

**FACTORS CONTRIBUTING TO DRY WEIGHT DIFFERENCES AMONG  
HERBIVOROUS ZOOPLANKTON IN TWO SOFTWATER LAKES**

**by**

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## ABSTRACT

The dry weight of zooplankton is an important parameter conventionally used to estimate secondary production in aquatic ecosystems. Estimates of zooplankton weight vary considerably across studies. This study examines various factors that contribute to differences in the individual dry weight of freshwater herbivorous zooplankton. In the first chapter, I quantified and compared the individual length and weight changes of Daphnia catawba and Diaptomus minutus resulting from preservation in either 4% sugar-formalin, 70% ethanol solution or freezing over dry ice. The results indicate that the dry weight of both animals was significantly altered by chemical preservatives. The length of Diaptomus was also significantly reduced due to preservation.

Site-specific differences in lakes, such as available food and the presence of predators, introduce another potential source of variation in herbivore dry weight. In Chapter 2, the food available to several herbivorous zooplankton in two softwater lakes was estimated using various methods. An index of "edible" phytoplankton biomass based on stomach content analyses was developed and compared to the traditional techniques used to estimate available food. The results indicate that the available was food different for

each herbivore and that estimates of food available based on stomach content analyses were not significantly related to the traditional techniques used to estimate available food.

In Chapter 3, I evaluate the relative impacts of "top-down" (predation) versus "bottom-up" (food) effects on the dry weight of several herbivores in two softwater lakes with contrasting food-web structures. The length-specific dry weights of Daphnia catawba, Diaptomus minutus and Holopedium gibberum varied seasonally and these changes were tax-specific and unique to each lake. Herbivore weights were regressed against length, available food, clutch size, population density and temperature to determine if "bottom-up" effects could explain between-lake differences in herbivore weight. Length and population density were the prominent predictor variables in the resulting regression models for the herbivores in these lakes. Predator effects were determined by comparing if the between-lake differences in herbivore weight were consistent with the presence or absence of planktivores. Holopedium dry weight was lower in the presence of planktivores, while Diaptomus dry-weight differences exhibited no consistent trend with the presence or absence of planktivores.

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## GENERAL INTRODUCTION

The dry weight of zooplankton is a meaningful parameter that is often used to estimate community biomass and secondary production in aquatic communities (Giguere et al. 1989). Although dry weight is highly desirable, it is infrequently measured directly because of the labour-intensive processing involved and expensive equipment required. Instead, body length is often measured and is then used to estimate dry weight from length-weight relationships previously developed in other studies (Bottrell et al. 1976). This practice, however, does not consider differences in length-specific dry weight of zooplankton which is known to vary significantly across studies.

Seldom is the source of this variation identified or considered when cross-study comparisons are made.

One of the most obvious sources of error is associated with using different chemical preservatives and ignoring their differential shrinkage or expansion effects on zooplankton dry weight (see review by Giguere et al. 1989). Another potential set of variations may be associated with site-specific differences in the lakes, such as food availability and the presence of predators. The effect of food availability has been referred to as "bottom-up" effects (McQueen et al. 1986) while those attributed to predators have been referred to as "top-down" effects, and both can influence the zooplankton community structure as well as biomass (see review by Vanni 1987).

The goals of this study are to first research the methodological problems encountered in the measurement of zooplankton dry weight associated with preservation, and to develop empirical relationships that would yield accurate estimates of dry weight by knowing such information as body length, type of preservative used, and the duration of preservation. A second goal is to evaluate the relative impacts of "top-down" versus "bottom-up" effects on the dry-weight of several common herbivorous taxa, including Daphnia catawba, Holopedium gibberum and Diaptomus minutus.

There is some evidence that predation by planktivores may affect zooplankton biomass (see review by McQueen et al. 1989). The lower biomass can arise simply as a result of a selection for smaller-sized individuals through size-selective predation, or as a result of individuals weighing less from being exposed to predation. Arts and Sprules (1988) found that Holopedium subjected to high fish predation had lower overall lipid reserves which may translate into a lower weight. Zooplankton subjected to intense predation may allocate more energy in to defence mechanisms (eg. a larger gelatinous sheath for Holopedium) or these animals may be ingesting less food if they have to remain still to avoid predation. If predation forces do cause animals of a certain length to weigh less than those not subjected to predation, then I would expect the length-specific weight of herbivorous zooplankton to be lower in a lake where planktivores are abundant than in one where they are scarce.

