

STUDIES OF SIZE SELECTIVE FEEDING BY ZOOPLANKTON  
DESIGNED FOR IMPLEMENTATION OF PROCESS MODELLING

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## ABSTRACT

Selective grazing by zooplankton upon phytoplankton may influence the rate of eutrophication of aquatic ecosystems. Experimentally three species of zooplankton were fed netplankton, nanoplankton and bacteria. The total phytoplankton (NETP. + NANNOP.) represented a natural assemblage from Lake George. Their filtering rates were measured on one tagged food resource in the presence of the other two. Experiments were limited to 10 min to eliminate the problem of excretion of radioactive matter. On phytoplankton foods, both Diaphanosoma and Diaptomus were shown to select small phytoplankters (NANNOP.), while Daphnia showed no preference. Both Daphnia and Diaphanosoma preferred bacteria over algae. These data will be valuable in calibration of zooplankton biomass and resource allocation models. (Key words: zooplankton, feeding, eutrophication, modeling).

## I. INTRODUCTION

An understanding of zooplankton grazing is essential to both the interpretation of secondary processes and the modelling of aquatic ecosystems. Comparing the filtering abilities of the zooplankton on algal and detrital resources of different sizes may provide insight into the competitive abilities of these herbivores as well as help us predict the effects that artificial perturbations may have on both individual species and aquatic ecosystems undergoing eutrophication.

The experimental program consisted of measuring the filtering rates of the dominant zooplankters on various resources found in Lake George. These resources were categorized for manipulation as the following:

- 1) Net phytoplankton ( $> 22\mu$  in one dimension),
- 2) Nannophytoplankton ( $< 22\mu$  in one dimension),
- 3) Free floating bacteria,
- 4) Total phytoplankton (NETP. & NANNOP.),
- 5) Artificial detritus, and
- 6) Concentrations of 2X net phytoplankton.

In essence, we set out to measure the filtering rate of the zooplankton on each of the first 3 resources in the presence of the other 2, while measuring the filtering rate of the zooplankton when fed either item 4, 5 or 6 (above). The main purpose was to determine whether or not selective feeding can occur on natural assemblages of resources.

## II. LITERATURE REVIEW

Considerable evidence exists suggesting that many zooplankters are size-selective grazers. In laboratory studies, the rotifer Keratella has been shown to prefer small chrysophytes, especially Chrysochromulina (1-25 $\mu$ ),

upon which it exhibits the best growth (Edmondson, 1965). From feeding experiments using sand grains to stimulate algae, it has been suggested that Keratella has a preference for even smaller 0-2 $\mu$  particles (Gliwicz, 1969).

Among the copepods, Eudiaptomus also selects small chrysomonads (Nauwerck, 1963). Most recently Wilson (1973) has shown that the marine calanoid Acartia prefers particles in the range 15-59 $\mu$ , again evidence of size-selective feeding.

The cladocerans also exhibit size-selective grazing. Bosmina has a preferred range for particles of 0-15 $\mu$ , while Chydorus selects smaller 0-4 $\mu$  particles (Gliwicz). Thus Porter (1973) has concluded that the impact of grazing on the phytoplankton community at any one time is determined by the proportion of suppressed (selected), increased (avoided) and unaffected algal food species present. This is an important concept with regard to the problem of eutrophication and noxious algal blooms.

### III. METHODS

The general experimental procedure can be found in EDFB-IBP Memo Report 72-69 (McNaught, Bogdan and O'Malley, 1972). However, as this research progressed new techniques were developed and these are now described. The techniques developed to produce the 6 experimental regimes for the resource selection experiment were both lengthy and complex, and are best detailed by a flow diagram (Fig. 1).

The above figure accounts for 5 of the 6 resource regimes, as detritus was obtained by autoclaving the TOTAL PHYTOPLANKTON (after the algal experiment) for 1 to 2 hours at 110°C and allowing it to set overnight. The next day the detrital feeding experiment was performed. The aim of this elaborate

procedure was to get 4 or 5 similar experimental regimes differing only in what fraction was labelled with  $C^{14}$ , by using organic carbon as a measure of similarity we see that this occurred in the later experiments (Table 1). It was assumed that the BACTERIAL regime was identical to the TOTALP. regime.

#### IV. RESULTS

Before proceeding to this year's research, further analysis of a data set found in IBP-MEMO REPORT 72-69 by McNaught, Bogdan and O'Malley (1972) has provided some interesting and useful data. The data set in question deals with the relationship between the filtering rate of Daphnia and body size, reported in Table 2 in the above report. Burns and Rigler (1967) have shown that for Daphnia filtering yeast cells, the filtering rate increases with the cube of the body length, while others have suggested the square of the body length. The general equation is:

$$\text{Filtering rate} = \text{constant (Body Length)}^X$$

$$\text{Filtering rate} = c (L)^X$$

Daphnia filtering rates and sizes were plugged into this equation and Fig. 2 shows the power function generated. As one can see, there is strong agreement with Burns and Rigler's cube root equation, the exponents being 2.79 (data of 9-21-72) and 3.02 (data of 9-29-72). In both cases the correlation was statistically significant at the .01% level, thus we can confidently predict filtering ability on total phytoplankton of all size classes of Daphnia by knowing the filtering rate of one size class.

