collected, estimates do not include these size classes. Highest densities were found in the uppermost transect of the Chowan and the lowest transect of the Blackwater River (Strata 14 and 15), and decreased sharply below Stratum 9.

(a)



(b)

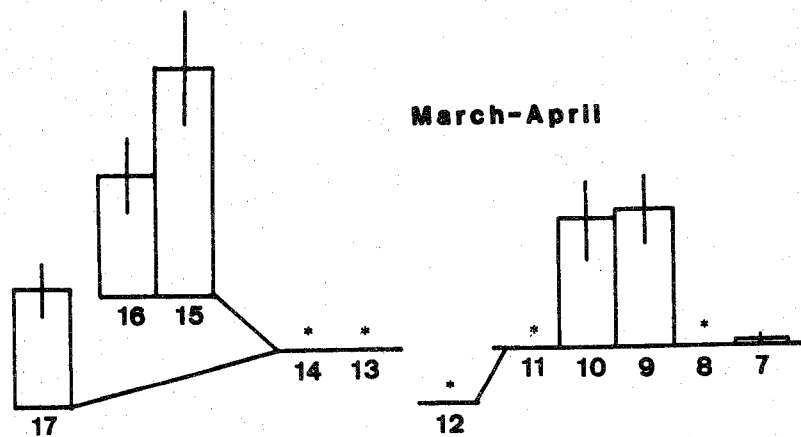


Figure 7. Schematic of Chowan River and tributaries, showing mean densities (no./m² ± 1 S.E.) of *Corbicula* by strata in (a) July (summer) and (b) March-April ("winter"), 1980. Stratum 12, Meherrin River; stratum 17, Nottoway River; strata 15-16, Blackwater River. * = no sample taken.

The lower Meherrin also had relatively low densities. Within strata, densities were extremely patchy but generally higher at depths over 2 m (Fig. 8). Stratum mean biomass ranged from 3.8 to 22.2 g·m⁻² dry flesh weight, following the same pattern as densities (Fig. 9a). Mean densities were similar in the March-April survey (Fig. 7).

To show the correspondence between densities of Corbicula and the hydrological environment, the annual mean discharge at each stratum (U.S.G.S. data) was divided by the cross-sectional area of the channel at the upper transect (mean depth x width) to estimate relative flow speeds (Fig. 10). Corbicula densities declined sharply below a hypothetical mean flow speed of 5 cm·sec⁻¹.

In July, size distributions of the populations tended to fall into 3 modal groups, one each near 8-10 mm, one near 15-20 mm, and one 21-24 mm (Fig. 11a and b). The March-April survey did not show the lowest population mode. Smaller clams were more numerous in the upriver strata than in the middle reaches of the river (compare strata 9 and 15). Pooled data for strata 15-17 show modes at 8, 15, and 22 mm in July (Fig. 12). The shift in modal locations from spring to summer indicates a growth rate of approximately 3-5 mm in length during this period (more in smaller size classes). Appearance of the 8 mm size class in July is presumed to represent growth of individuals which were

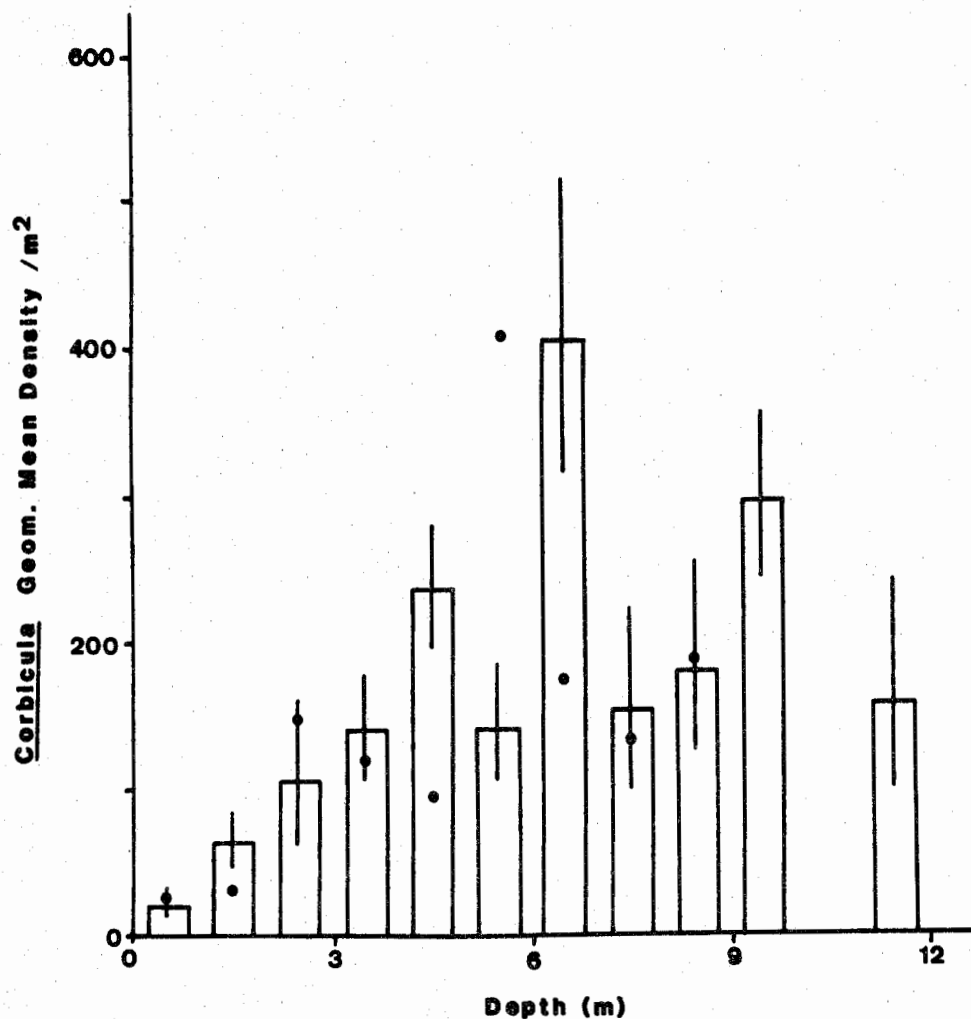


Figure 8. Geometric mean density (no.·m⁻² ± 1 S.E.) of Corbicula versus depth for all samples in the Chowan and tributaries in July (bars) and March-April (dots), 1980.