By comparison, considerably less is known or reported, about possible bottom-up forces. Because the quality and quantity of food available to herbivores tend to vary seasonally (eg. Geller and Muller 1985; Kerfoot et al. 1988; Lynch 1989; McQueen et al. 1989; Gaedke 1992; Sterner et al. 1993), researchers in the past have suggested that changes in food quality and availability may account for variations in weight at length (Schindler 1971; Goulden et al. 1982; Williamson and Butler 1987; Lynch 1989; Sterner et al. 1993). If bottom-up forces (ie. food) are responsible for differences in weight of a given herbivore length in any two lakes, I would expect animals to weigh more in the lake with more available food (ie. higher biomass of algae). Since bottom-up effects may also be reflected in differences in clutch size and animal density (Maly 1973; Checkley 1980; Elmore 1983; Williamson and Butler 1987; Chow-Fraser and Maly 1991), I would also expect to see zooplankton weight correlated with animal density and clutch size.

This study originated as part of a collaborative, multidisciplinary study designed to assess the relative impacts of inter-lake differences in food-web structure on the partitioning within and exchange of mercury among compartments in Mouse and Ranger Lakes located near the town of Dorset, Ontario. These two lakes were chosen because they have very similar edaphic characteristics and morphometries, but contrasting food-web structures (see Table 1). Ranger Lake (45 09'N, 78 51'W) and Mouse Lake (45 11'N, 78 51' W) are both small, single-basin, oligotrophic lakes located on granite and

Table 1

Summary of some of the physical and chemical characteristics of Ranger and Mouse Lakes in 1992. All values are seasonal means and standard errors in parentheses (n = 9 to 11 sampling dates)

<u>Physical Characteristics:</u>	<u>Ranger L.</u>	<u>Mouse L.</u>
Lake Surface Area (ha)	11.25	8.99
Mean Depth (m)	6.25	4.88
Maximum Depth (m)	13.00	9.00
Volume ( $10^5$ m <sup>3</sup> )	6.32	4.39
<u>Chemical Characteristics:</u>	<u>Ranger L.</u>	<u>Mouse L.</u>
pH (mean epilimnetic)	6.06 (0.068)	5.65 (0.052)
ph (mean metalimnetic)	5.65 (0.035)	5.47 (0.055)
HCO <sub>3</sub> <sup>-</sup> (mean epilimnetic)	0.16 (0.011)	0.10 (0.024)
HCO <sub>2</sub> <sup>-</sup> (mean metalimnetic)	0.56 (0.094)	0.40 (0.120)
TP (mean epilimnetic; µg/L)	5.91 (0.377)	7.80 (0.580)
TP (mean metalimnetic; µg/L)	15.92 (1.697)	13.79 (2.430)

---

Note: All data pertaining to physical and chemical information were taken from Ramcharan et al. (in press)



sand basins at the southern margin of the Precambrian Shield (Ramcharan et al. 1993 unpub.). Ranger Lake is deeper than Mouse Lake in both mean depth and maximum depth and has a larger surface area. Some of the physical and chemical parameters of these lakes have been summarized in Table 1.

Mouse Lake has a mainly planktivorous fish community consisting of small populations of common white sucker, creek chub, long-nose sucker, golden shiner, pumpkinseed and a large population of yellow perch. Ranger Lake, in contrast, contains few yellow perch and pumpkinseed and quite large populations of largemouth bass, smallmouth bass and common white sucker. Both lakes contain populations of the crustacean zooplankter Diaptomus minutus and Holopedium gibberum. Ranger Lake also contains a large population of Daphnia catawba which is a rare component in Mouse Lake.

