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# Trophic Interactions: the Relative Importance of Dreissena Filtration and Daphnia Grazing on Phytoplankton Abundance and Water Clarity

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TROPHIC INTERACTIONS: THE RELATIVE IMPORTANCE OF DREISSENA  
FILTRATION AND DAPHNIA GRAZING ON PHYTOPLANKTON ABUNDANCE  
AND WATER CLARITY

A Thesis

Presented to the Faculty of the  
Department of Biological Sciences  
of the

State University of New York College of Brockport  
in Partial Fulfillment for the Degree of  
Masters of Science

by

Eileen M. Malloy Desormeaux

December 1993

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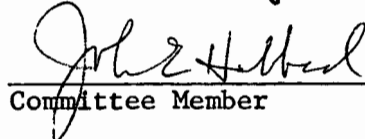
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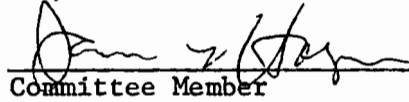
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## ABSTRACT

A series of controlled laboratory experiments were performed ( $n=4$ ) to determine the effects of Dreissena filtration and Daphnia grazing on phytoplankton abundance and water clarity. Dreissena consumed significantly more phytoplankton than Daphnia at 48 and 72 hours in vessels containing a single herbivore (Daphnia or Dreissena). Dreissena reduced phytoplankton abundance by 39% overall, while Daphnia reduced 19% of the phytoplankton. However, an additive effect was not observed in vessels containing both herbivores. Phosphorus cycling by Daphnia and cycling and retention by Dreissena changed the dynamics of the vessels significantly. Ultimately, it is likely that Dreissena will increase water clarity to a greater extent than Daphnia due to the differences in phosphorus cycling exhibited by both herbivores.

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## INTRODUCTION

The introduction of Dreissena polymorpha into North American freshwater ecosystems has resulted in major impacts to industrial and municipal water systems (Clarke, 1952; Miller et al, 1992) as well as natural aquatic ecosystems (Nepszy, 1992; Stewart, 1993; Griffith, 1993). One impact frequently attributed to Dreissena is increased water clarity (Reeders, et al., 1989; O'Neill and MacNeill, 1989) due to Dreissena's ability to filter large quantities of phytoplankton from the water column (Morton, 1971; Walz, 1978; Stancykowska, et al., 1975). Indeed, research conducted in the western basin of Lake Erie in 1989 demonstrated a twofold increase in water clarity (O'Neill and MacNeill, 1989) since the introduction of Dreissena.

However, research indicates that water clarity in Lake Erie was improving prior to the introduction of Dreissena and was generally attributed to the phosphorous abatement program and a shift in zooplankton composition from inefficient (e.g. Bosmina) to efficient phytoplankton grazers (e.g. Daphnia pulicaria) (Makarewicz, 1993; Bertram, 1993; Makarewicz and Bertram, 1991).

Thus, increased water clarity in the western basin of Lake Erie may result from several factors: 1) the reduction in phosphorous loading and the resulting decrease in phytoplankton biomass; 2) the shift in zooplankton community from inefficient to efficient grazers; 3) the introduction of Dreissena; and 4) a combination of the above.

This study was done to answer the following questions: 1) Which herbivore population, Dreissena or Daphnia, causes the greatest reduction in phytoplankton biomass and subsequent increase in water clarity? and 2) When the two herbivores are present in the same ecosystem, does either herbivore have an effect on the other herbivore's ability to reduce phytoplankton quantities? To answer these questions, a series of controlled laboratory experiments were done to determine the relative importance of Daphnia grazing and Dreissena filtration on

phytoplankton abundance and water clarity. The experiments were designed to mimic conditions observed in the western basin of Lake Erie relative to population densities of Daphnia and Dreissena (Appendix I).

## METHODS

### Cultures

**Phytoplankton:** Separate batch cultures of Chlamydomonas reinhardtii and Chlorella vulgaris were maintained at 20°C in a 14:10 light:dark cycle in Guillard's medium (Provasoli, 1971).

**Daphnia magna:** Daphnia were cultured in a 75.7 L aquarium of aerated distilled water augmented with 0.12 g of Natural Brewer's yeast as a food source. Aquarium temperatures ranged from 15°C to 22°C, while lighting was natural except from December to February when a 14:10 light:dark cycle was maintained with a fluorescent light.

**Dreissena polymorpha:** Dreissena from Lake Ontario and the Erie Canal were maintained in an aerated aquarium (37.8 L) filled with treated lake water. Treated Lake Ontario water was produced by addition of activated charcoal (2 g/L), aeration for one hour and filtration through a 0.45 µm Supor-450 142 mm membrane filter to remove zooplankton, phytoplankton and bacteria (Provasoli, 1957). Every two weeks feces, pseudofeces and one-half of the water in the aquarium was removed and replaced by freshly treated water. The temperature ranged from 17°C to 22°C. Dried finely ground Spirulina (1 g) was placed in the aquarium every other day as the food source. Four days prior to the start of an experiment Dreissena were isolated and fed Chlamydomonas and Chlorella.

## Experimental Design

General: The experimental plexi-glass vessels (n=5) were 152 cm in height and 14.5 cm in diameter with 11 sampling port depths (Figure 1). The duration of each experiment was 72 hours during which a 12:12 light:dark cycle was maintained. Each vessel was filled with 20 L of treated Lake Ontario water and enough Chlamydomonas reinhardtii and Chlorella vulgaris to obtain a concentration of 80,000 phytoplankton/ml. In addition, four of the five vessels contained various concentrations of Daphnia magna and Dreissena polymorpha separately and in combination (Table 1).

Daphnia (0.5 to 2.5 mm in size) and Dreissena (0.7 to 1.7 cm in size) were added to the experimental vessels 15 minutes prior to the start of the experiment (0 hour reading). Dreissena, on their natural substrate (i.e., a rock), were placed in a fiber-glass mesh cylindrical cage 7.5 cm in diameter and 11 cm in height and lowered to the bottom. The cage was secured 6 cm from the bottom between sampling ports 10 and the water outlet (Figure 1). Water samples for chemistry and phytoplankton abundance were taken every 24 hours. Number of zooplankton at each depth were visually counted every 24 hours.

Phosphorus was added to each vessel, if necessary, to obtain an initial reading of at least 10 µg P/L. Thus, phosphorus was not a limiting factor in phytoplankton growth at the start of the experiment.

To simulate unstratified temperature conditions which exist in lakes during spring and fall overturn, a series of experiments (n=4) were conducted where vessels were maintained at 20°± 1C. Initial sampling (0 hour) occurred when the phytoplankton were evenly distributed throughout the vessels as determined by direct phytoplankton counts and chlorophyll a levels.

## Water Chemistry and Physical Measurements

**Chlorophyll:** Chlorophyll *a* was determined directly by the fluorometric method with a Turner Model 111 Fluorometer (Wetzel and Likens, 1979).

**Phytoplankton abundance:** Abundance was measured using a Model Z<sub>r</sub> Coulter Counter. Polystyrene microspheres (3.14, 5.00 and 10.09  $\mu\text{m}$ ) were used to calibrate the counter. Each phytoplankton abundance value represents the average of five Coulter Counter readings. The precision of the Coulter Counter was measured by determining the standard deviation of the average readings (Appendix II).

**Soluble Reactive Phosphorus:** SRP was determined by the ascorbic acid method (APHA, 1989) on a Technicon autoanalyzer.

Temperature and turbidity were measured with YSI temperature probes and Turner Nephelometer (APHA, 1989), respectively.

**Shell Analysis:** Shells were first rinsed in fresh Nanopure water several times to remove organic material, placed in a 100°C drying oven for one hour and then crushed in an acid washed mortar. The crushed material was digested in sulfuric-nitric acid (APHA, 1989) and analyzed for phosphorus on a Technicon autoanalyzer.

## RESULTS

### Phytoplankton Abundance (Table 2)

All vessels, including the control, showed a decrease in phytoplankton abundance from the initial to the 72 hour readings. Since herbivores were not present in the control, the reduction

in phytoplankton in the control was attributed to settling and natural mortality. Any additional reduction in phytoplankton in vessels containing herbivores was attributed to the herbivores present (Table 2).

### 1. Comparison of Dreissena Only and Daphnia Only Vessels (Figure 2a)

The vessel containing 54 "Dreissena Only", showed a significant decrease in phytoplankton abundance and a progressive net decrease over the control. Although phytoplankton abundance decreased in the "Daphnia Only" vessel, there was not a progressive net decrease in phytoplankton. Initially, the net decrease in phytoplankton was as high as the Dreissena vessel at 24 hours but then decreased and leveled off at approximately 19%. A significant difference ( $p < 0.05$  level) between the "Dreissena Only" and "Daphnia Only" vessels occurred at 48 and 72 hours (net and absolute)(Figure 2, Table 2).

### 2. Comparison of Dreissena Only and High Dreissena Vessels (Figure 2b)

At 48 hours, the "Dreissena Only" vessel reduced phytoplankton significantly more ( $p < 0.05$ ) than the "High Dreissena/Low Daphnia" vessel. No significant difference was observed at 24 and 72 hours (Figure 2).

The "Dreissena Only" vessel had a progressive net decrease in phytoplankton from 0 to 72 hours. The "High Dreissena/Low Daphnia" vessel showed a large reduction in phytoplankton at 24 and 72 hours with a slight net reduction at 48 hours (Figure 2, Table 2).

### 3. Comparison of Daphnia Only and High Daphnia/Low Dreissena Vessels (Figure 2c)

No significant difference ( $p < 0.05$ ) in phytoplankton reduction occurred between the "Daphnia Only" and "High Daphnia/Low Dreissena" vessels throughout the experiment (Figure 2).

### Soluble Reactive Phosphorus (SRP) (Table 3)

Elevated SRP values were observed in all vessels throughout the experiment. The largest SRP values were observed at 24 hours in all experimental vessels. The "Daphnia Only" and "High Daphnia" vessels had higher ambient SRP values than the "Dreissena Only" vessel throughout the experiment (Figure 3, Table 3).

#### 1. Comparison of Dreissena Only and Daphnia Only Vessels (Figure 3a)

The "Daphnia Only" vessel had significantly ( $p < 0.05$ ) higher SRP values than the "Dreissena Only" vessel throughout the experiment (24 to 72 hours). Although both vessels had elevated SRP levels, the "Dreissena Only" vessel showed only a slight SRP increase throughout the experiment while the "Daphnia Only" vessel had a net average increase of 439% over 72 hours. For both vessels, the largest SRP increase occurred at 24 hours (Figure 3a, Table 3).