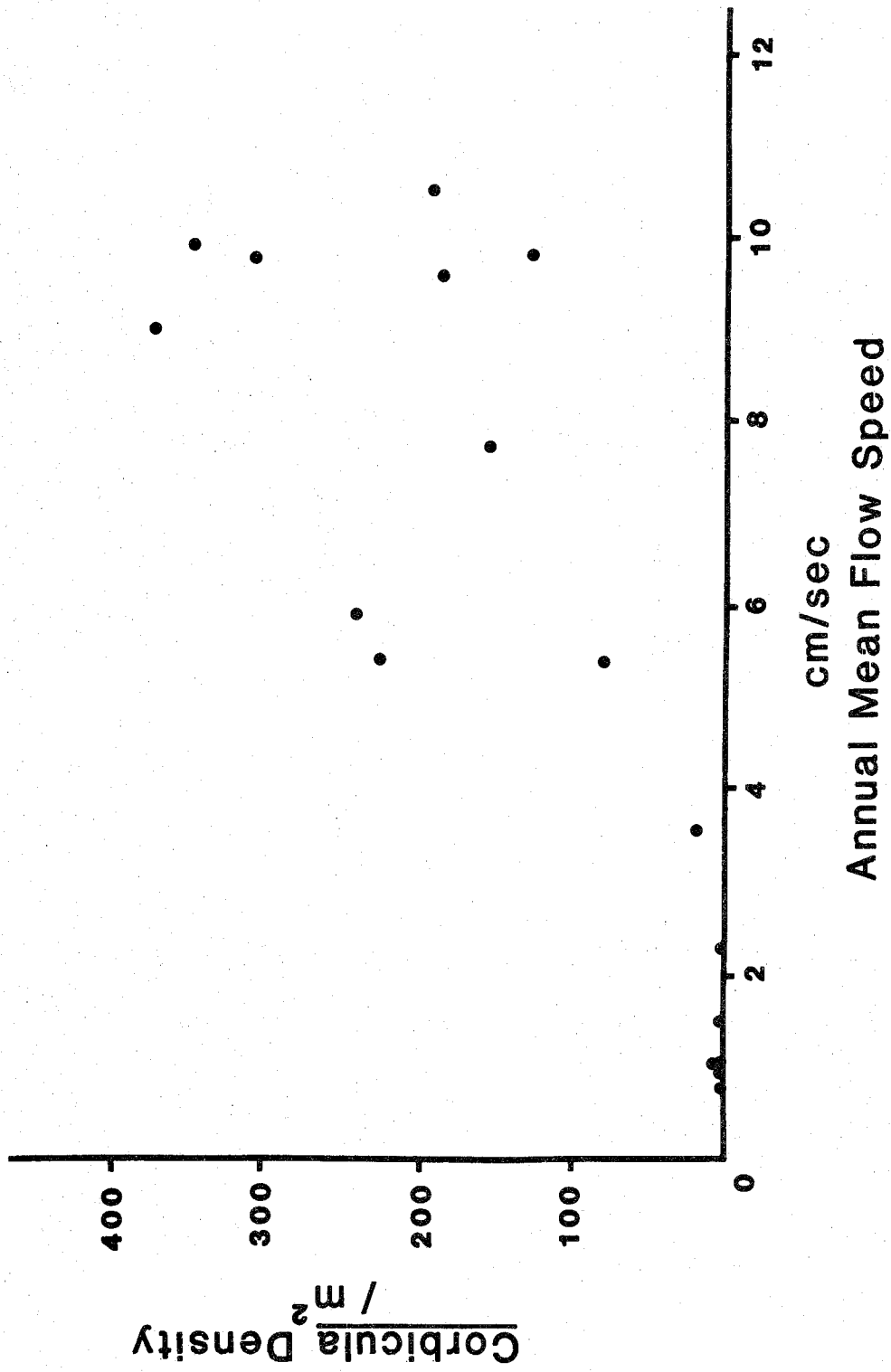


Figure 10. Stratum mean densities (no. \cdot m⁻²) of Corbicula versus annual mean flow speed (mean yearly discharge divided by mean stratum cross-sectional area) in each stratum.

MARCH - APRIL



JULY

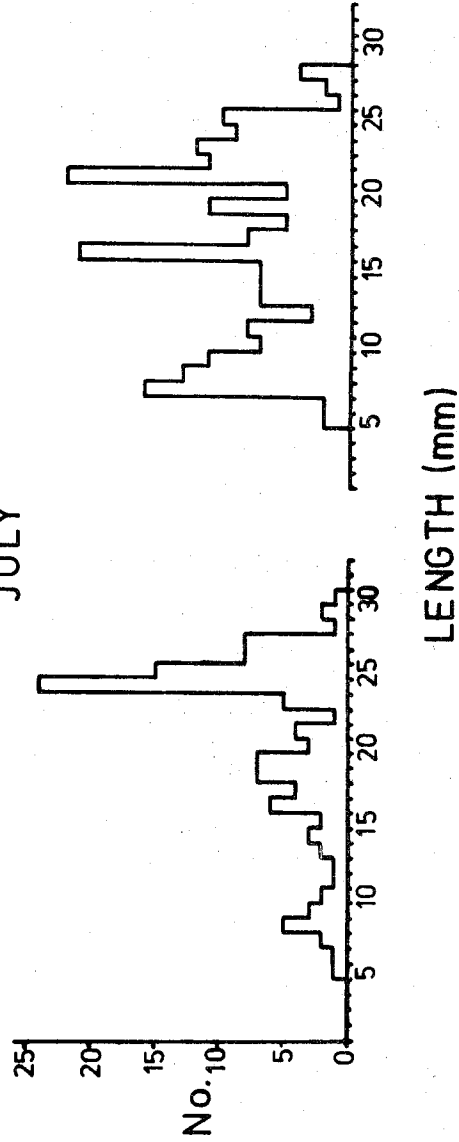


Figure 11a. Shell length frequency distributions for *Corbicula* in March-April and July, 1980 for strata 9 and 15. Each histogram represents 12 grab casts, or about 0.25 m².