The contrasting fish food-web structures found in these two lakes provided an excellent opportunity to compare and evaluate the impacts of lake-specific properties on the dry weights of herbivorous zooplankton. For this study I chose to compare the dry-weight differences of Diaptomus minutus and Holopedium gibberum between the two lakes and to compare Holopedium and Daphnia catawba in Ranger Lake since Daphnia accounts for most of the cladoceran biomass in this lake (Ramcharan et al. 1993, unpub.). These herbivores are also commonly found in the Precambrian Shield lakes of central Ontario and represent a broad range of zooplankton size and body shape.

To test the top-down hypothesis, I predict that for a given length, the weight of these herbivores would be lower in Mouse Lake than in Ranger Lake because Mouse Lake has a very large population of planktivorous predators. To test the bottom-up hypothesis, I predict that for a given length, the weight of herbivores would be higher in the lake with more available food, regardless of the predator structure. Because information available from 1991 indicated that the chlorophyll a concentrations were almost identical for the two lakes (Ramcharan et al. 1993 unpub.), it is more difficult to judge in advance which of these two lakes should have more food available to zooplankton, since not all algae present in the lake are necessarily eaten (e.g. Chow-Fraser and Maly 1992).

In Chapter 1, I examine the current methodological problems associated with measuring zooplankton dry weight. A review of the literature shows that one of the largest errors incurred in cross-study comparisons is the unknown or unquantified effects of preservatives in different studies (Giguere et al. 1989). Here, I compare the effect of common preservatives on the length and dry weight measurements of two of the herbivorous species in the study lakes, Daphnia catawba and Diaptomus minutus. The methods of preservation include freezing with dry ice, and chemical preservation with 4% sugar-formalin and 70% ethanol. The goal of Chapter 1 is to provide a means to account for the differential effects of these common methods of preservation so that unpreserved dry weight may be calculated from measurements of preserved specimens.

In Chapter 2, I explore the methods used to measure available food for herbivorous zooplankton. In nature, the phytoplankton community undergoes changes both qualitatively and quantitatively throughout the season. If all algae are assumed to be available and ingested at the same rate, then a suitable index of food may be an estimate of the total phytoplankton biomass measured either as wet weight of algal cells or the amount of chl a in the cells. If, however, different herbivore taxa prefer different diet items (ie. not all algae are ingested, or ingested at the same rate), then the "food" that is "edible" may differ for each animal. In Chapter 2, I use stomach content analyses to develop an index of "edible" phytoplankton that is then used to calculate the amount of food available to the animals of interest. This quantity which I operationally define as "edible" algae is then compared to other more conventional measures of available food such as the biomass of all phytoplankton <30  $\mu\text{m}$ , (eg. Chow-Fraser and Knoechel 1985), total phytoplankton biomass (McCauley and Kalff 1981; Kerfoot et al. 1988), and chlorophyll a (McQueen et al. 1989; Elser and Goldman 1991).

Chapter 3 evaluates the relative impacts of lake-specific characteristics on herbivore weight in Mouse and Ranger Lakes. First, length-weight relationships are developed for each of the herbivores throughout the ice-free season to determine the changes in weight at length between lakes. Since animals used for these measurements had to be preserved when collected, the results of Chapter 1 are used to correct for the effects of preservation. To determine bottom-up

effects, herbivore weights are regressed against various direct measures of food (as discussed in Chapter 2), as well as other indirect indicators of resource competition such as clutch size and population density. To determine fish predator effects, herbivore weights will be compared between lakes to determine if differences are consistent with the presence or absence of planktivores.

This study will contribute information that is pertinent not only to the collaborators of the biomanipulation project on Mouse and Ranger Lakes, but to limnological researchers in general. First, establishing and comparing the relevant effects of common preservatives on the length and weight of zooplankton should permit investigators to correct for any differences in length and weight such that a standardized unpreserved weight estimate can be generated regardless of the preservative used. These correction factors should improve both the accuracy and comparability of these basic parameters and facilitate between-study comparisons. Second, exploring the use of various estimates of "edible" food should reveal which of these is most appropriate for future studies. Third, evaluating the roles of top-down and bottom-up forces on the length-specific dry weight of herbivorous zooplankton may provide an indication of the relative impacts of these forces on secondary production estimates. Finally, by considering variables other than length, such as food, density and clutch size, I will develop models that will more accurately predict herbivore dry weight for these two lakes that are undergoing biomanipulation.