#### 2. Comparison of Dreissena Only and High Dreissena/Low Daphnia Vessels (Figure 3b)

The "High Dreissena/Low Daphnia" vessel had significantly ( $p < 0.05$ ) higher SRP values than the "Dreissena Only" vessel at 24 and 72 hours. In both vessels, the greatest amount of SRP was generated within the first 24 hours. In the "High Dreissena/Low Daphnia" vessel, the lowest SRP increase occurred at 48 hours (5%) followed by elevated levels at 72 hours (66%)(Figure 3b, Table 3).

#### 3. Comparison of Daphnia Only and High Daphnia/Low Dreissena Vessels (Figure 3c)

There was a significant difference between the "Daphnia Only" and "High Daphnia/Low Dreissena" vessel throughout the experiment (24 - 72 hours). At 24 and 48 hours, the "High Daphnia/Low Dreissena" vessel had higher SRP values. At 72 hours, the "Daphnia Only" vessel had higher ambient SRP levels. The "High Daphnia/Low Dreissena" vessel had the highest net percent increase in SRP (816%) found in any experimental vessel (Figure 3c, Table 3).

### Chlorophyll a (Table 4)

Chlorophyll a levels decreased uniformly in each vessel throughout the experiment. Although a net percent decrease in chlorophyll a occurred at each time interval, the largest decrease was observed at 48 hours (Figure 4, Table 4). Although chlorophyll a and phytoplankton abundance values did not mimic each other at all time intervals, there was a correlation between these values. Generally, as phytoplankton abundance decreased, chlorophyll a values also decreased.

#### 1. Comparison of Dreissena Only and Daphnia Only Vessels (Figure 4a)

The "Dreissena Only" vessel had significantly ( $p < 0.05$ ) less chlorophyll a than the "Daphnia Only" vessel at 48 and 72 hours (Figure 4a, Table 4).

#### 2. Comparison of Dreissena Only and High Dreissena/Low Daphnia Vessels (Figure 4b)

There was no significant difference between these vessel at any time interval throughout the experiment (Figure 4b, Table 4).

#### 3. Comparison of Daphnia Only and High Daphnia/Low Dreissena Vessels (Figure 4c)

The "High Daphnia/Low Dreissena" vessel had significantly ( $P < 0.05$ ) less chlorophyll a than was observed in the "Daphnia Only" vessel at 48 and 72 hours (Figure 4c, Table 4).

### Turbidity (Table 5)

Turbidity values fluctuated throughout the experiment. The vessels containing 54 Dreissena both had a progressive net decrease in turbidity throughout the experiment while the vessels containing 540 Daphnia had net turbidity increases at 24 and 72 hours.

Epiphytic growth was observed in the vessels containing two herbivores and the "Daphnia Only" vessel during two of the four experiments. Epiphytic growth could be readily seen on the inside surface of the vessels as well as on each of the plugs, probably as a result of the high SRP values. Epiphytic growth resulted in increased cloudiness and increased turbidity in the "Daphnia Only" and "High Daphnia/Low Dreissena" vessels.

### 1. Comparison of Dreissena Only and Daphnia Only Vessels (Figure 5a)

The "Dreissena Only" vessel had significantly ( $p < 0.05$ ) reduced turbidity levels in comparison to the "Daphnia Only" vessel at 24 and 72 hours. Although turbidity values decreased throughout the experiment in the "Dreissena Only" vessel, the "Daphnia Only" vessel actually had increased turbidity values at 24 and 72 hours (Figure 5a, Table 5).

### 2. Comparison of Dreissena Only and High Dreissena/Low Daphnia Vessels (Figure 5b)

The "Dreissena Only" vessel had significantly lower ( $p < 0.05$ ) turbidity values at 48 and 72 hours in relation to the "High Dreissena/Low Daphnia" vessel. Both vessels exhibited a progressive net decrease in turbidity from 0 to 72 hours (Figure 5b, Table 5).

### 3. Comparison of Daphnia Only and High Daphnia/Low Dreissena Vessels (Figure 5c)

The "Daphnia Only" vessel had significantly ( $p < 0.05$ ) less turbidity at 48 hours than the "High Daphnia/Low Dreissena" vessel. A similar turbidity pattern was observed in these vessels: a slight increase in turbidity at 24 hours, decreased levels at 48 hours followed by increased turbidity at 72 hours (Figure 5c, Table 5).

## Daphnia Distribution (Figures 6-9)

Daphnia distribution was measured once every 24 hours during daylight conditions. Since distribution measurements were made only once every 24 hours, vertical migration was not observed. However, vertical migration by Daphnia has been observed in natural aquatic ecosystems (Lampert, 1989) as well as in laboratory experiments (Orcutt et al., 1983). Although a consistent pattern of Daphnia distribution was not found, Daphnia were generally observed within the top 72 cm of the experimental vessels (Figures 6-9).



## DISCUSSION

### Phytoplankton Abundance

In the experiments that measured the effects of a single herbivore on phytoplankton density and water clarity, Dreissena filtered significantly more phytoplankton than Daphnia at 48 and 72 hours. Over a 72 hour period, Dreissena filtered 39% of the phytoplankton available compared to 19% filtered by Daphnia. This result was generally supported by the chlorophyll *a* (Figure 4) and turbidity data (Figure 5) and suggest that Dreissena is a more significant contributor in increasing water clarity than Daphnia. That Dreissena is a more significant contributor in increasing water clarity than Daphnia is also suggested in the literature (Morton, 1971; Stanczykowska et al, 1976; Walz, 1979; Shevtsova and Kharchenko, 1981; Piesik, 1983; Stanczykowska and Planter, 1985).

Based on the amount of phytoplankton removed by each herbivore in the "Dreissena Only" and "Daphnia Only" experiments, vessels containing both herbivores were expected to remove considerably more phytoplankton than vessels containing a single herbivore. However, in experiments in which Dreissena and Daphnia were combined in a single vessel (Figure 10) to determine their joint effect on a phytoplankton community, an additive effect did not occur. In fact, the "Dreissena Only" vessel filtered more phytoplankton than vessels containing both Dreissena and Daphnia and "Daphnia Only". How did the two herbivore vessels differ from the vessels containing a single herbivore? Did the presence of one herbivore have an inhibiting effect on the other herbivore's ability to filter phytoplankton, or did either herbivore affect the environment in such a way that less phytoplankton was filtered by one or both of the herbivores?

In comparing the single and two herbivore vessels, one parameter clearly separated the "Dreissena Only" vessel from the combined Dreissena/Daphnia vessels and the "Daphnia Only" vessel. Although all vessels showed an increase in soluble reactive phosphorous (SRP)

throughout the experiment, significantly larger quantities of SRP were found in vessels containing Daphnia (Table 3). The "Dreissena Only" vessel had significantly less SRP than the "Daphnia Only" and "High Daphnia" vessels at all time intervals (24-72 hours) and had significantly less SRP than the "High Dreissena" vessel at 24 and 72 hours (Figure 3).

Consequently, these experiments may not adequately reflect Daphnia's filtration rate due to the confounding variable of phosphorous. Likewise, the filtration rates of both herbivores in the combined vessels may be underestimated because the large quantities of SRP found in these vessels could have been utilized by phytoplankton for growth and reproduction.

### Soluble Reactive Phosphorus (SRP)

The importance of phosphorous in relationship to phytoplankton consumption in these experiments is significant for two reasons: a) phosphorous cycling by Daphnia and b) phosphorous cycling and retention by Dreissena.

The role of Daphnia in cycling phosphorous, a nutrient needed for primary productivity in aquatic ecosystems, is well documented (Dodds, et al. 1991; McCarthy & Goldman, 1979; Ejsmont-Karabin, 1990). The large amount of SRP undoubtedly recycled in vessels containing Daphnia was available for uptake, growth and reproduction by phytoplankton. The phytoplankton used in the experiments could have reproduced between the 24-hour interval readings and the increased numbers would not have been measured.

Figure 11 shows the relationship between SRP and phytoplankton values for the "Daphnia Only" and "Dreissena Only" vessels. In the "Dreissena Only" vessel, as the amount of phytoplankton that was filtered increased, the SRP values increased, on average, by 15% over a 72 hour period. For Daphnia, the SRP increased on average 439% over the same period. Clearly, the dynamics of the vessels were changed appreciably by the way in which phosphorous was utilized by the herbivores. At 24 hours, all experimental vessels had approximately the

same phytoplankton reduction (Table 2), however, greatly elevated SRP values (Table 3) were observed in vessels containing Daphnia and not in the "Dreissena Only" vessel. At 48 hours, the "Dreissena Only" vessel continued to show a net progressive decrease in phytoplankton (Table 2) while the vessels containing Daphnia showed slight decreases or no change in the amount of phytoplankton consumed (Figure 2). The elevated phosphorous levels observed at 24 hours in Daphnia vessels could have been utilized by phytoplankton for reproduction (Lehman, 1980; Ejsmont-Karabin and Spodniewska, 1990). Both herbivores may have been decreasing phytoplankton at a constant rate but the amount of phytoplankton generated by the large SRP available was masking the trend.

If large SRP values resulted in higher abundance of phytoplankton, Daphnia could have been grazing not only the existing phytoplankton but also the newly-formed algae. Therefore, results of phytoplankton consumption by Daphnia in these experiments are underestimated and vessels containing both herbivores may not adequately reflect the total amount of phytoplankton consumed.

Although Daphnia grazed down the phytoplankton population, they also cycled back into the water column a large amount of phosphorous thus providing a necessary nutrient for further phytoplankton growth. Dreissena, however, filtered large amounts of phytoplankton out of the water column while releasing a relatively small amount of phosphorous (Stanczykowska and Planter, 1985).

Increased SRP values were observed in the "Dreissena Only" vessels (Table 3, Figure 3). However, the net increase was significantly less than that recorded for vessels containing Daphnia (Table 3, Figure 3). Research by Stanczykowska and Planter (1985) indicates that Dreissena cycles phosphorous through a) an accumulation in mussel shells and tissues and b) feces and pseudofeces.

Any accumulation of phosphorous in shells and tissue is locked up and unavailable to the aquatic ecosystem for several years. Tissue matter would be removed from cycling for the life of the mussel (4-6 years); while phosphorous deposited in shells may be unavailable for up to 20 years (Stanczykowska, 1984). Analysis of a small number of Dreissena shells, indicated that approximately 0.13% of shell mass was phosphorous. These results are similar to those obtained by Kuenzler (1961) for Modiolus, a marine mussel similar to Dreissena in physical appearance (Stanczykowska, 1984). Also, Stanczykowska (1984) indicates that there is more phosphorous in mussel tissue than that found in shell material.

Stanczykowska and Planter (1985) estimate that approximately 40% of the phosphorous taken in by Dreissena through filtration is released in the form of feces and pseudofeces. These materials settle to the bottom but could enter the water column due to water currents and may account for the small increase in SRP observed in the "Dreissena Only" vessel in my short term experiments.