Proceeding to this year's results, we decided that before doing the lengthy and complex resource allocation experiment, we must show that the experimental technique was reliable. This required a major effort and

involved 3 main questions:

(1) Was the feeding period of 10 minutes short enough to preclude any excretion of radioactive food, a phenomenon that would bias the measurement of filtering rates. In order to test this hypothesis, we conducted an experiment on which 4 successive groups of animals collected from the lake were fed the same phytoplankton assemblage for periods of 5 min, 10 min (I), 10 min (II), and 15 min. If radioactive food was egested by the animals during the longer feeding periods, there would be a lower filtering rate for these animals than for those feeding the shorter times. As you can see from Table 2, there was no obvious decrease at all. Thus, 10 min was not too long of a feeding period.

(2) What was the degree of replication within an experiment, or how large was the experimental error? This problem was approached two ways: (a) If 2 groups of animals collected from the lake are exposed to the same phytoplankton assemblage, will they show the same filtering rate? (b) If 2 groups of animals collected from the lake are exposed to different aliquots of one larger phytoplankton sample, will they show the same filtering rate? In other words, the former approach discloses the error variance due to differences among animals, while the latter discloses the error variance due to differences in animals as well as differences due to variability in what we assume to be identical phytoplankton assemblages. The error variance in both these areas must be low. For if one cannot get similar filtering rates on what we usually assume to be identical conditions, the technique must be faulty and we can go no further. This is a very crucial point because when we did the resource selection experiment, we were physically unable to do replicates, so it was absolutely necessary to have a reliable technique. Looking at both Table 3 and Table 4, we see that in both experimental types the error term was initially high (> 10% of experimental values), but as we became experienced it was reduced to

successively lower levels, so by the time of the resource selection experiments, it was usually less than 10% of the experimental values. From this, we concluded that replication was not absolutely necessary and we had a reliable technique.

(3) Did the number of animals within the feeding chamber influence the magnitude of the filtering rate? This is an important factor to examine if we wanted to compare data from experiment to experiment because even though we tried to keep the number of animals constant by collecting zooplankton from 56 l of lake water, one finds seasonal variation as well as daily variation in the number of animals in such a volume. If a density factor is in effect, it may obscure our interpretation of the data. Our experimental test of this question was simple. Two groups of animals, one at 12X normal concentration and one at 25X normal concentration were exposed to the same phytoplankton assemblage and their filtering rates compared. Analysis of the data (Table 5) shows that although there are differences it is unlikely that the differences are significant and are probably no greater than those differences found in the replication experiments. For if we assume that density has no effect and treat the 2 experiments as replicates, we see from Table 5 that the S.E. x 100/EXP. VALUE ratios of the means are similar to those of the replication experiments. In other words, we have introduced no additional source of error by clumping data on 12X and 25X normal concentrations of herbivores.

The cumulation of this summer's work was the resource selection experiment. The experiment was performed 4 times. The general trends are discussed below, but first a comment on the interpretation of the experiment. We have produced 4 similar food regimes, differing only in what resource was radioactive. A simple summary of treatments will illustrate the 4 experimental regimes (a box surrounding a component indicates radioactivity).

- 1)  $\boxed{\text{NETPLANKTON + NANNOP.}} + \text{BACTERIA} : \text{"HOT" TOTALP. (NETP. + NANNOP.)}$
- 2)  $\boxed{\text{NETP.}} + \text{NANNOP.} + \text{BACT.} : \text{"HOT" NETP.}$
- 3)  $\text{NETP.} + \boxed{\text{NANNOP.}} + \text{BACT.} : \text{"HOT" NANNOP.}$
- 4)  $\text{NETP.} + \text{NANNOP.} + \boxed{\text{BACT.}} : \text{"HOT" BACT.}$

Thus, the animals in the experiment faced similar food regimes in all 4 chambers and probably showed similar ingestion patterns. However, the calculated filtering rates are dependent only on how many radioactive cells are ingested, so we can have 3 possible results if we compare, for example, the filtering rates of animals taken from the HOT NETP. and HOT NANNOP. regimes.

- 1) If Filtering Rate  $\frac{\text{NANNOP.}}{\text{NETP.}} = \text{Filtering Rate}$   
then there was no selective feeding;
- 2) If Filtering Rate  $\frac{\text{NANNOP.}}{\text{NETP.}} > \text{Filtering Rate}$  then NANNOP. was selected;
- 3) If Filtering Rate  $\frac{\text{NANNOP.}}{\text{NETP.}} < \text{Filtering Rate}$  then NETP. was selected.