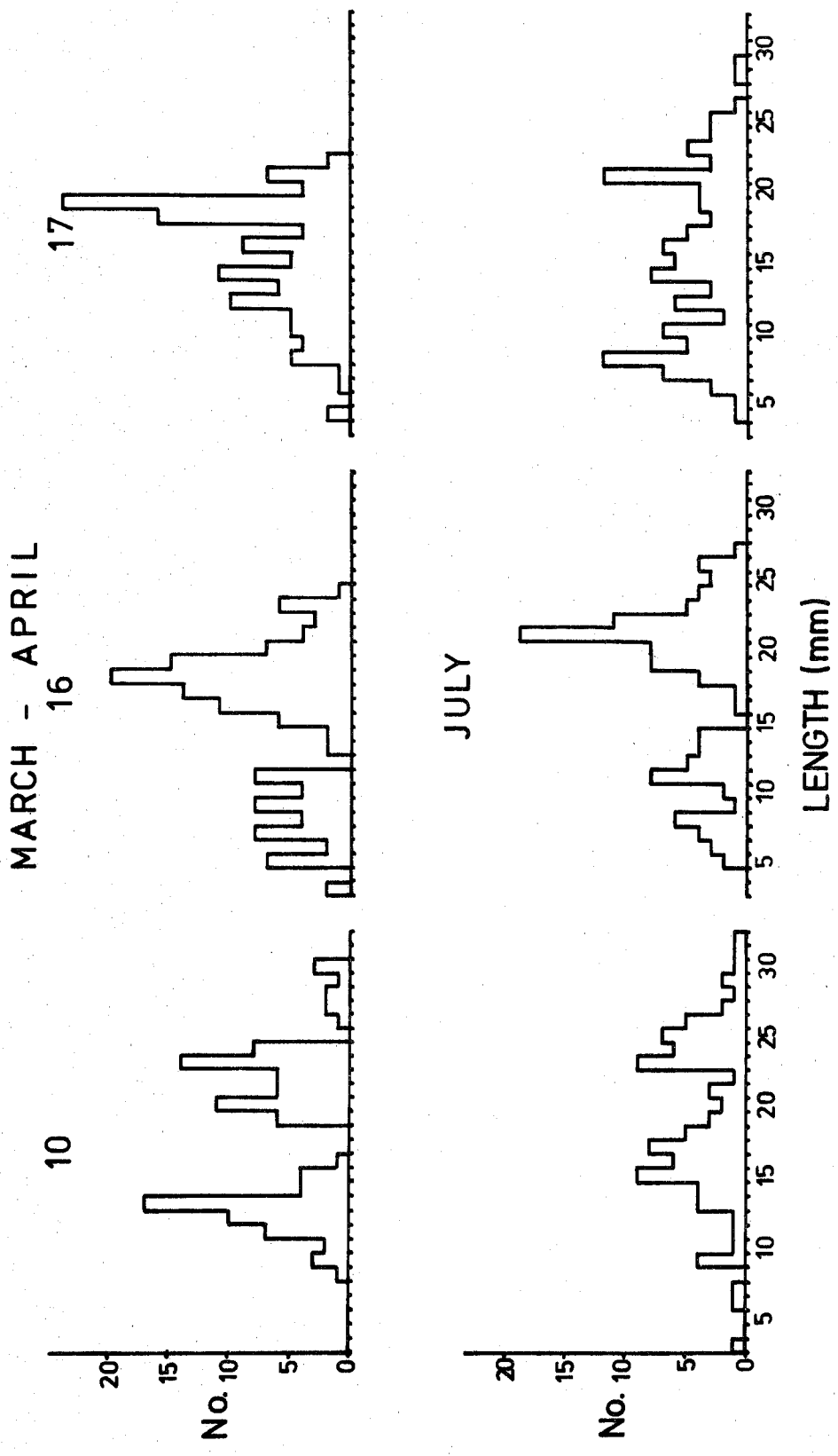


Figure 11b. Shell length frequency distributions for Corbicula in March-April and July, 1980 for strata 10, 16 and 17.

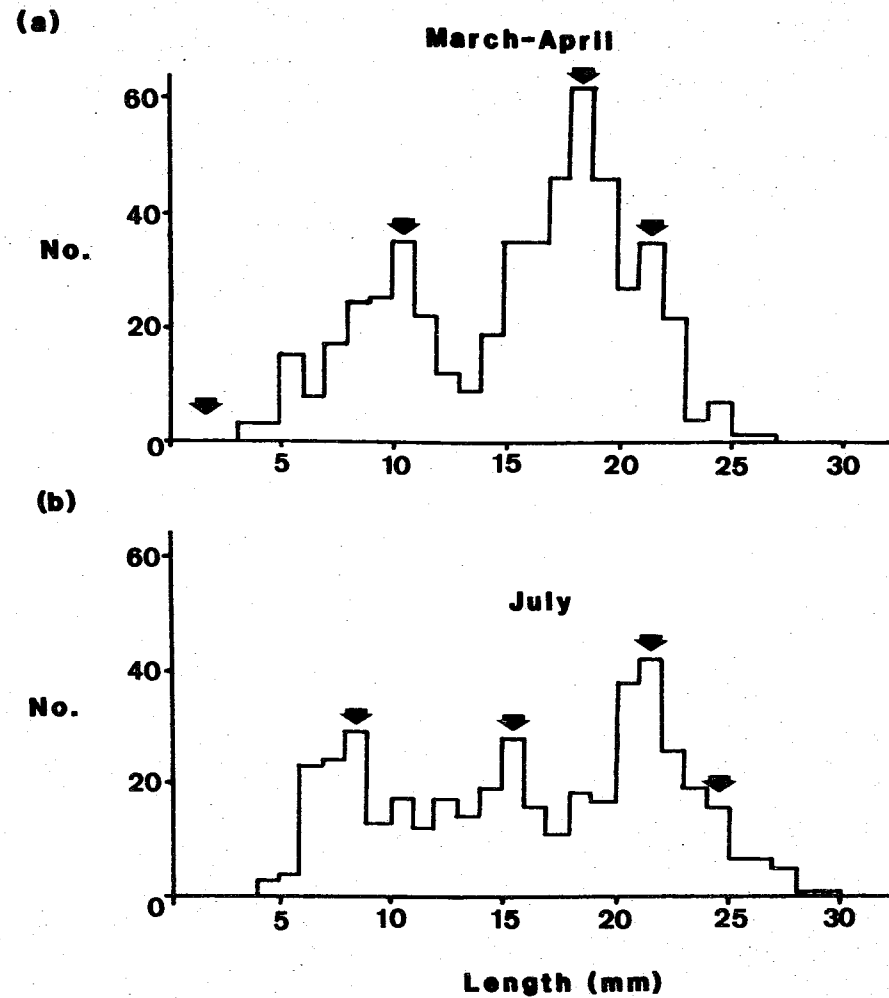


Figure 12. Shell length frequency distributions for *Corbicula* from upriver strata (pooled data from 15, 16 and 17) to show cohort length progression from March-April to July, 1980. Arrows indicate modal length classes for four successive cohorts (see text).

smaller than 4 mm in March-April. The largest Corbicula in survey samples were 32 mm long, but other collections produced specimens as long as 35 mm.