Dreissena filtered large amounts of phytoplankton out of the water column while releasing a relatively small amount of phosphorous. Dreissena may inhibit additional phytoplankton growth by limiting available phosphorous. As a result, Dreissena may have a more significant long-term role in increasing water clarity in natural ecosystems than Daphnia.

The manner in which phosphorus was utilized by the zooplankton in these experiments significantly changed the composition of any vessel containing Daphnia (alone or in combination) in relation to the control or "Dreissena Only" vessels. Phosphorus cycling by Daphnia appears to be the major influence in the vessels containing both herbivores in relation to the amount of phytoplankton that was consumed. However, other factors that could have an influence on the filtration process in suspension feeders must also be considered for all the experimental vessels. These factors include: temperature, phytoplankton quantity and phytoplankton quality.

## Temperature

For Dreissena, an increase in temperature corresponds with an increase in filtration rate up to 30°C (Morton, 1971; Winter, 1978). Walz (1978) found the optimal temperature in terms of growth rate for Dreissena to be 15°C. The experimental vessels were maintained at 20°C, slightly above the optimal temperature for growth but within the range found acceptable for normal physiological processes. Consequently, the temperature in these experiments would not appear to limit Dreissena's ability to filter phytoplankton.

Daphnia demonstrate an optimum filtering rate at 22°C (Kersting and van der Leeuw, 1976) which is just slightly above the temperature used in these experiments. Although neither herbivore was maintained at their optimal temperature, neither were they hindered by the experimental temperatures. It is unlikely that temperature had a negative effect on either herbivore in relation to their ability to filter phytoplankton and increase water clarity.

## Phytoplankton Abundance

A phytoplankton abundance of 80,000 organisms/ml was used in each experimental vessel. Similar quantities are frequently used in filtration studies for Dreissena (Morton, 1971; Sprung and Rose, 1988) and Daphnia (McMahon and Rigler, 1965) when small phytoplankton, such as Chlamydomonas reinhardtii and Chlorella vulgaris, are used. Morton (1971) suggested these quantities may better reflect true filtration rates because lower algal concentrations may not be enough to stimulate all tactile receptors while larger concentrations may stimulate tactile receptors too much, thus irritating the herbivore resulting in a decreased filtering rate.

Filtration rate is defined as the volume of water filtered completely free of particles per unit of time (Winters, 1978; Sprung and Rose, 1988). The relationship between filtration rate and phytoplankton concentration has been demonstrated for several species of lamellibranchiate bivalves (Winter, 1978). Similar results were obtained by Morton (1971) in analyzing the

filtration rates of Dreissena in particular. In general, filtration rate increases with increasing phytoplankton quantities up to a maximum filtration. Thereafter, filtration rate decreases with increasing phytoplankton concentration. The average filtration rate of Dreissena after 24 hours in my experiments was found to be 11.6 ml/hr. These results correspond with Stanczykowska et al (1976) (10-100 ml/hr); Morton (1971 A) (5-180 ml/hr); and Mikheev (1967) (2-50 ml/hr) (Appendix III). The phytoplankton quantities I used did not seem to hinder Dreissena's filtration ability nor did they appear to stimulate a high filtration rate. In all experiments (n=3), Dreissena's filtration rates were always found to be at the low end of those cited in the literature.

The average filtration rate for Daphnia in these experiments was found to be 0.47 ml/hr after 24 hours. These results are considerably lower than those found by Kersting and van der Leeuw (1976): 3.2 ml/hr; McMahon and Rigler (1965): 2.7 - 3.4 ml/hr or Ryther (1954): 3.3 ml/hr. (Appendix III). The low filtration rates observed in my experiments may be due to the amount of time between sampling periods (24 hours) and also due to the large phosphorus quantities being used by phytoplankton for growth. Generally, Daphnia filtration rates are analyzed every 10 - 30 minutes. By using small sampling periods, the confounding variable of phosphorus is minimized (Lehman, 1980). By 24 hours, extremely high SRP values were observed in all vessels containing Daphnia (Table 3). Because this phosphorus was available to phytoplankton for growth and reproduction, phytoplankton abundance could have increased within this time period but would not have been measured. Consequently, observed Daphnia filtration rates are very low and do not truly reflect Daphnia's ability to reduce phytoplankton numbers.

The concentrations of phytoplankton used in these experiments should not have inhibited the filtration rate of either herbivore. The fact that Daphnia's filtration rates do not coincide with those in the literature is most likely due to the high phosphorus values and not the quantity of phytoplankton.

### Phytoplankton Quality

Although food selection by bivalves is mainly considered a quantitative rather than qualitative process, Morton (1971) has shown that the culture medium in which algae are grown can either increase or decrease Dreissena's filtration rate. He suggests that this could be due to chemical products released by algal cells into the medium. Other researchers have also suggested that the metabolic products of algae may also affect the feeding habits of bivalves (Davids, 1964; Walne 1956). This indicates that both quantity and quality of food should be considered when the filtration rates of herbivores are studied.

In many studies on the filtration rates of Dreissena and Daphnia, Chlamydomonas reinhardtii and Chlorella vulgaris are frequently used as food sources (Morton, 1971; Sprung and Rose, 1988; Arnold, 1971; Kersting and van der Leeuw, 1976; Sarnell, 1986; McMahon and Rigler, 1965). They are considered important nutrient sources for herbivores due to their size (5 - 15  $\mu\text{m}$ ) (Gliwicz, 1977), shape (Spherical), and lack of a gelatinous sheath (Sarnell, 1986; Porter and Orcutt, 1980). Studies indicate that neither algae is toxic to the herbivores; consequently they are used often to determine filtration rates.

Although neither alga is considered toxic, the use of monocultures of these organisms may not provide the best nutrient source for the herbivores. Walz (1978) found that Dreissena fed on mixed phytoplankton diets (natural lake algal assemblages) had better growth rates than those fed on monoculture. Since Dreissena were fed on a Spirulina monoculture between experiments, it is possible that they were not in optimum condition which could have affected their ability to filter phytoplankton.

In this study, it is likely that the difference in phosphorus recycling by Daphnia and Dreissena had the most significant effect on the herbivore's ability to increase water clarity.

## The Effects of Dreissena Filtration on-an Aquatic Ecosystem

Dreissena's ability to reduce phytoplankton and increase water clarity may have profound effects on aquatic ecosystems. By significantly reducing phytoplankton quantities, the primary productivity of a system may decline. Reductions in productivity could ultimately lead to reduced zooplankton, planktivores and top carnivores. An entire ecosystem shift could occur. Since Dreissena not only reduces phytoplankton but also removes nutrients from the pelagic to the benthic zone, it is possible that a primarily pelagic-based ecosystem could be replaced by a benthic system.

Fisher (1992, unpublished) suggests that such a shift may be occurring in Lake Erie as a result of the Dreissena invasion. The increased populations of Gammarus observed in Lake Erie are generally attributed to Dreissena because Gammarus readily consume Dreissena feces and thus benefits directly from benthic depositions by Dreissena. Stewart (1993) also found that native macroinvertebrate species diversity increased in benthic areas (cobble and reef) in Lake Ontario since the introduction of Dreissena.

If such an ecosystem shift occurs, the effects may be far-reaching. Mackie (1991) suggests that severe socio-economic impacts, especially for the fishing industry, are likely to follow a pelagic to benthic ecosystem change.

## Future Research

This study examined the relative importance of Dreissena and Daphnia filtration on an ecosystem when the temperature of the water was uniform. Because of this, phytoplankton were found throughout the experimental vessels and were readily available as a food source for either Dreissena or Daphnia. Consequently, Dreissena consumed significantly more phytoplankton than Daphnia. However, different results may be observed if these experiments



were done under thermally stratified conditions. In a thermally stratified experiment, Daphnia would be expected to affect phytoplankton more in the epilimnion, while Dreissena would do the same in the hypolimnion. If Daphnia were also able to remove phytoplankton from the metalimnion, Daphnia would then be more important in reducing phytoplankton than Dreissena. A thermally stratified experiment would complement this study and add to our knowledge of Dreissena's affects on a lake during summer and winter stratification.

Both thermally stratified and non-stratified experiments could also be done using various phytoplankton assemblages, especially diatoms that are typically found in lake ecosystems.

## SUMMARY

Dreissena reduced phytoplankton abundance significantly more than Daphnia at 48 and 72 hours, following their introduction into an aquatic ecosystem. However, the differences in the amount of phytoplankton reduced by each herbivore may have more to do with the way in which phosphorous is utilized and cycled by the herbivores rather than their filtration ability.

Phosphorous cycling also had an effect on the amount of phytoplankton that could be reduced by the herbivores when they were both placed in the same vessel. Consequently, an additive grazing effect was masked by increased SRP production in the two herbivore vessels.

Therefore, ultimately it is likely that Dreissena will increase water clarity more thoroughly than Daphnia due to the differences in phosphorous cycling exhibited by both herbivores. While Daphnia reduced phytoplankton numbers by grazing, it also supplied the necessary nutrient

phosphorous into the water column so that additional phytoplankton growth could occur. Dreissena, however, while grazing heavily on phytoplankton, only cycled small amounts of phosphorous back into the aquatic ecosystem.

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Table 1. Abundance of Daphnia magna and Dreissena polymorpha in control and experimental vessels. Abundance in vessels corresponds to 1989 abundance in the western basin of Lake Erie (MacNeill, 1989).

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Vessel 1: Control + Phytoplankton only

Vessel 2: Phytoplankton and 54 Dreissena polymorpha

Vessel 3: Phytoplankton with 54 Dreissena polymorpha  
and 209 Daphnia magna

Vessel 4: Phytoplankton and 540 Daphnia magna

Vessel 5: Phytoplankton with 540 Daphnia magna  
and 25 Dreissena polymorpha

Table 2. Values represent the average ( $X \pm S.E.$ ) net decrease (%) in phytoplankton ( $n=3$ ). Net values were obtained by subtracting any reduction in phytoplankton that occurred in the control from each of the experimental vessels. Temperature was uniform throughout the vessels at  $20 \pm 1^\circ\text{C}$ .

Time Interval	<u>Dreissena</u> <u>Only</u> Mean $\pm$ S.E.	<u>High Dreissena</u> <u>Low Daphnia</u> Mean $\pm$ S.E.	<u>Daphnia Only</u> Mean $\pm$ S.E.	<u>High Daphnia</u> <u>Low Dreissena</u> Mean $\pm$ S.E.
24	25 $\pm$ 5.0	27 $\pm$ 4.5	24 $\pm$ 4.5	25 $\pm$ 3.9
48	29 $\pm$ 3.6	18 $\pm$ 2.2	20 $\pm$ 2.9	26 $\pm$ 3.9
72	39 $\pm$ 2.1	36 $\pm$ 3.5	19 $\pm$ 3.6	23 $\pm$ 8.1

Table 3. Values (%) represent the average ( $X \pm S.E.$ ) net percent increase in soluble reactive phosphorus (SRP) ( $n=2$ ). Net values were obtained by subtracting any SRP changes that occurred in the control from the experimental vessels.