This same logic can be expanded and applied to all 4 resource regimes to see if there was any resource selection by the zooplankton. These data appear in Table 6 and upon observation one immediately sees that the filtering rates on TOTALP. equal those on NANNOP. Attempting to quantify this similarity we clumped the 2 experimental groups together and calculated a S.E. MEAN x 100/EXP. VALUE ratio to see if these ratios were any higher than the ratios we found in the replication experiments (10%). In all cases except 2, the ratio was less than 10%, and we concluded that the rates were similar enough to be considered equal, the artificial clumping did not introduce a new source of variance. Isolated, these data suggest that the animals were selecting nannoplankton and ignoring netplankton since the filtering rate in the presence

of HOT NETP. + HOT NANNOP. = TOTALP. was the same as in the presence of COLD NETP. + HOT NANNOP. However, we have other data that clouds this interpretation. Other experiments performed by us have shown that 80-90% of the radioactivity found in a TOTALP. sample passes through a 50 $\mu$  net, how much of that is < 22 $\mu$  is not known, however this suggests that in a TOTALP. sample only a small amount of radioactivity was taken up by the netplankton and possibly overshadowed by the nanoplankton, so that in essence, it was really the same regime as HOT NANNOP.-COLD NETP. regime. This second explanation is supported and the first weakened by the fact that when faced with HOT NETP. + COLD NANNOP., the animals do show filtration rates. This would be impossible, if according to our first interpretation, the animals were rejecting netplankton. The filtration rates on NETP. are a problem, with no consistent pattern. For on 8-15, and 9-26, they were lower than TOTALP. and NANNOP. for all 3 species, while on 8-22, 9-17, they were higher for Daphnia and Disphanosoma and about the same for Diaptomus. Further analysis of these data sets must wait until the standing crops of phytoplankton involved in these experiments are analyzed, perhaps then, the paradox will be resolved by some pattern in the phytoplankton.

However, obvious and consistent differences appear when one compares the species filtering rates on TOTALP. and 2 X NETP. Here we have 2 regimes with the same level of organic carbon but differing in what type of cells made up the available resource. The vast majority of the 2 X NETP. were cells having at least one dimension > 22 $\mu$ , while the TOTALP. had cells in the entire range of 0 to 100 $\mu$ , and which we know contained cells below 22 $\mu$  in size. The trend is consistent for all 3 species; the filtering rate on TOTALP. or NANNOP. was greater than that on 2 X NETP. Table 7 is a summary of easily quantified data. The data are not conclusive enough to detail species-specific abilities but are strong enough to show the greater ability of the animals to ingest

nannoplankton than netplankton. This is especially interesting if we consider that one of the trends of eutrophication is a preponderance of larger algal cells. Although there exists numerous studies of selection in zooplankton, these have mainly been with one or two cell types or sizes at a time, while in nature a species faces a myriad of cell shapes and sizes. The fact that this selective ability is still present in the animal, even when faced with a diverse phytoplankton assemblage in Lake George, should be especially exciting to aquatic modelers.

Examining the detrital filtering rates, one is surprised to see that the zooplankton were able to handle dead cells as easily as live cells, since the filtering rates on detritus were comparable to those on TOTALP. or NANNOP. One must remember that this is an artificial situation since the only food available was detritus and that in order to get a more natural situation one must determine what percentage of the organic carbon is detritus and then label detritus at that percentage and measure the filtering rates. Nevertheless, these data are a good indication that detritus is a readily ingested food resource.

The species' filtering rates on bacteria are as puzzling as those on netplankton. A comparison to TOTALP. or NANNOP. (Table 8) shows great variability in the ability of the zooplankton to filter bacteria. However, for Daphnia and Diaphanosoma there is a general pattern of great selectivity for bacteria showing the availability of bacteria as a food source and the rapid rate at which the zooplankton can filter bacteria out of the water. The case is not so clear for Daphnia, but it too can, on occasion, take advantage of the bacterial food source. If one compares filtering rate vs size (sizes from Table 9) on the 4 dates in question, one realizes that on the 2 dates the rates were lower than NANNOP. or TOTALP., the animals in the experiment were 1.27 mm

on 8-22 and 1.29 mm on 9-26-73 (large Daphnia for Lake George!), while in the 2 days the rates were high the animal sizes were .91 mm on 8-15, and 1.11 mm on 9-17. Thus, with Daphnia and not the other species, size may influence the ability to ingest bacteria.

The final analysis deals with the summer pattern of the zooplankton for filtering on TOTAL phytoplankton. Table 9 reveals that Diaptomus a species present in the lake all year, shows very little variation in filtering rate over 3 months, perhaps indicating it can filter a large variety of resource equally well. However, with the cladocerans there is a different pattern. Diaphanosoma, a seasonal species, shows great variability in its filtering ability. When data on the seasonal pulse of Diaphanosoma becomes available, it will be interesting to see if there is any correlation between population and filtering rate peaks. Daphnia cannot be considered at this time since the wide variance in the sizes of the animals involved in the experiment preclude any discussion of possible influence on these rates. However, in an attempt to determine what was influencing the magnitude of the filtering rates for Diaptomus and Diaphanosoma, whose size was consistent during the summer, we plotted T°C versus filtering rate and organic carbon versus filtering rate. As can be seen in Figures 3 and 4, there is no observed correlation between T°C or organic carbon and filtering rates, although there may be a slight temperature effect in Diaptomus. What then, is the controlling factor? Our hopes for answering this question lie in the analysis of the quality of the phytoplankton. Fortunately, we have preserved the assemblages used in the feeding experiment and after analysis hope to discover the critical key to understanding zooplankton filtering rates.

Table 1. Experimental food rations described by fraction labelled with  $C^{14}$ .