Excretion Rates

Excretion rates of ammonium (NH_4) and orthophosphate (PO_4) averaged over 14 hr were expressed as power functions of dry flesh weight according to the following equation: $V = aW^b$, where V is in $\mu\text{moles}\cdot\text{l}^{-1}\cdot\text{hr}^{-1}$, W is in g of clam dry flesh weight, and a and b are regression constants. An orthogonal contrast (ANOVA) of May and September NH_4 excretion rates was not significant ($F = 3.8$, $p > .05$) so data from these two experiments were pooled and a single regression line was fitted to these data (Table 3; Fig. 13). However, contrasts of the pooled summer and winter regressions showed a highly significant difference, even between means adjusted by analysis of covariance, with dry flesh weight as the covariate ($F = 145.2$, $p < .001$). The slopes of the winter and pooled summer regression lines were not significantly different ($F = 2.01$, $p > .15$) indicating the relationship between excretion rate and dry flesh weight was the same (Fig. 13) but the rates were significantly lower.

Orthophosphate excretion rates between May and September were also not significantly different ($F = 0.46$, $p > .50$) so the data were pooled to give a summer

Table 3. Relationship of ammonia and orthophosphate excretion by Corbicula (V, in $\mu\text{mol}\cdot\text{hr}^{-1}$) to dry flesh weight (W, in g). n = number of animals tested; T = water temperature in $^{\circ}\text{C}$ during tests; r = correlation coefficient.

<u>Date</u>	<u>n</u>	<u>T</u>	<u>Regression Equations and Coefficients</u>			
			<u>NH₃</u>	<u>r</u>	<u>PO₄</u>	<u>r</u>
13-V-82 and 2-IX-82	90	20- 21	$V = 1.491W^{0.477}$	0.833	$V = -0.479W^{0.337}$	0.823
20XII-82	45	6	$V = 0.750W^{0.496}$	0.947	$V = -0.715W^{1.920}$	0.773

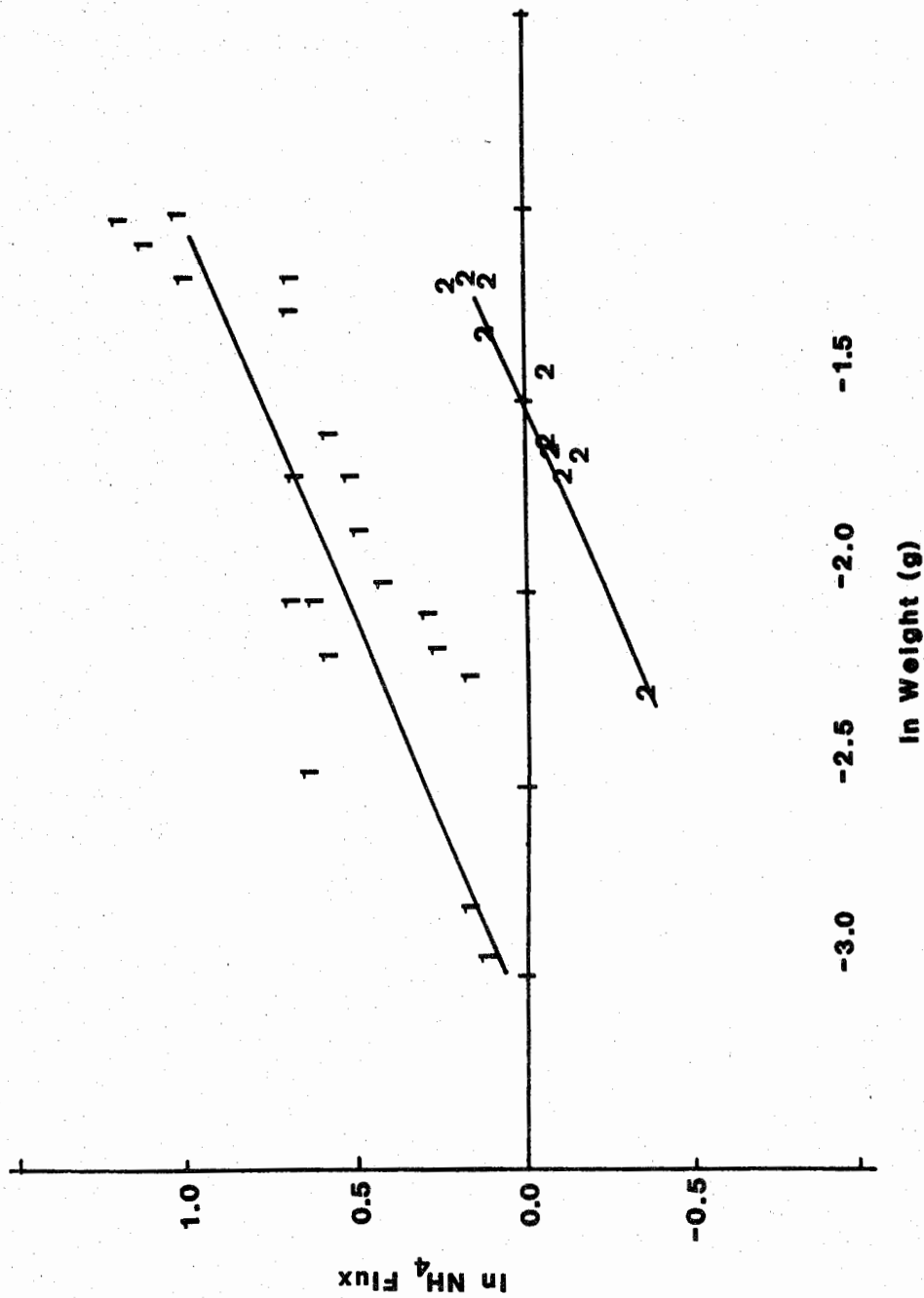


Figure 13. Regressions of dry flesh weight (g) on ammonium excretion rates (moles·l⁻¹·hr⁻¹) for Corbicula freshly collected from the Chowan River in May and September (1) and in December (2), 1982.

regression (Table 3). Summer and winter rates were significantly different ($F = 170.3$, $p < 0.001$), due to the difference in slope ($F = 17.4$, $p < .001$) as well as the generally lower rates (Fig. 14). In addition to rates being generally lower in winter, the size-rate relationship did not hold so that there was little difference between excretion rates of large and small clams.