Time Interval	<u>Dreissena</u> Only Mean $\pm$ S.E.	High <u>Dreissena</u> Low <u>Daphnia</u> Mean $\pm$ S.E.	<u>Daphnia</u> Only Mean $\pm$ S.E.	High <u>Daphnia</u> Low <u>Dreissena</u> Mean $\pm$ S.E.
24	31 $\pm$ 15.0	311 $\pm$ 75.6	1044 $\pm$ 149.0	2144 $\pm$ 348.8
48	9 $\pm$ 4.7	5 $\pm$ 6.4	124 $\pm$ 27.3	221 $\pm$ 45.2
72	4 $\pm$ 3.0	66 $\pm$ 23.2	148 $\pm$ 23.3	84 $\pm$ 8.0



Table 4. Values (%) represent the average ( $X \pm S.E.$ ) net percent decrease in chlorophyll a levels for the unstratified experiments ( $n=4$ ). Net values were obtained by subtracting any chlorophyll a changes that occurred in the control from the experimental vessels.

Time Interval	<u>Dreissena</u> Only Mean $\pm$ S.E.	High <u>Dreissena</u> Low <u>Daphnia</u> Mean $\pm$ S.E.	<u>Daphnia</u> Only Mean $\pm$ S.E.	High <u>Daphnia</u> Low <u>Dreissena</u> Mean $\pm$ S.E.
24	20 $\pm$ 4.4	26 $\pm$ 4.4	14 $\pm$ 4.0	20 $\pm$ 3.6
48	27 $\pm$ 3.6	28 $\pm$ 2.2	23 $\pm$ 2.7	31 $\pm$ 2.5
72	23 $\pm$ 2.9	24 $\pm$ 3.3	16 $\pm$ 2.1	24 $\pm$ 3.0

Table 5. Values (%) represent the average ( $\bar{X} \pm \text{S.E.}$ ) net percent change in turbidity levels ( $n=4$ ). Net values were obtained by subtracting any turbidity changes that occurred in the control from the experimental vessels. Negative values represent decreases in turbidity levels, positive values represent increases.

Time Interval	<u>Dreissena</u> Only Mean $\pm$ S.E.	High <u>Dreissena</u> Low <u>Daphnia</u> Mean $\pm$ S.E.	<u>Daphnia</u> Only Mean $\pm$ S.E.	High <u>Daphnia</u> Low <u>Dreissena</u> Mean $\pm$ S.E.
24	-27 $\pm$ 6.4	-19 $\pm$ 6.8	6 $\pm$ 7.9	13 $\pm$ 8.7
48	-93 $\pm$ 12.4	-38 $\pm$ 10.8	-76 $\pm$ 13.0	-4 $\pm$ 10.8
72	-105 $\pm$ 10.1	-72 $\pm$ 15.2	46 $\pm$ 35.7	16 $\pm$ 42.3

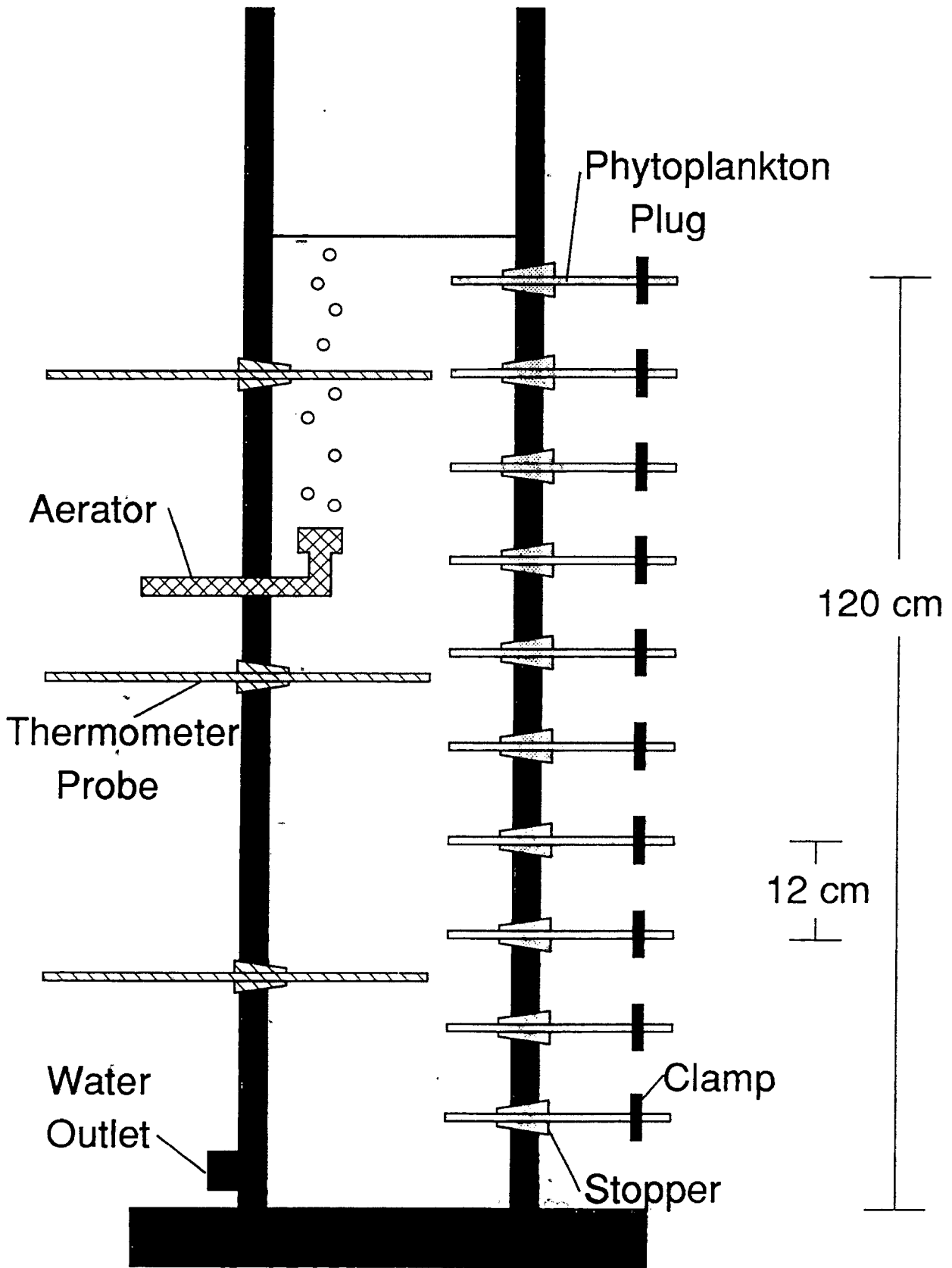


Figure 1 - Schematic of experimental vessel

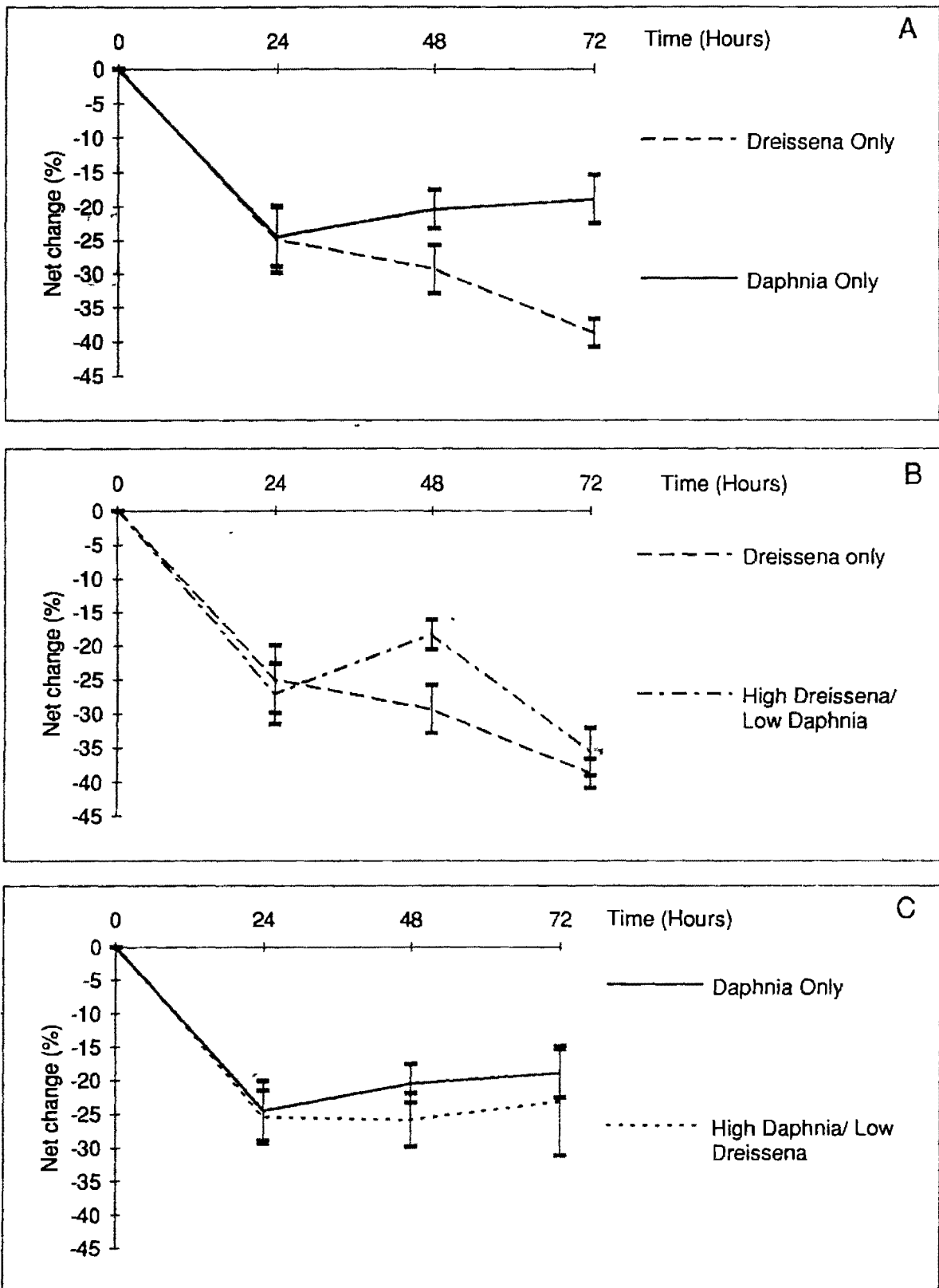


Figure 2 - Average net percent decrease in phytoplankton for all experimental vessels