Date	Particulate Organic Carbon ( $\mu\text{g C/l}$ )				
	Hot Total	Hot Nanno	Hot Net	Hot 2 x Net	Hot Detritus
8-15	165	731	285	763	309
8-22	174	383	546	371	203
9-17	1341	1185	1193	1200	-
9-26	1380	1220	1031	1242	-

Table 2. Results of feeding experiments of 5, 10 and 15 min duration to explore effect of egestion on estimation of filtering rate.

Date	Species	Feeding Time			
		5'	10' I	10' II	15'
6-26-73	Daphnia	$.05 \pm .004$	$.05 \pm .002$	$.06 \pm .007$	$.03 \pm .005$
		4/25	4/18	4/22	4/21
6-26-73	Diaptomus	$.07 \pm .01$	$.07 \pm .004$	$.06 \pm .002$	$.05 \pm .009$
		4/22	4/20	4/25	4/23

- NOTES: (1) For all filtering rates reported, the 2 numbers in the right hand corner represent the number of scintillation vials used to obtain the filtering rate and the number of animals in each vial, i.e. 4/22 = 4 vials with 22 animals per vial or 88 animals.
- (2) The standard errors associated with the filtering rates are standard errors of the mean and represent the error introduced by processing the animals after they have been killed; this applies to all filtering rates reported.

Table 3. Error term for sequential feeding in same feeding chamber.

Date	Species	Resource	Mean of 2 Successive Exp. $\pm$ S.E. Mean	S.E. x 100 Exp. Value
7-29	Daphnia	Total I	.24 $\pm$ .05	20.8
7-29	"	" II	.20 $\pm$ .03	15.0
7-29	"	Detritus	.18 $\pm$ .03	16.6
7-29	Diaptomus	Total I	.13 $\pm$ .02	15.3
7-29	"	" II	.10 $\pm$ .006	6.0
7-29	"	Detritus	.06 $\pm$ .01	16.6
8-6	Daphnia	"	.28 $\pm$ .007	2.5
8-6	Diaptomus	"	.02 $\pm$ .000	0.0
8-6	Diaphanosoma	"	.09 $\pm$ .007	7.7
9-10	Daphnia	Total I	.14 $\pm$ .02	14.2
9-10	"	" II	.13 $\pm$ .01	7.6
9-10	Diaphanosoma	" I	.11 $\pm$ .007	6.3
9-10	"	" II	.10 $\pm$ .007	7.0
9-10	Diaptomus	" I	.10 $\pm$ .008	8.0
9-10	"	" II	.11 $\pm$ .005	4.5

Table 4. Error term for feeding in two chambers at same time.

Date	Species	Resource	Mean of 2 Successive		S.E. x 100
			Exp. ± S.E.	Mean	Exp. Value
8-6	Diaptomus	Total	.14 ± .007		6.3
8-6	Daphnia	Total	.44 ± .04		9.0
9-10	Daphnia	Total I	.14 ± .02		14.2
9-10	"	" II	.12 ± .02		16.6
9-10	Diaphanosoma	" I	.11 ± .007		6.3
9-10	"	" II	.10 ± .005		5.0
9-10	Diaptomus	" I	.12 ± .004		3.3
9-10	"	" II	.09 ± .005		5.5

Table 5. Effect of number of herbivores per chamber on filtering rate.

Date	Species	F. Rate		Mean ± S.E. Mean	S.E. x 100
		12 x animals	25 x animals		Exp. Value
7-11	Diaptomus	.11 ± .02 3/12	.08 ± .01 4/15	.09 ± .01	11.1
7-29	"	.11 ± .02 3/20	.09 ± .01 4/22	.10 ± .01	10.0
7-29	"	.15 ± .01 2/18	.10 ± .01 4/28	.12 ± .01	8.3
7-29	Daphnia	.22 ± .06 2/4	.15 ± .01 2/4	.19 ± .03	16.3
7-29	"	.24 ± .10 2/6	.24 ± .00 2/6	.24 ± .00	16.7

Table 6. Filtering rates (ml/hr/animal) for Daphnia, Diaphanosoma and Diaptomus upon various resources.

Date	Species	"Hot" Nanno	"Hot" Net	"Hot" 2 x Net
8-15-73	Daphnia	3/31 .16 ± .009	2/26 .07 ± .01	2/24 .07 ± .01
8-22-73	"	5/30 .43 ± .02	5/24 .52 ± .01	5/25 .33 ± .03
9-17-73	"	3/7 .49 ± .07	3/5 .78 ± .03	3/6 .18 ± .006
9-26-73	"	3/20 .41 ± .01	3/17 .28 ± .02	3/11 .34 ± .02
8-15-73	Diaphanosoma	4/30 .20 ± .008	4/23 .06 ± .02	3/21 .08 ± .01
8-22-73	"	3/15 .15 ± .007	2/5 .45 ± .09	3/20 .07 ± .02
9-17-73	"	4/30 .17 ± .007	3/17 .18 ± .03	4/17 .11 ± .006
9-26-73	"	4/22 .13 ± .01	3/14 .05 ± .001	4/23 .06 ± .009
8-15-73	Diaptomus	4/50 .11 ± .005	4/48 .03 ± .005	4/40 .03 ± .005
8-22-73	"	5/40 .09 ± .005	4/33 .10 ± .02	5/50 .05 ± .003
9-17-73	"	5/35 .14 ± .005	5/50 .08 ± .007	4/50 .05 ± .002
9-26-73	"	5/40 .09 ± .004	5/35 .02 ± .002	5/50 .03 ± .002

Table 7. Mean filtering rates on food resources, expressed as a percentage of total and nanno phytoplankton.