Summer ammonium fluxes (hourly) due to Corbicula were calculated for the upper river and tributaries (Strata 7-17) using the pooled summer excretion rates and biomass estimates from the July 1980 survey (Fig. 9b). Fluxes followed the same patterns in the river as clam biomass, with the highest rates at strata 9, 11, and 14 in the Chowan, and stratum 15 in the Blackwater River. Calculated on a 24 hr basis, rates ranged from 357-8642 $\mu\text{moles}\cdot\text{m}^{-2}$ (Table 4). Summer fluxes of orthophosphate also showed the same pattern, with rates ranging from 160.8-3923.76 $\mu\text{moles}\cdot\text{m}^{-2}$ (Table 4).

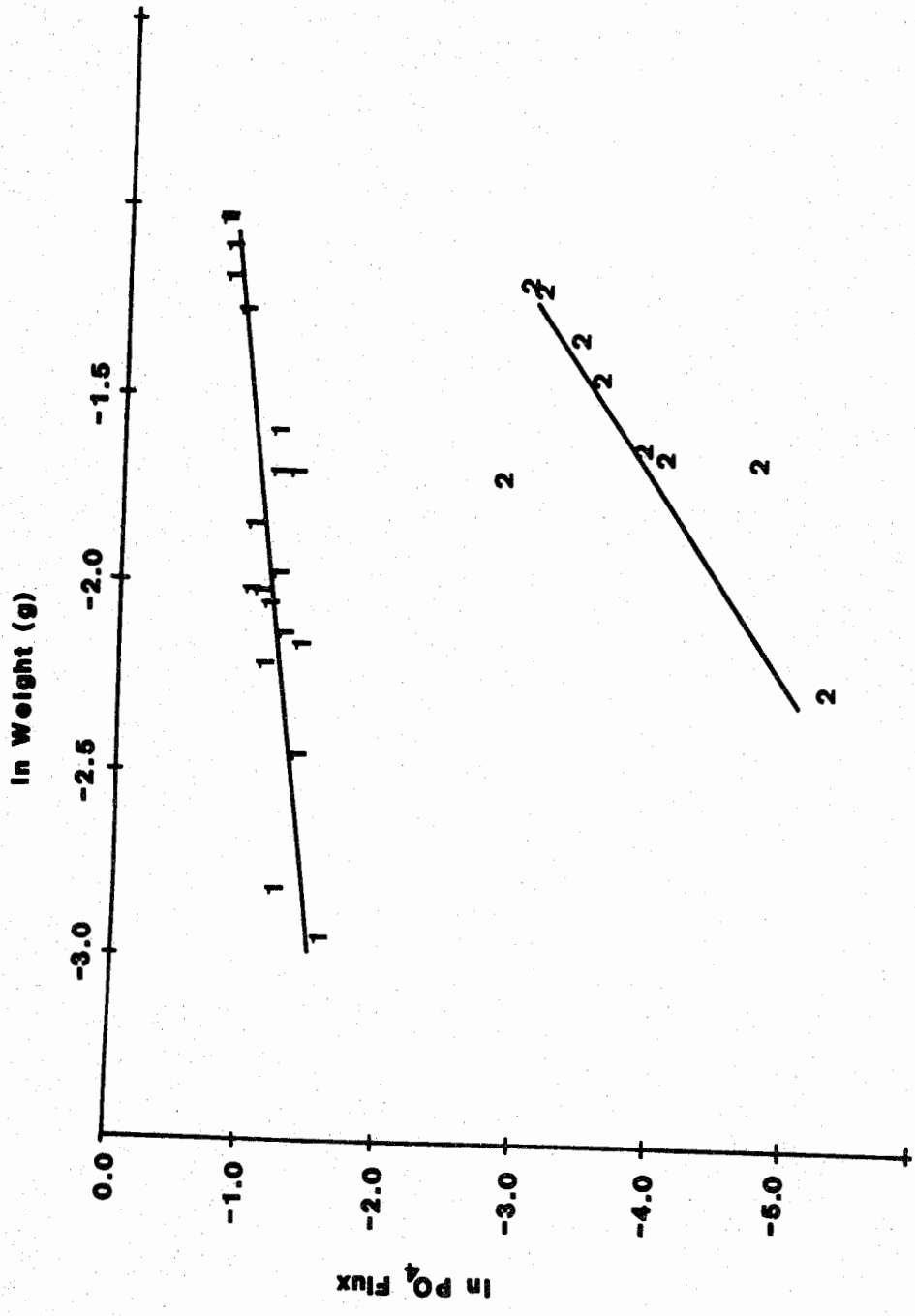


Figure 14. Regressions of dry flesh weight (g) on orthophosphate excretion rates (moles·l⁻¹·hr⁻¹) for *Corbicula* freshly collected from the Chowan River in May and September (1) and in December (2), 1982.

Table 4. Corbicula mean biomass (g dry flesh wt. $\cdot m^{-2} g^{-1}$ July 1980) and summer excretion rates ($\mu mol \cdot m^{-2} \cdot hr^{-1}$) of ammonia and orthophosphate in the upper Chowan River. Biomass is estimated from length frequency distributions and excretion rates are calculated from biomass and weight-specific summer excretion rates (Table 3). Standard errors are based on 12 sampling sites within each stratum.