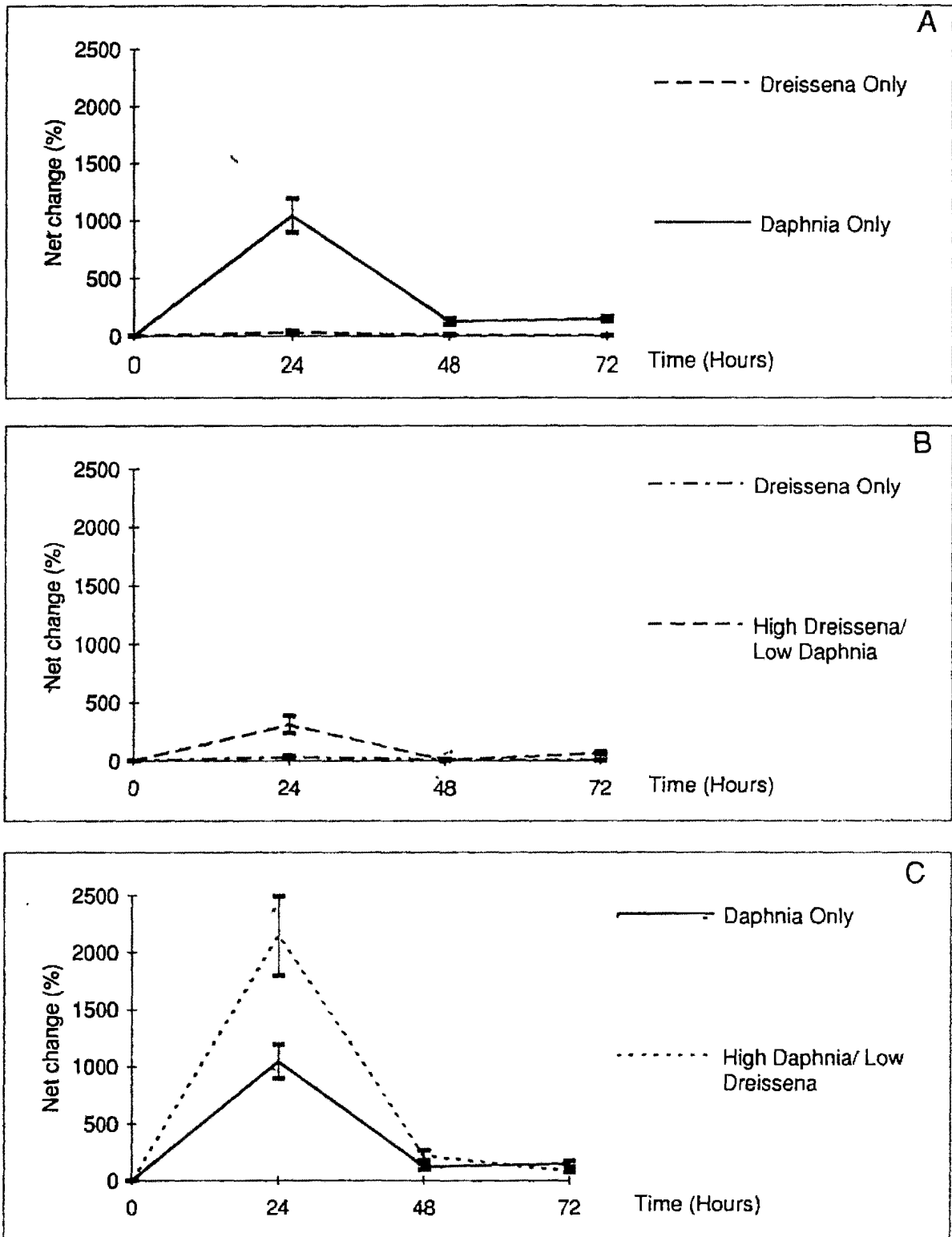


Figure 3 - Average net percent increase in soluble reactive phosphorus (SRP) for all experimental vessels

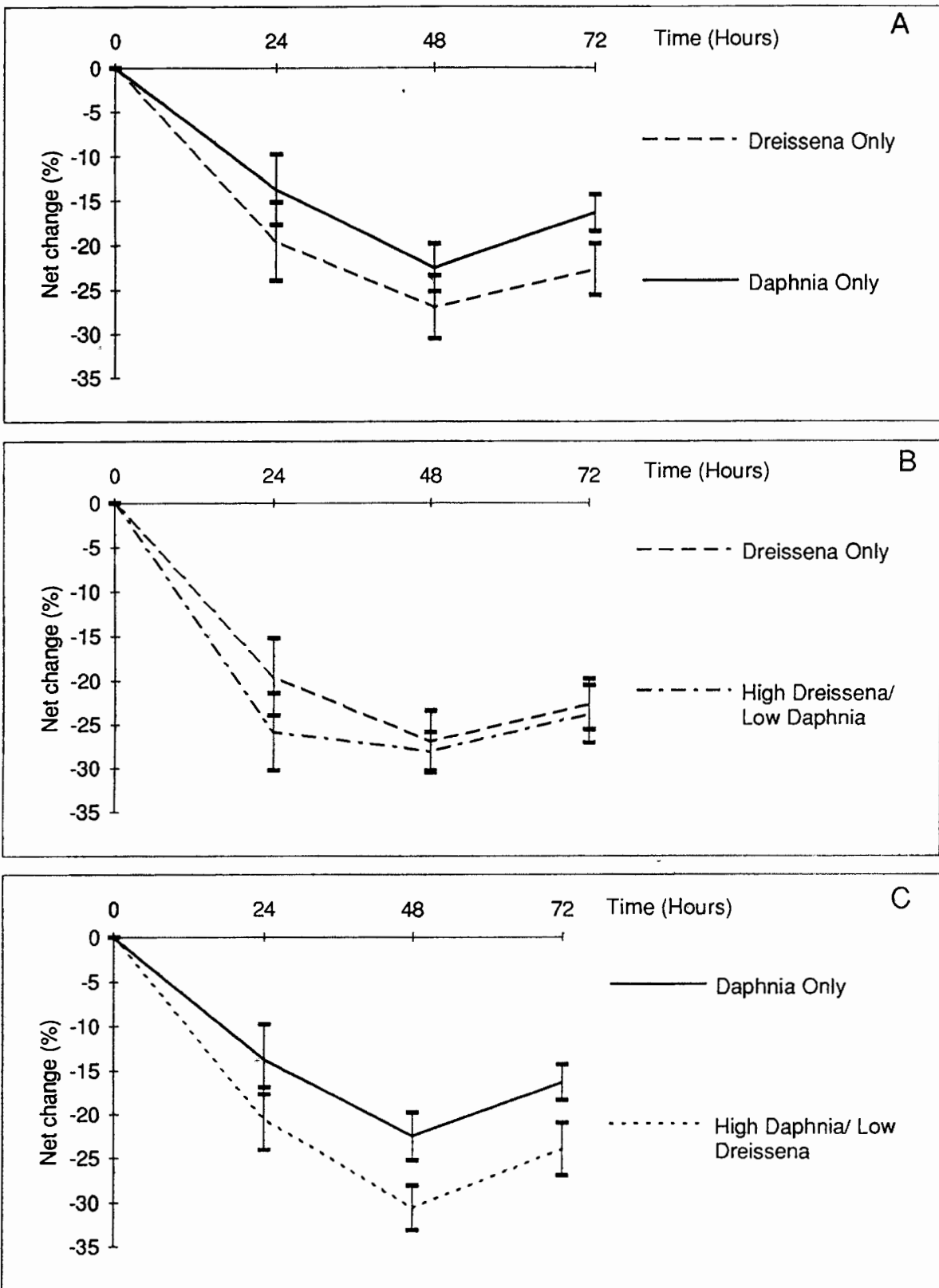


Figure 4 - Average net percent decrease in chlorophyll a for all experimental vessels