Species	Mean of 4 Exp. (Filtering Rates)	
	2 x Net x 100	2 x Net x 100
	Total	Total
Daphnia	70	60
Diaphanosoma	62	50
Diaptomus	46	38

Table 8. Mean filtering rates on bacterial foods.

Date	Daphnia Filtering Rate Ratios		Diaphanosoma Filtering Rate Ratios		Diaptomus Filtering Rate Ratios	
	Bact. x 100	Bact. x 100	Bact. x 100	Bact. x 100	Bact. x 100	Bact. x 100
	Total	Nanno	Total	Nanno	Total	Nanno
8-15	4.00	4.00	2.43	2.55	6.00	4.90
8-22	.62	.65	5.75	3.07	2.43	1.88
9-17	30.34	14.24	15.23	11.64	6.11	3.93
9-26	.68	.68	.88	1.15	.27	.33

Table 9. Seasonal patterns for filtration rates on total phytoplankton.

Date	Species	Size $\pm$ S.D.	T <sup>o</sup> C	Organic Carbon µg/l	F.R. $\pm$ S.E.
6-26-73	Daphnia	.82 $\pm$ .06	22.2	225	.05 $\pm$ .002
"	"	1.08 $\pm$ .05	22.2	225	.24 $\pm$ .03
7-11-73	"	.80 $\pm$ .10	24	-	.10 $\pm$ .005
7-29-73	"	.86 $\pm$ .07	24	635	.15 $\pm$ .01
8-6-73	"	1.37 $\pm$ .08	26	580	.44 $\pm$ .04
8-15-73	"	.91 $\pm$ .08	24	165	.16 $\pm$ .006
8-22-73	"	1.27 $\pm$ .09	23	174	.45 $\pm$ .02
9-10-73	"	.90 $\pm$ .06	23	1278	.13 $\pm$ .01
9-17-73	"	1.11 $\pm$ .08	18	1341	.23 $\pm$ .01
9-26-73	"	1.29 $\pm$ .08	19	1389	.41 $\pm$ .12
8-6-73	Diaphanosoma	.91 $\pm$ .07	26	657	.15 $\pm$ .00
8-15-73	"	1.00 $\pm$ .04	24	165	.21 $\pm$ .006
8-22-73	"	.92 $\pm$ .06	23	174	.08 $\pm$ .009
9-10-73	"	.95 $\pm$ .05	23	1278	.11 $\pm$ .005
9-17-73	"	1.09 $\pm$ .06	18	1341	.13 $\pm$ .008
9-26-73	"	.94 $\pm$ .04	19	1380	.17 $\pm$ .02
6-26-73	Diaptomus	.84 $\pm$ .10	22.2	225	.07 $\pm$ .004
7-11-73	"	.78 $\pm$ .05	24	-	.08 $\pm$ .006
7-29-73	"	.89 $\pm$ .06	24	635	.10 $\pm$ .008
8-6-73	"	.79 $\pm$ .04	26	580	.11 $\pm$ .007
8-15-73	"	.87 $\pm$ .04	24	165	.09 $\pm$ .002
8-22-73	"	.90 $\pm$ .05	23	174	.07 $\pm$ .005
9-10-73	"	.91 $\pm$ .05	23	1278	.11 $\pm$ .005
9-17-73	"	.97 $\pm$ .06	18	1341	.09 $\pm$ .002
9-26-73	"	.90 $\pm$ .04	19	1380	.11 $\pm$ .004

Figure 1. Flow diagram describing resource selection experiment. A = algal cell retained by net. Each box represents one of the 5 resource regimes which was fed to the zooplankton.