<u>Stratum</u>	<u>Biomass</u>	<u>NH₃</u>	<u>PO₄</u>
7	0.8 ± 0.4	15 ± 7	7 ± 3
8	3.0 ± 0.9	64 ± 18	29 ± 8
9	20.4 ± 8.2	294 ± 111	134 ± 51
10	14.1 ± 4.1	201 ± 61	92 ± 28
11	22.2 ± 4.5	360 ± 71	163 ± 32
12	6.1 ± 1.7	119 ± 28	54 ± 13
13	7.6 ± 1.4	178 ± 33	79 ± 15
14	17.9 ± 4.6	357 ± 95	161 ± 43
15	19.3 ± 5.3	346 ± 95	156 ± 43
16	13.1 ± 4.2	213 ± 71	97 ± 32
17	10.1 ± 2.7	185 ± 42	84 ± 19

DISCUSSION

Filtration Rates

Most feeding studies of bivalve molluscs have been done under laboratory conditions. The advantages of this are obvious, allowing control and manipulation of specific variables such as temperature, food quantity and quality. There are, however, certain disadvantages which must be taken into consideration when interpreting their results and applying them to natural systems. For example, bivalves can be very sensitive to disturbances and test conditions, resulting in significant deviations in important physiological functions. This is evidenced by the wide fluctuations in filtration rates reported for bivalves. The freshwater mussel Dreissena polymorpha, an introduced species in Europe, has relatively low filtration rate estimates of $< 100 \text{ ml}\cdot\text{hr}^{-1}$ (Stanczykowska et al. 1976; Walz 1978) compared with rates of the saltwater mussel Mytilus edulis of $1400 \text{ ml}\cdot\text{hr}^{-1}$ (Foster-Smith 1975). Previous estimates of filtration rates of Corbicula show a wide range of variability ($20\text{-}150 \text{ ml}\cdot\text{hr}^{-1}$, Prokopovich 1969; a mean of $11 \text{ ml}\cdot\text{hr}^{-1}$, Habel 1970; a mean of $816 \text{ ml}\cdot\text{hr}^{-1}$, Auerbach et al. 1977; $500\text{-}600 \text{ ml}\cdot\text{hr}^{-1}$, Mattice 1979). These fluctuations are probably an artifact of test conditions, since results of our study indicate that even

the type of food used can have an influence on filtration rate. The relationship between filtration rate and food (or seston) concentration that we observed has also been documented in salt water mussels (e.g., Winter 1973; Walz 1978), and gives another possible explanation for the variability in previous filtration rate estimates. Rates of filtration have also been correlated with body size in saltwater mussels (Winter 1978), but we observed no pattern within the relatively small size range of Corbicula tested.

Inducement of pseudofeces production by Anabaena may have been a response to the filamentous nature of the algae. Its presence in the water column in the Chowan may serve to render a large proportion of the material that is filtered by the clams as "unobtainable" since it may clog the gills and be rejected. Work with the saltwater mussel M. edulis indicates that pseudofeces are produced after the gut and/or digestive gland of the animal fills with filtered material (Foster-Smith 1975). Therefore the amount of utilizable food ingested by a non-selective filter-feeder in a natural situation is determined by the total particulate concentration and the proportion of non-utilizable organic and inorganic material present in the seston. Inorganic material such as silt would dilute the amount of food ingested, so that food availability would likely be inversely proportional to particle concentration (Widdows et al. 1979).

Importance of Corbicula Filtration in the Chowan

Although clams for which filtration rates were determined were slightly larger than the mean size of the population in the Chowan (17.4 mm), filtration rate was relatively insensitive to size, and a conservative estimate (250 ml·hr⁻¹·individual; Fig. 3) was adopted for filtration rate. Using the mean density of 200·m⁻², we estimate that Corbicula in the middle reach of the Chowan from Virginia to Holiday Island could filter 50 liters of water per m²·hr. The mean depth of our sampling sites in this reach is 4.7 m, and the volume is about 2 x 10⁸·m³. Multiple-year mean discharge is 132 m³·sec⁻¹ (NCDEM 1982), so hydraulic renewal time is about 16 days. An average number of Corbicula in one m² then, could filter a volume equivalent to the volume of the overlying water column (4.7 m³) every four days, removing particulate material and depositing mucus-bound feces and pseudofeces. Prokopovich (1969) reports massive quantities of apparently biodeposited sediments in a California canal with a large Corbicula population, and the same may occur to some extent in the Chowan. Such biodeposition would have an influence on materials transport and biogeochemical cycles in the middle river. Suspended particles adsorb most of the inorganic phosphorus, pesticides and trace metals which are transported from the catchment, so flushing of pollutants

and nutrients out of the river may be delayed or prevented by this deposition. But until in situ experiments are done, interpretations of clam filtering impact in the river must be made with caution.

Assimilation Efficiencies

Assimilation efficiency allows a comparison of food quality of the material ingested, although it is not a direct measure of the nutritional value of the food source. Walz (1978) determined that the freshwater mussel Dreissena assimilated the diatom Nitzschia with an efficiency of 41 %, while in a Polish lake Stanczykowska et al. (1975) found nearly the same Dreissena mean assimilation efficiency in situ (40.5 %).

Zooplankton assimilation efficiencies for different algal species has received more study by freshwater biologists. Arnold (1971) determined ingestion, assimilation, and survivorship of the cladoceran Daphnia pulex fed a variety of blue-green and green algal species. He found that the filtration rate of Anabaena flos-aquae by Daphnia was relatively low, but assimilation of the algae ingested was essentially 100 %. Chlorella vulgaris was filtered at a higher rate and was also assimilated at nearly 100 %, but the green alga that was filtered the fastest, Ankistrodesmus falcatus, was assimilated at a lower rate, probably because the food was passing through

the gut at a rapid rate. This may have happened in our feeding experiments, where Chlorella was filtered rapidly but assimilation was low, and much viable material was passed through the clams. In longer-term assessments of reproduction and survival of D. pulex however, the blue-greens proved to be less suitable, and these results were even more pronounced at higher food levels (Arnold 1971). This suggests that there was some inhibition of feeding by the blue-greens rather than poor nutritional value of the algae; similar conclusions have been reached in other studies with Daphnia (Lampert 1977; Porter and Orcutt 1980). In the upper Chowan River where Corbicula is most abundant, blue-green algae may dominate in the plankton during summer months, but do not reach high population densities or form surface scums as in the lower river. The presence of blue-greens in clam diets in the upper river may do no harm other than clog their gills and cause a certain amount of food to be rejected, but growth and reproduction studies similar to those that have been done with zooplankton are needed on Corbicula to determine long-term effects of blue-greens in their diets.