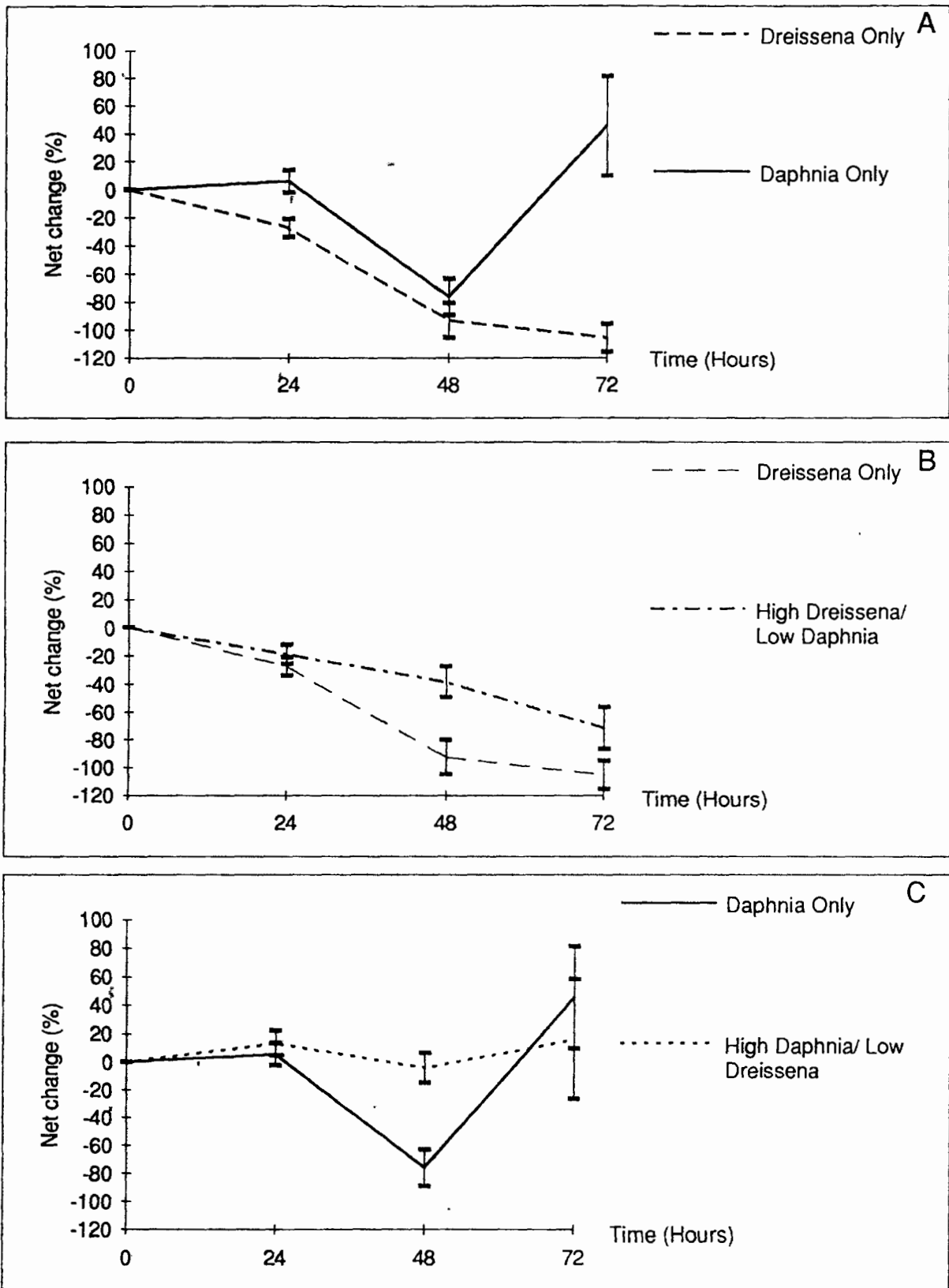


Figure 5 - Average net change in turbidity for all experimental vessels

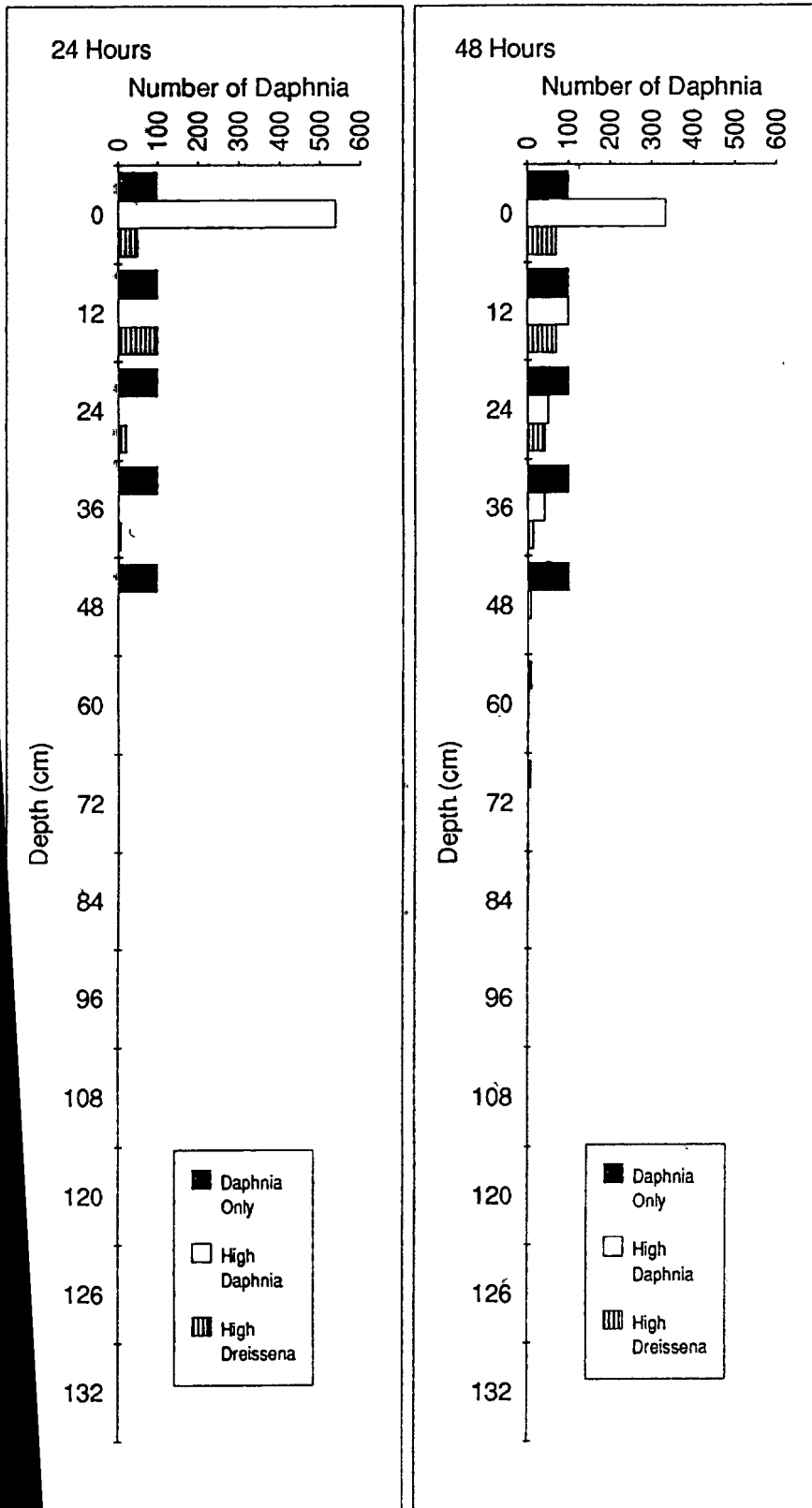


Figure 6 - Distribution of Daphnia at 24 and 48 hours for experiment 1



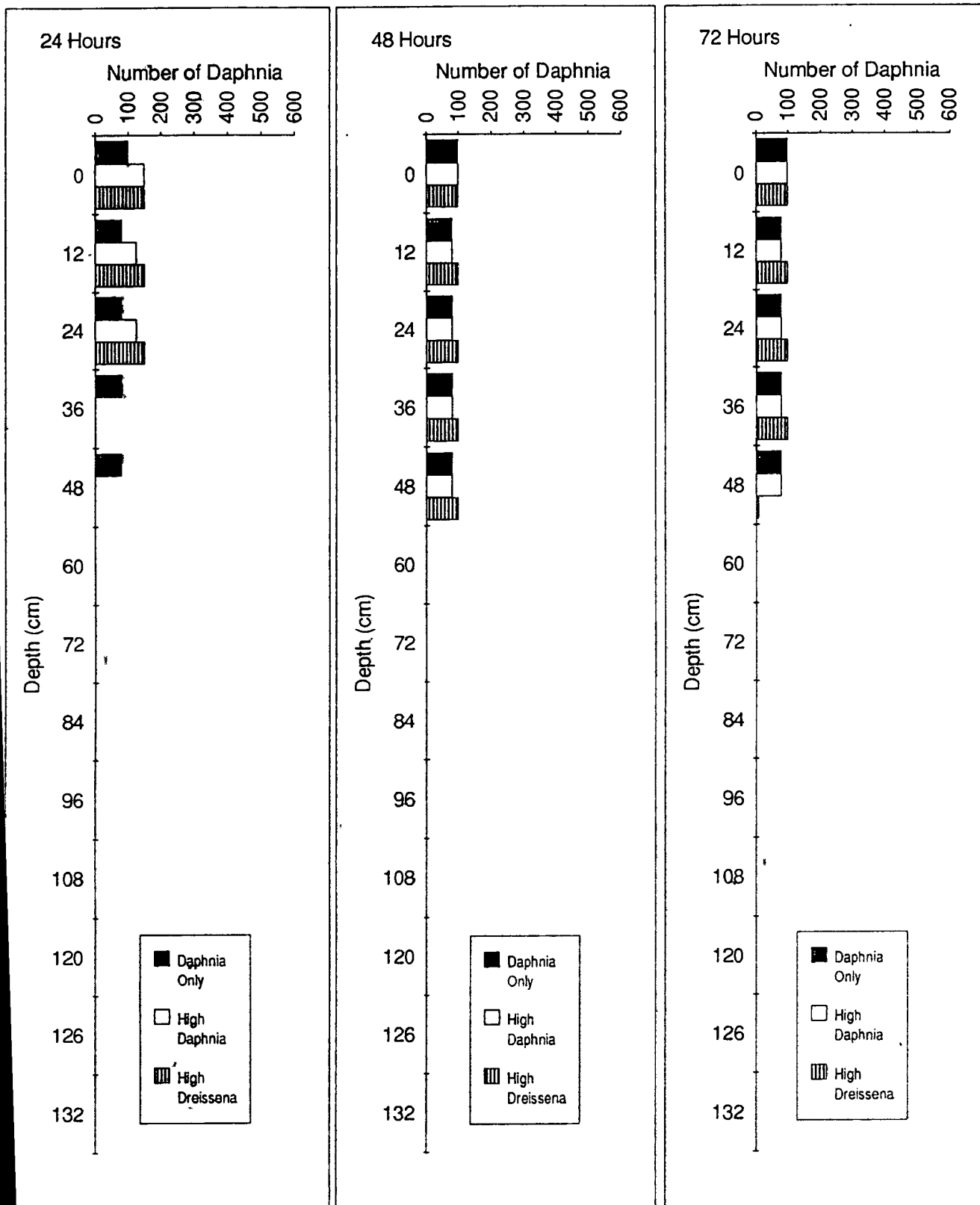


Figure 7 - Distribution of Daphnia at 24, 48 and 72 hours for experiment 2