## CHAPTER 1

### Differential effects of chemical preservatives and freezing on the length and weight of Diaptomus and Daphnia

#### INTRODUCTION

The dry weight and length of individual zooplankters are basic information collected by limnologists on a routine basis (Bird and Prairie 1985). Because it is rarely practical to take such measurements from unpreserved zooplankton, ecologists generally have to take measurements from preserved samples. Investigators seldom correct for any effect of preservatives on either the length or the dry weight of zooplankton, even though several studies have shown that zooplankton lose a significant amount of their dry weight in various preservatives (see review by Giguere et al. 1989), and the possible effects of preservatives on zooplankton length are not yet known. Neglecting to correct for potential effects may produce substantial errors when cross-study comparisons are made in cases where different preservatives have been used, or when length-weight regressions corresponding to preserved animals are subsequently used to estimate the dry weight of unpreserved animals.

Establishing and comparing the relevant effects of these preservatives on the length and weight of zooplankton, and evaluating the appropriateness of using a standard wet-dry conversion factor should permit investigators to correct for any differences in length and weight such that a standardized unpreserved weight estimate can be generated regardless of the preservative used. These correction factors should improve both the accuracy and comparability of these basic parameters and facilitate between-study comparisons.

The aim of this study is to compare the effect of common preservatives on the length and dry weight measurement of two herbivorous zooplankton, Daphnia catawba and Diaptomus minutus. These animals which occur commonly in oligotrophic lakes of south central Ontario, have disparate body shapes and dry weights. As well, they represent the extremes with respect to calcium content in their carapace (Yan et al. 1989), a variable that may be important if calcium is related to the degree of shrinkage (Steedman 1976). I examined three methods of preservation: freezing, formalin and ethanol. In addition to quantifying the effects of preservatives on dry weights, I also determined the relationship between the dry weight and wet weight of individuals so that wet weights can be predicted empirically from dry weight data.

## METHODS

### Description of the study lake and sampling methods

Ranger lake is an oligotrophic softwater lake located in south central Ontario near the town of Dorset. It has a surface area of approximately 12 ha, a maximum depth of 13 m and mean Secchi depth transparency of 2.7 m. The physical and chemical parameters have been summarized in Table 1.

Zooplankton samples were collected by vertical haul (80  $\mu\text{m}$  mesh square Wisconsin net) at an established pelagic station (3 m). Animals were immediately filtered through modified Petri Plates (equipped with mesh), rinsed with filtered lakewater and frozen on dry ice. Within 2 h, they were transferred into Ziploc freezer bags and kept frozen for up to 30 d. These were subsequently used in experiments to determine the effect on zooplankton length of two chemical preservatives, 4% sugar-formalin (Prepas 1978) and 70% ethanol. Other animals were collected and placed directly in chemical preservatives. In order to conduct experiments with unpreserved animals, I collected animals from Ranger L. and transported them back to the laboratory at McMaster University and maintained them in aquaria on a culture of Scenedesmus and Ankistrodesmus. Animals were fed daily and maintained for approximately one month prior to being used in the experiments.

### Effects of preservatives on length over time

Animals frozen in the field (n=20 for each Daphnia and Diaptomus) were thawed, rinsed with distilled water and transferred onto depression slides where their individual lengths were measured to the nearest 0.001 mm with an Optimas Image Analysis System (Bioscan Inc., Edmonds, Washington). To avoid the effect of variable clutch size, I used non-ovigerous females in all my experiments. Daphnia were measured from the top of the head to the base of the tail spine (Fig. 1.1). Diaptomus were measured from the top of the head to the base of the caudal rami (prosome + urosome; Fig. 1.2) to avoid errors which may result when the angle of the caudal rami relative to the long axis of the body is changed from measurement to measurement (Culver et al. 1985). Immediately following the initial length measurement, animals were placed into individual 1.5 mL centrifuge capsules with sealing lids and filled to 1.0 mL with one of the chemical preservatives. The length of each animal was measured again after 1,7,14 and 40 d; animals were returned to their respective capsules after each measurement, and these were topped up with the appropriate preservative. To account for any effect of initial freezing on zooplankton length, cultured animals were measured unpreserved and then frozen for 8 d or 30 d, after which length measurements were repeated.