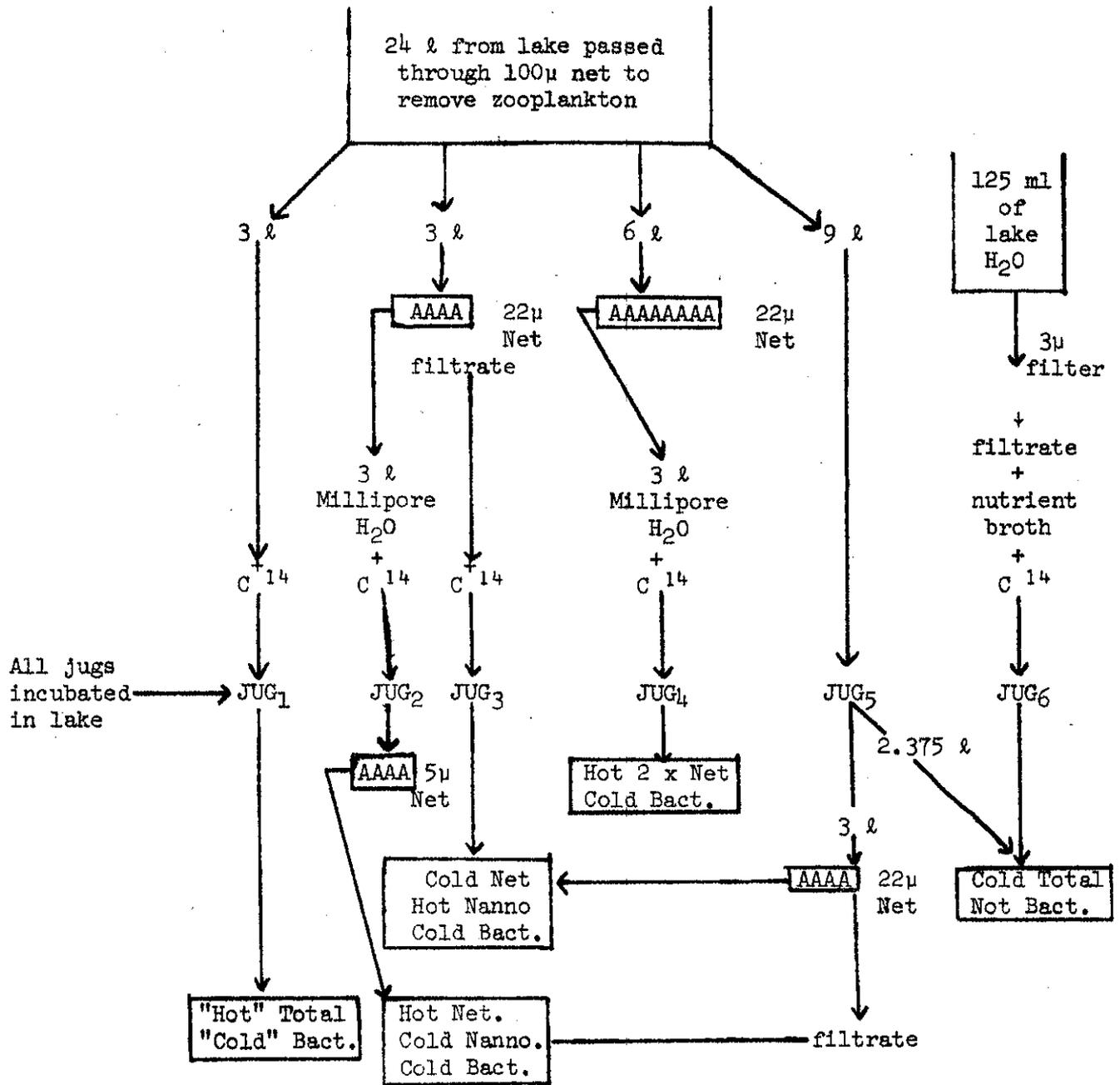


Figure 2. Power function for relationship between body size and filtering rate in Daphnia illustrating increase in filtering rate with cube of the body length.

(F) FILTERING RATE

ml./anim./hr.

0.50

0.40

0.30

0.20

0.10

0.0

0.50

1.00

1.50

(L) BODY LENGTH (mm)