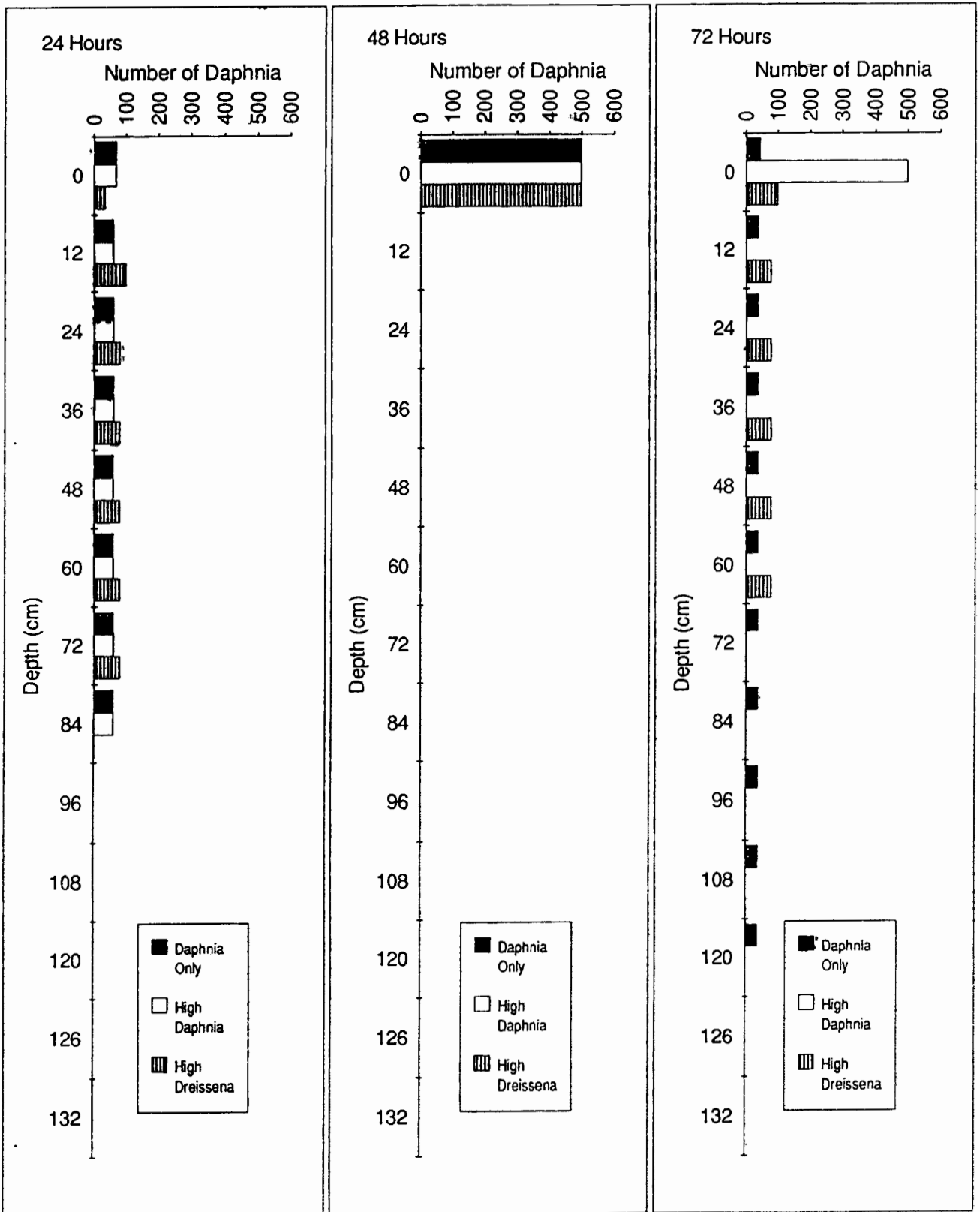


Figure 8 - Distribution of Daphnia at 24, 48 and 72 hours for experiment 3

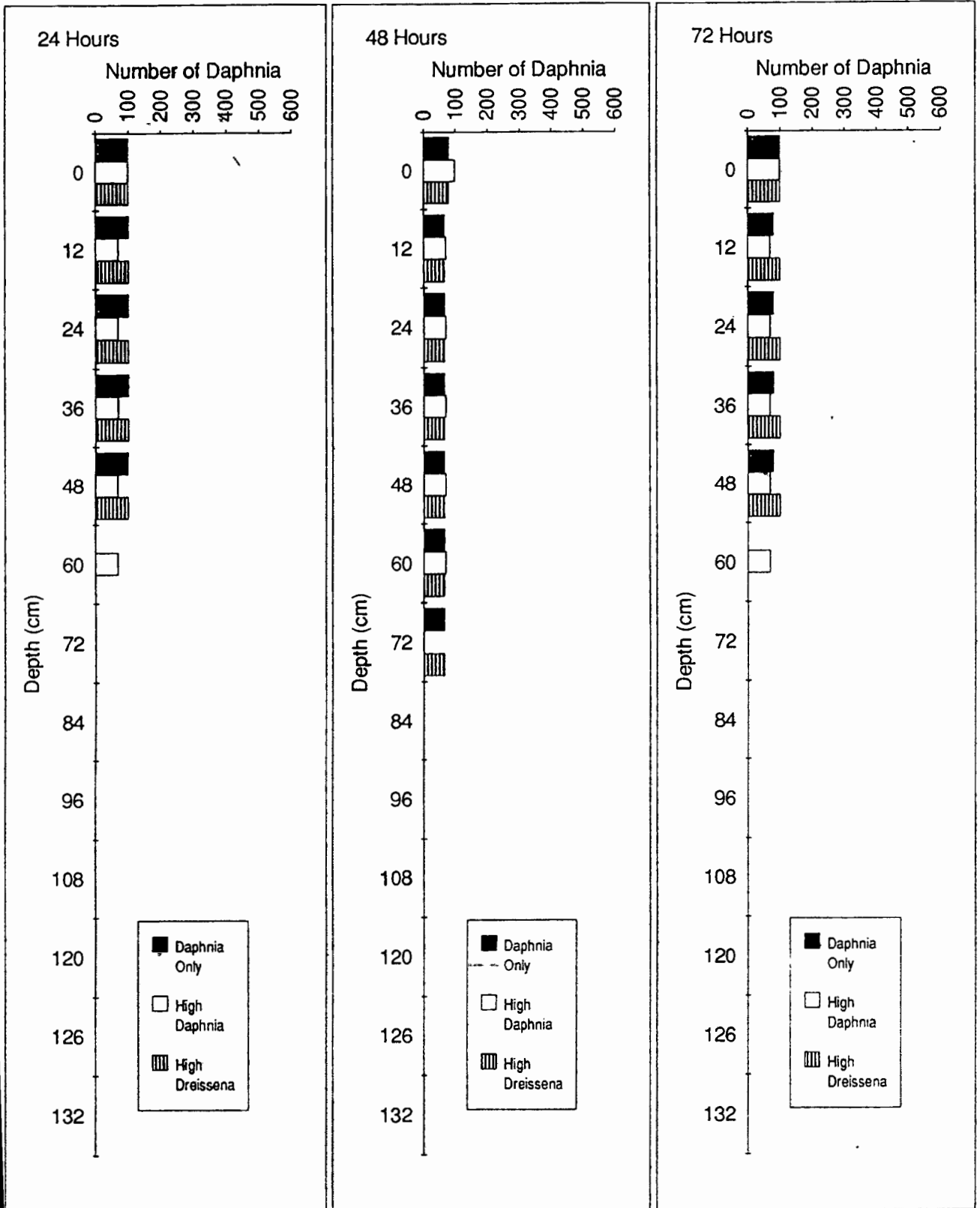


Figure 9 - Distribution of Daphnia at 24, 48 and 72 hours for experiment 4

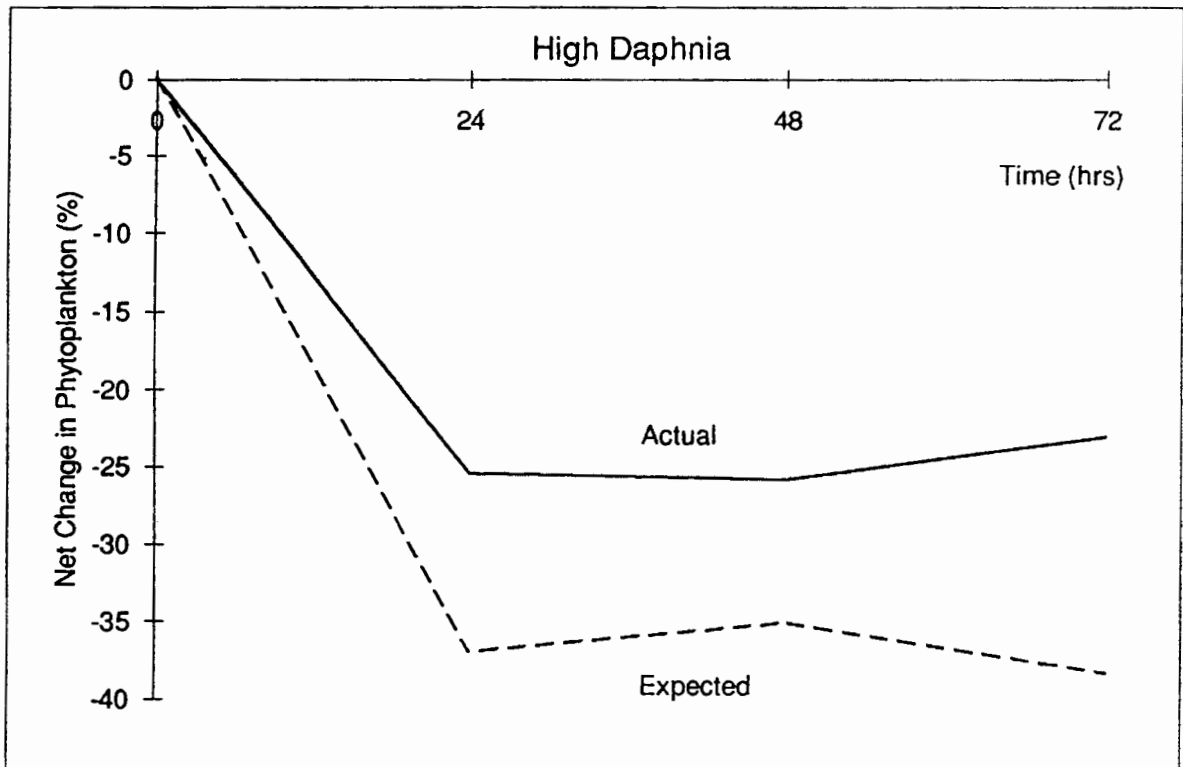
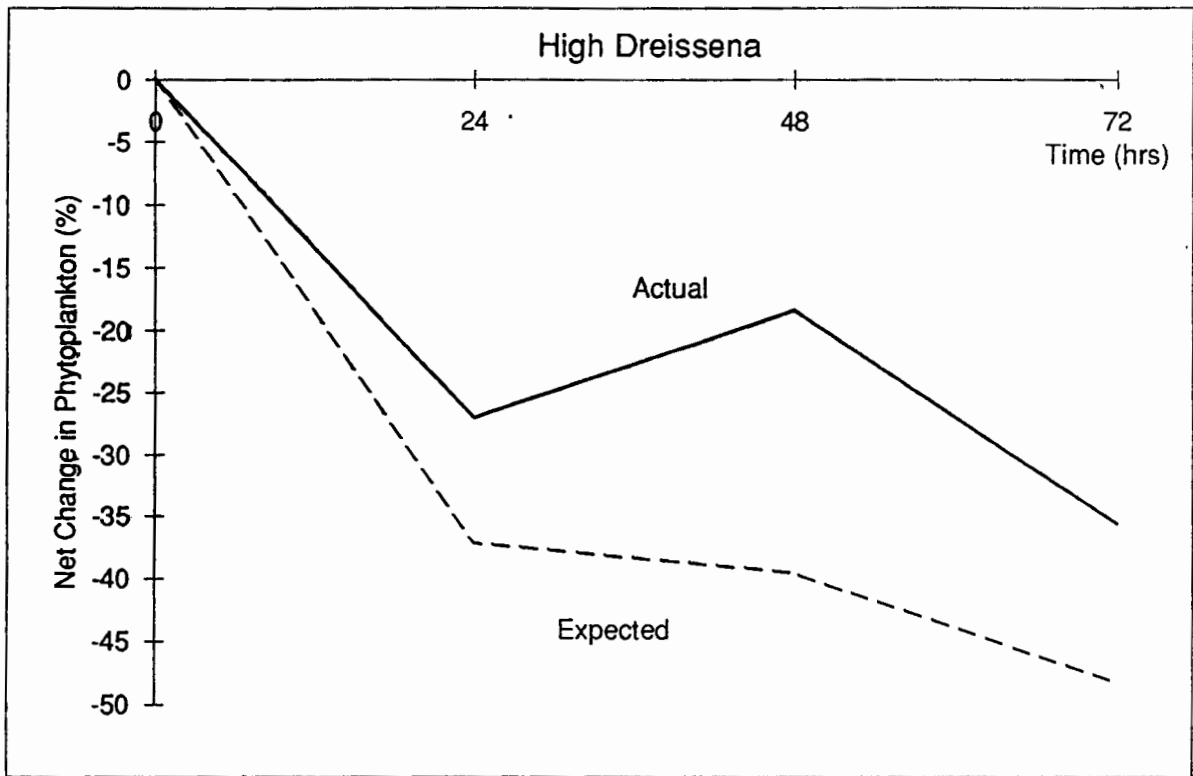