Corbicula Distributions

The strongest pattern in density was the virtual disappearance of Corbicula from samples near and downstream of Holiday Island (Stratum 6). The few individuals

collected in the lower section were in sandy sediments near shore, where wave action keeps the water moving near the bottom. Lacking detailed information on near-bottom currents, we approximated flow by dividing the annual mean discharge by cross-sectional area of the channel and the number of seconds per year (Fig. 10). Within transects of the upper reaches, fine sediments are most heavily deposited near the banks while mid-channel bottoms are usually sand or gravel (Kuenzler et al. 1982). Corbicula was least dense near the banks upstream, again suggesting a minimum flow threshold for Corbicula persistence near that at which silts and clays are deposited. In its native Asia most Corbicula species are considered to be rheophilic--usually occurring only where there is a certain minimum water movement (Britton and Morton 1979). Flow rate has been shown to affect filtration rate and, therefore, feeding activities in several species of saltwater mussels (Walne 1972).

Within the upper section, highest mean densities were observed immediately downstream of the Union Camp pulp and paper mill discharge into the Blackwater River and below the confluence of the Meherrin River near Winton (Fig. 7). These strata had higher mean flow velocities than most others, but effluent from the pulp mill may also have had a stimulatory effect by increasing the concentration of

suspended organic particles during winter discharge periods.

Corbicula densities are usually patchy, and none of the available data from the Atlantic coastal rivers are based on sampling as intense as our survey. Diaz (1974) reports densities up to $1452 \cdot m^{-2}$ at an organically enriched site of the James River, but mean densities from the regions where Corbicula was found was $371 \cdot m^{-2}$. Dresler and Cory (1980) record a density of $665 \cdot m^{-2}$ in the Potomac near Washington, D.C., but a second estimate only months later was just $53 \cdot m^{-2}$, probably due to small sample size and patchy distribution of the clams. Sickel (1973) notes a mean of about $200 \cdot m^{-2}$ after an initial large set in excess of $10000 \cdot m^{-2}$ had died back in the Altamaha River in Georgia. It appears that stable populations in the Atlantic drainage rarely exceed $400 \cdot m^{-2}$ in the absence of heavy organic loading.

Density controls other than food availability have not been detected in most studies. Predation by waterfowl, raccoons and flatworms is known or suspected (Diaz 1974; Perry and Uhler 1981). Many bottom feeding fish such as hogchokers and catfish take younger clams (Hinshaw pers. comm.), but their effect on clam populations has not been assessed.

Size frequency distributions of Corbicula in the Chowan are similar to those in the Altamaha River (Sickel 1972) and can be similarly interpreted to represent two main reproductive periods each year in spring and fall. Small clams present but not well sampled in March-April seemed to grow to about 8 mm in length by July (Fig. 12). If the next larger cohort, which grew from about 11 mm to 16 mm over the same time period, resulted from reproduction in spring 1979, then the annual growth of Corbicula would be about 14-15 mm the first year, 10 mm (to 25 mm length) the second, and for the few individuals living for a third year, another 5 mm (to 30 mm length). Mortality estimates from comparing the two larger modal classes for the uppermost strata between spring and summer (cf. Fig. 12) were about 22 % for one-year-old and 43 % for 1 1/2 years and older over the 3 1/2 month period. Since few predators can handle older, larger Corbicula, much of the higher mortality must be from disease or senescence.

Despite higher mortality of older clams, the largest modal class was still the most abundant. This suggests that the older class was the first to become well-established in the Chowan probably in 1978. Sickel (1972) describes the clam's invasion of the Altamaha with a similar pattern. According to McMahon (1982) most Atlantic coast rivers were invaded by 1972, but verbal reports from

N.C. DNRC biologists who sampled benthos in the Chowan in 1974 indicate that the clam was not yet present.

Ammonium Excretion

In the saltwater mussel Mytilus edulis, ammonium forms the major excretory end product of protein and amino acid catabolism (Bayne et al. 1976), so that the rate of NH_4 excretion may be regarded as reflecting the rate of protein catabolism. Rates of excretion increase when the animals are starved, and this change is more marked for small individuals (Bayne and Scullard 1977). During the period of gametogenic quiescence in autumn and early winter, ammonium excretion is at a minimum, increasing in spring and summer when the animal maintains mature gametes in the mantle. This most likely reflects a marked seasonal shift from reliance on carbohydrate as the main energy reserve in the autumn to a greater reliance on protein reserves in spring (Gabbott and Bayne 1973). At higher temperatures (25°C) near the upper limit of environmental and physiological temperature range for M. edulis, there is a marked increase in the rates of metabolism and ammonium excretion, which indicates a greater degree of protein catabolism in order to meet the increased metabolic energy demand (Widdows 1978).

The variability that we found in Corbicula NH_4 excretion rates between summer and winter was probably a

function both of the seasonal gametogenic cycle and of the metabolic effects of seasonal changes in ration and temperature. Particulate nitrogen levels in the river remain relatively high in winter, although most is detrital (Stanley and Hobbie 1981), so food levels probably do not decrease enough to induce winter starvation. There is also evidence from lentic environments that particulate humic materials, which complex with protein and act as a food buffer system, decreasing the utilization of food when its production is high but conserving it for future use when food supply might otherwise be inadequate (Blazka 1971). Since particulate humic materials are abundant in the Chowan in winter, the potential for complexation may affect Corbicula food availability as well.

The highest excretion rates occur from late spring to early fall, when allochthonous loading of NH_4 to the river is at a minimum, and phytoplankton uptake rates are highest. Uptake rates were determined by Kuenzler in 1980, which was a bloom year in the river, and in 1981. Summer (May-September) mean gross NH_4 uptake rates near Winton were $1095 \mu\text{moles}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$ in 1980 and $779 \mu\text{moles}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$ in 1981 (Kuenzler et al. 1982). Corbicula mean NH_4 excretion rates estimated near Winton ($360 \mu\text{moles}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$; Table 4) could have supplied 33 % of 1980 and 46 % of 1981

summer phytoplankton uptake rates in that part of the river.

Orthophosphate Excretion

Little is known of phosphate excretion in aquatic invertebrates although recent studies indicate that zooplankton may excrete enough PO_4 (and NH_4) to support observed levels of primary productivity in nutrient-poor waters (Jawed 1973). The most thorough investigation of phosphorus flow through a saltwater mussel population (Geukensia) was undertaken by Kuenzler (1961). He found that 87 % of the particulate P removed (filtered) by the mussels was deposited as pseudofeces, and that $260 \mu\text{g PO}_4 \cdot \text{m}^{-2} \cdot \text{da}^{-1}$ was excreted by the population.