9-21-72  
 $F = 0.08(L)^{2.79}$   
 $r = 0.99$

9-29-72  
 $F = 0.04(L)^{3.02}$   
 $r = 0.99$

2 points

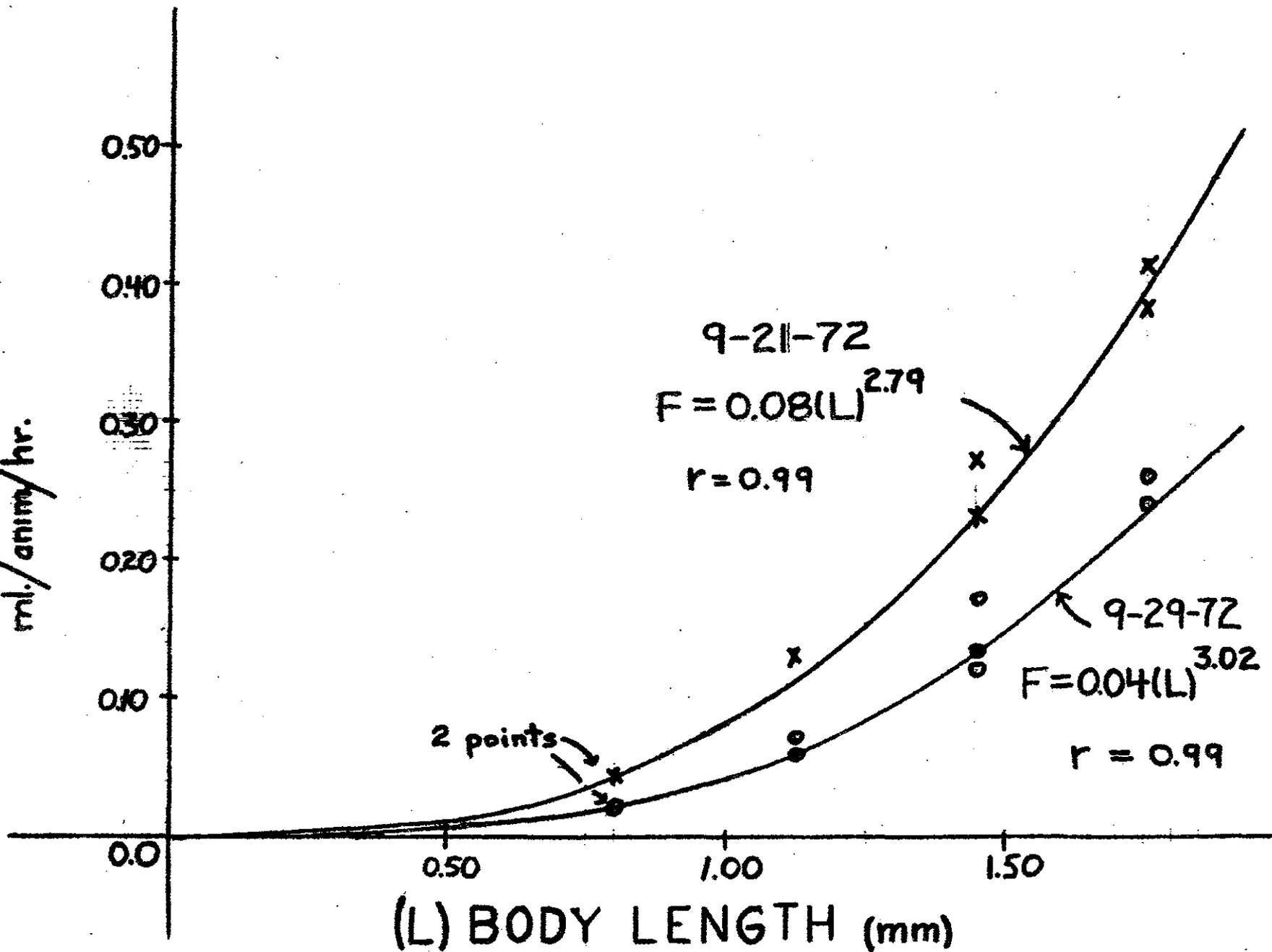


Figure 3. Relationship between temperature ( $^{\circ}\text{C}$ ) of lake water and filtering rate of Diaphanosoma and Diaptomus.