Figure 10 - Phytoplankton removal from vessels containing both Dreissena and Daphnia

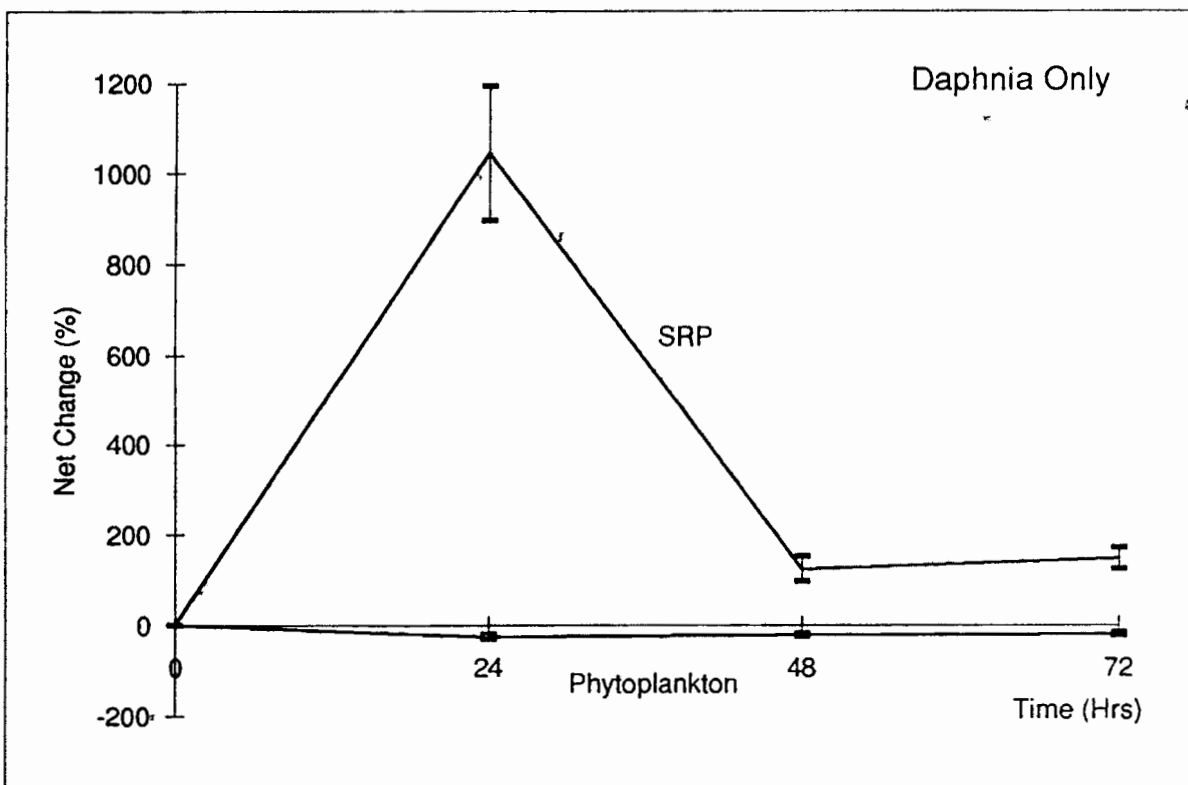
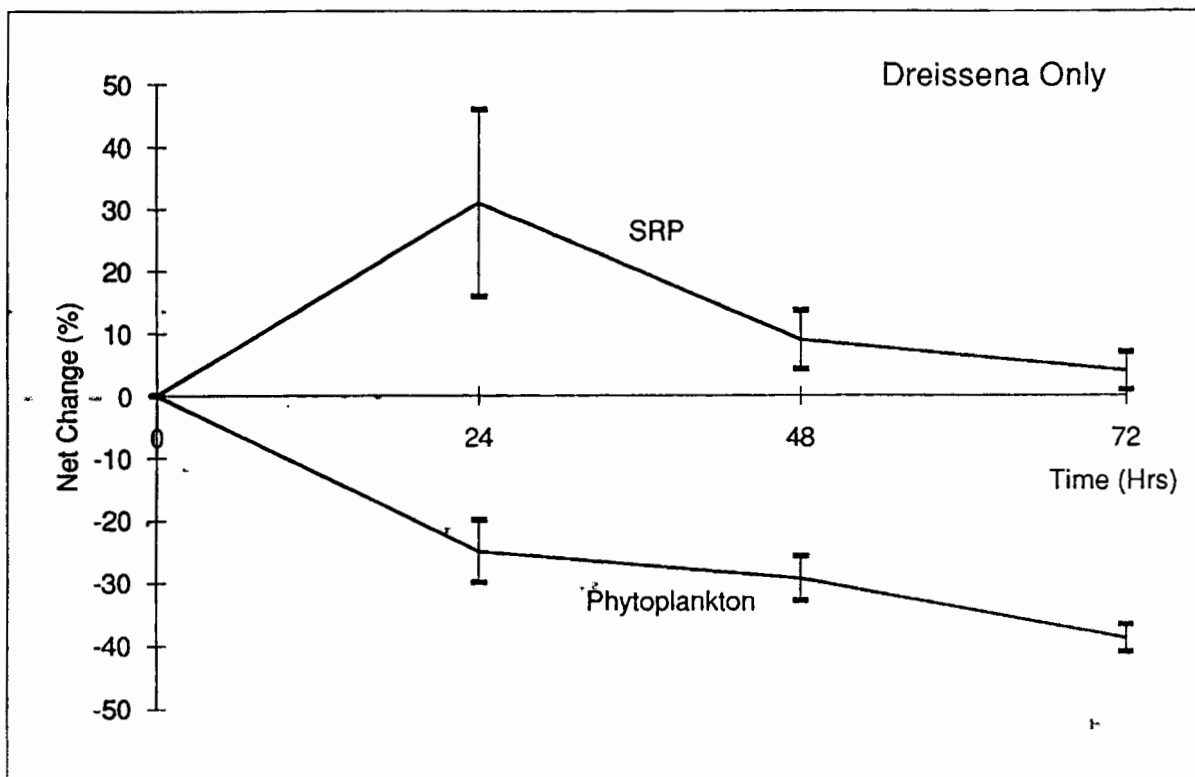


Figure 11 - Net % Change in Phytoplankton and SRP vs Time (Hrs) for Daphnia Only and Dreissena Only

## APPENDIX I

The following criterion were used to determine the amount of Daphnia and Dreissena that each experimental vessel would contain.

### Daphnia Only and Dreissena Only Vessels

To determine what effect Daphnia grazing and Dreissena filtration have on water clarity, a series of experimental vessels; which mimicked the western basin of Lake Erie Daphnia (30,000/m<sup>3</sup>) (EPA, 1984) and Dreissena (30,000/m<sup>2</sup>) (MacNeill, 1989) populations densities, were established.

Both Dreissena and Daphnia are herbivores which utilize phytoplankton in the water column as their food source. The depth of the western basin of Lake Erie is approximately 10 m. An assumption was made that any phytoplankton found throughout the 10 m depth could be considered a food source for the herbivores. Therefore, 30,000 Dreissena and 300,000 Daphnia are supported (obtain nutrients) from 10 m<sup>3</sup> (10,000 L) of water. To simulate these conditions in the experimental vessels which contained 18 L of water, 54 Dreissena and 540 Daphnia were used.

### Vessels Containing Both Dreissena and Daphnia

Vessels containing both herbivores were established to determine: 1) if one herbivore had an effect on the other herbivore's ability to reduce phytoplankton numbers and increase water clarity; 2) which type of population (High Dreissena/Low Daphnia or High Daphnia/Low Dreissena) would most effectively reduce phytoplankton numbers and 3) the effects of a small population of an exotic species on an established zooplankton population (High Daphnia/Low Dreissena).

## APPENDIX II

To determine the precision of the Coulter Counter each phytoplankton sample was analyzed three to five times. The average of the replicates was used in all further calculations. The samples below are typical Coulter Counter readings. The precision of the instrument was measured by determining the standard deviation and standard error.

Reading	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5
1	17784	16958	17468	17878	18431
2	17961	16810	17467	17635	18444
3	17812	16464	17488	17984	18417
4	17991	16866	17408	17949	18441
5	17882	16679	17414	17974	18382
Average	17886	16755	17449	17884	18423
Standard Deviation	80.68	171.47	31.97	130.03	22.57
Standard Error	36.08	76.68	14.31	58.15	10.09

## APPENDIX III

The following equation from Coughlan (1969) was used to calculate the filtration rates of Dreissena and Daphnia:

$$m = \frac{M}{n \cdot t} \left[ \left( \ln \frac{conc_o}{conc_t} \right) - \left( \ln \frac{conc_o'}{conc_t'} \right) \right]$$

where

$m$  = filtering rate (mls/hr)

$M$  = volume of suspension

$n$  = number of animals

$t$  = time (hours)

$conc_o$  = initial concentration - experimental

$conc_o'$  = initial concentration - control

$conc_t$  = concentration at time  $t$  - experimental

$conc_t'$  = concentration at time  $t$  - control

### Dreissena Filtration Rate

Experiment	24 Hours	48 Hours	72 Hours
1	8.2 mls/hr	7.2	*
2	1.8	3.2	11.8
3	25.2	18.0	16.4

All Dreissena filtration rates were multiplied by 2 in accordance with Morton's (1971) research on the filtration rate of Dreissena. Morton found that Dreissena filtered discontinuously. Over a 24 hour period, they filtered only 12 hours, therefore Morton adjusted his filtration rates accordingly.

\* The first experiment was done for 48 hours, not 72 hours.



Daphnia Filtration Rate

Experiment	24 Hours	48 Hours	72 Hours
1	0.56 mls/hr	0.20	*
2	0.38	0.20	0.20
3	0.46	0.43	0.30

\* The first experiment was done for 48 hours, not 72 hours.