We were interested more simply in determining the relative magnitude of PO_4 excretion in the Chowan. As with NH_4 , rates were lower in winter, with reductions in rates probably due to changes in food available and temperature. It is unclear why the fundamental relationship between rates and flesh dry weight (slope of the regression) changed in winter. Kuenzler and coworkers (1982) found little seasonal variability in gross phosphate uptake rates near Winton, with rates averaging about $500 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$. Corbicula mean excretion rates estimated near Winton ($163 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$; Table 4) could have supplied 31 % of 1980-1981 summer phytoplankton uptake of phosphate in that part

of the river. We were unable to analyze fecal and pseudofecal samples for N and P, but it is quite likely that significant amounts of both nutrients are released in those forms. This material is deposited in sediments in the river and is then available for microbial decomposition and eventual re-release into the water column as well.

Importance of Corbicula Excretion in the Chowan

Although assessments have not yet been made of the role of other benthic organisms in nutrient regeneration in the Chowan, Corbicula excretion almost certainly is the single largest invertebrate source of NH_4 and PO_4 . The highest excretion rates of both nutrients occurred in summer, when allochthonous loading to the river is at a minimum and phytoplankton nutrient uptake rates are highest (Stanley and Hobbie 1981). Albert (1980) determined in situ nutrient fluxes in Chowan sediments in June 1980, and we have used his data from stations north of Holiday Island (which compare with our Strata 8-9) to compare with Corbicula excretion rates. Sediments in this part of the river are primarily sand (60 %) and clay (22 %), with higher percentages of C (7.77), N (0.42) and P (0.11) than in the lower river. Mean ammonia flux from sediments to the overlying water was $1220 \mu\text{moles}\cdot\text{m}^{-2}\cdot\text{da}^{-1}$ (S.E. = 201.6), while sediment phosphate release occurred at lower rates (mean = $95 \mu\text{moles}\cdot\text{m}^{-2}\cdot\text{da}^{-1}$, S.E. = 17.6). Several of the

sediment chambers used to measure in situ rates contained a few Corbicula, and excretion probably augmented the sediment fluxes measured by Albert (1980) in the upper river. In addition, exposure to increasing PO_4 concentrations in the overlying water (for example, by clam excretion) shifts adsorption equilibria in oxidized sediments to favor increased adsorption (Kuenzler et al. 1982). Mean daily excretion rates of NH_4 were about 4 times sediment flux rates, with daily phosphate excretion rates of about 24 times the sediment release rates. Combining this with the relatively high potential contribution of Corbicula excretion to summer phytoplankton NH_4 uptake rates (33 % in 1980; 46 % in 1981), it is clear that the clam population in the river can make a significant contribution to nutrient recycling in the river. Any future attempts to model nutrient regeneration must take Corbicula abundance into consideration.

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Appendix 1. Mean shell length (in cm) and total dry flesh weight (n=5 clams) used in excretion experiments. Corbicula were freshly collected from the Chowan River in May, Sept., and Dec. 1982.

	\bar{x} SL (cm)	Dry Flesh Wt. (mg)
May	2.5	295.0
	2.6	320.0
	2.7	342.5
	1.5	57.5
	1.7	105.0
	1.8	127.5
	1.9	152.5
	2.4	270.0
Sept.	2.6	196.7
	2.5	175.3
	2.5	175.4
	2.4	133.5
	2.3	123.6
	2.2	112.6
	2.0	110.8
	1.9	82.2
	1.5	50.0
Dec.	2.5	229.8
	2.6	289.4
	2.6	291.3
	2.0	186.9
	2.1	190.7
	2.3	255.4
	1.9	174.6
	2.0	185.4
	1.3-1.7	100.8

Appendix 2. Physical-chemical data from the Chowan River near Winton, N. C. at times when clams were collected for excretion measurements in 1982. Data collected by N. C. Dept. Environmental Management.

Date	Depth (m)	T (°C)	DO (ppm)	pH	Secchi (m)	mg·l ⁻¹					Chla (µg·l ⁻¹)
						TKN	NH ₃	Total P	Ortho P		
10 May	0.3	19.4	5.8	6.3	1.08	.80	.10	.07	< .05		
	6.9	19.3	5.8								
30 Aug	0.3	24.5	4.2	5.8	0.97	.70	.05	.08	.02	2.07	
	6.9	24.1	4.4								
20 Dec	0.3	5.1	10.5	6.3	0.75	.40	.08	.11	.03	1.00	
	7.3	5.1	10.6	6.2							

Appendix 3. ASM-J Medium Preparation (from Paerl 1983) a modification and combination of ASM-1 (Gorham et al. 1964) and Jansen (J) (Corbett and Parker 1976).

Stock solutions for solution A

<u>Compound</u>	<u>g/l</u>
NaNO ₃	170.00
Na ₂ HPO ₄ (7H ₂ O)	26.79
K ₂ HPO ₄	17.40
Na ₂ SiO ₃ (9H ₂ O)	56.80

Stock solutions for solution B

<u>Compound</u>	<u>g/l</u>
MgSO ₄ (7H ₂ O)	49.27
MgCl ₂ (6H ₂ O)	40.57
CaCl ₂ (6H ₂ O)	43.78
Na ₂ EDTA (2H ₂ O) / FeCl ₃ (6H ₂ O)	7.35/1.08

G9 trace element solution (modified)

<u>Compound</u>	<u>g/l</u>
H ₃ BO ₃	3.25
MnSO ₄ (H ₂ O)	1.80
ZnSO ₄ (H ₂ O)	0.30
(NH ₄) ₆ Mo ₇ O ₂₄ (4H ₂ O)	0.08
CuSO ₄ (5H ₂ O)	0.05
CoCl ₂ (6H ₂ O)	0.12
AlCl ₃ (6H ₂ O)	0.47
NiSO ₄	0.10
KI	0.09

Solution A: To a final volume of 500 mls, add 25 mg of Tricene buffer and one ml of each of the stock solutions. Adjust the pH of the solution to 8.2.

Solution B: To a final volume of 500 mls, add one ml of each of the stock solutions and one ml of the G9 trace element solution.

Autoclave the two solutions separately, then combine.