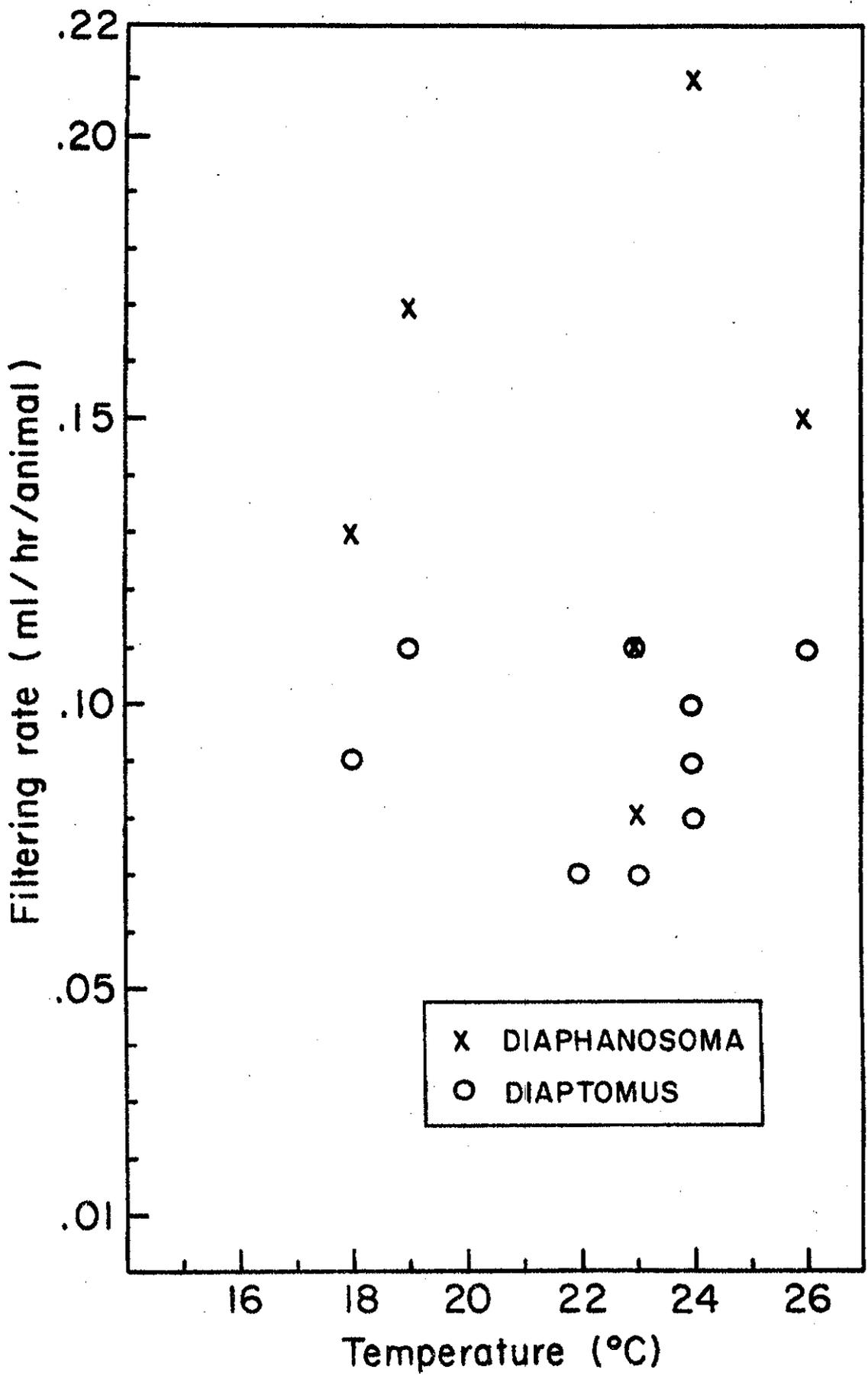
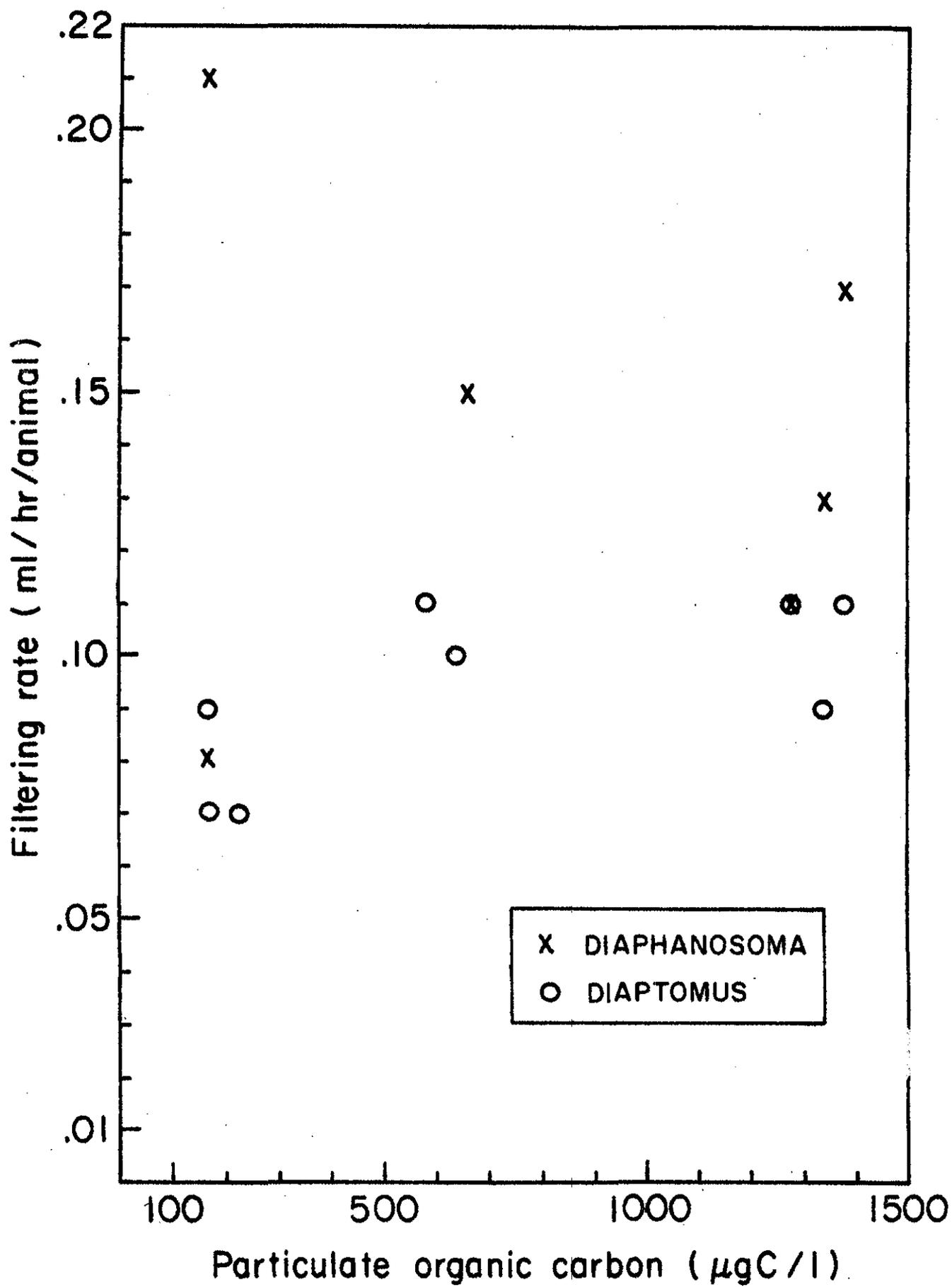


Figure 4. Relationship between concentration of particulate organic carbon ( $\mu\text{g C/l}$ ) and filtering rate ( $\text{ml/hr/animal}$ ) of Diaphanosoma and Diaptomus.



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