I determined the accuracy of all length measurements for this study on each measurement day by randomly measuring a 10% subsample of animals three times. The repeated measures were always less than



Figure 1.1 Length measurement of Daphnia catawba

Figure 1.1. Daphnia

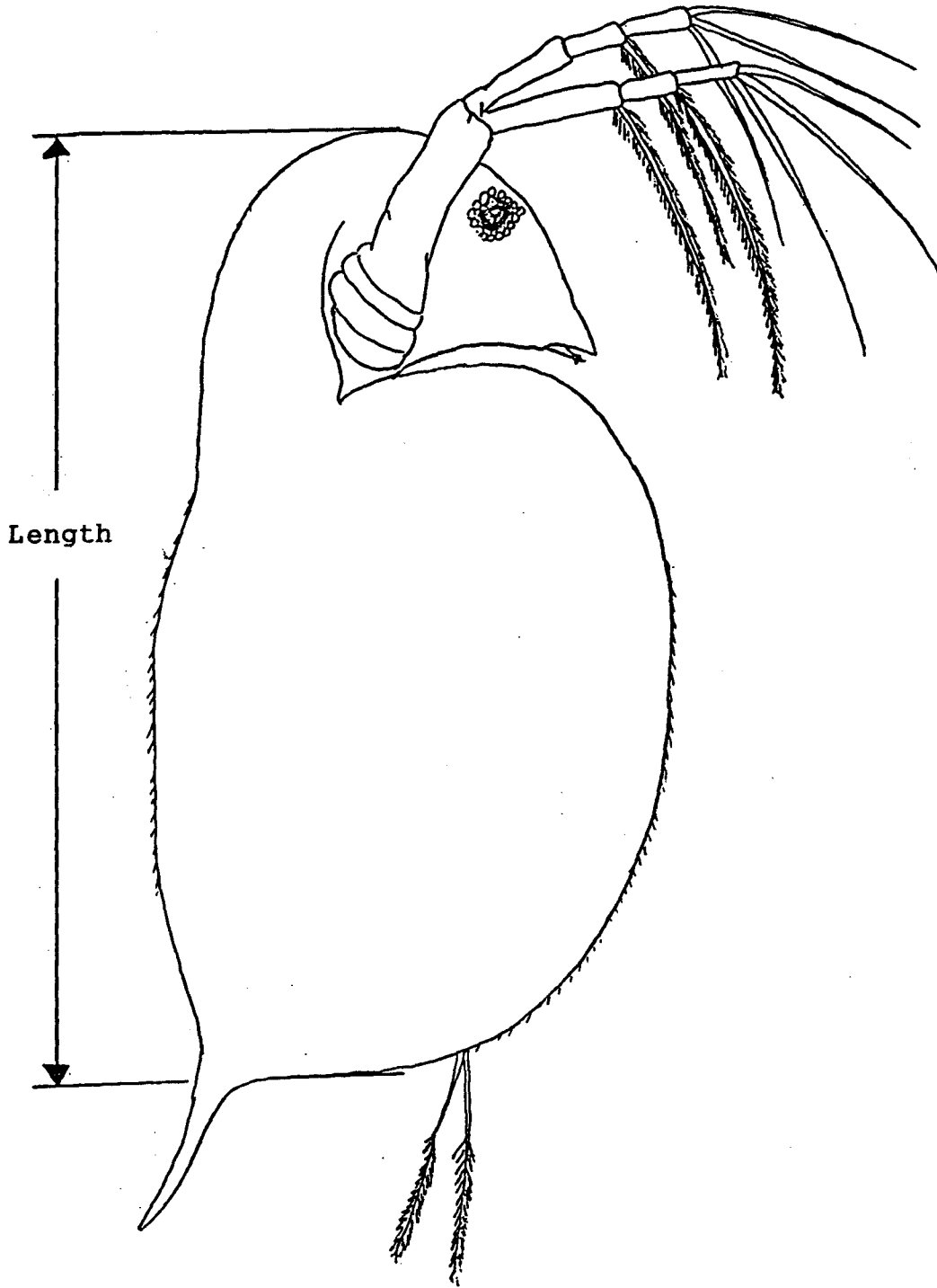
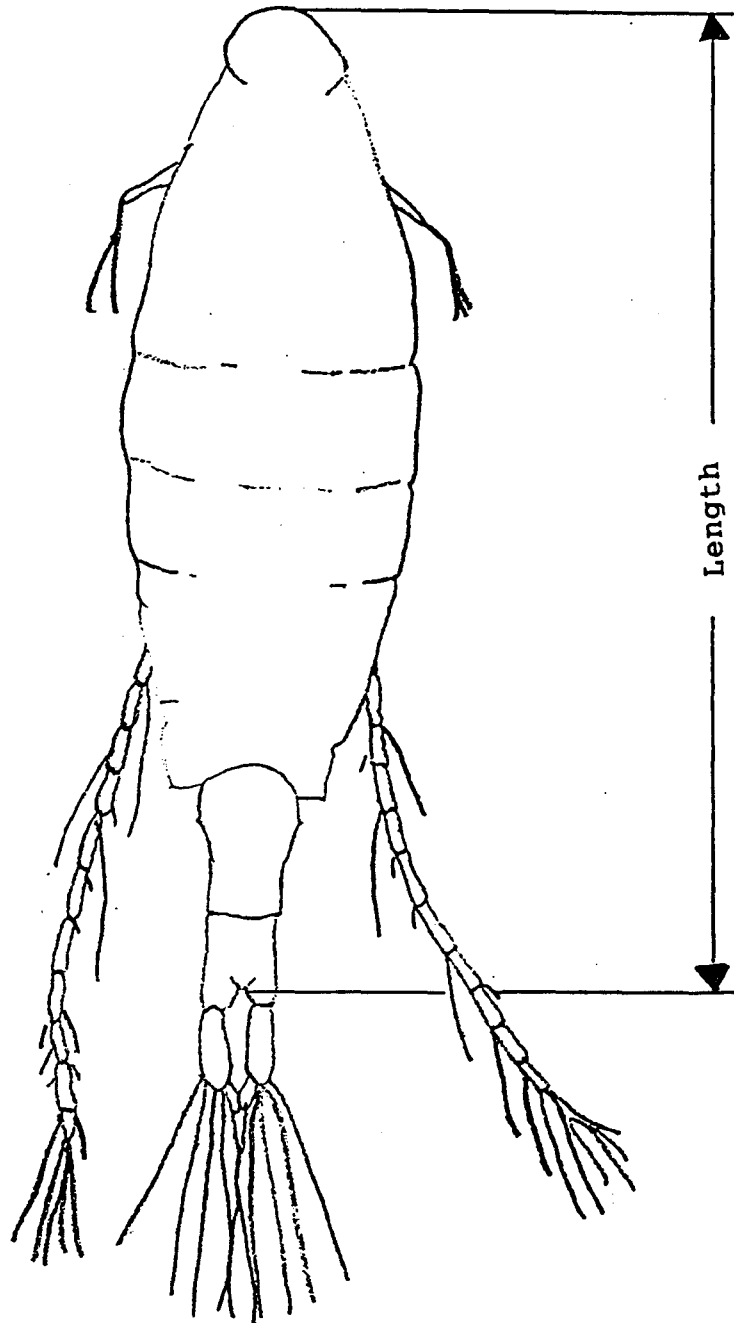


Figure 1.2 Length measurement of Diaptomus minutus

Figure 1.2 Diaptomus



0.5% of the total body length. As well, the length measurements were well within the practical measurement intervals of 5% of the shortest body length recommended by Bird and Prairie (1983).

### **Effects of preservatives on dry weight over time**

To determine the effects of chemical preservatives on dry weight over time, field-caught animals were placed in the two chemical preservatives for 9 or 21 days. To eliminate any confounding effects due to season, I conducted all of the experiments with animals collected from a single visit to Ranger L. At the end of the chosen preservation period, random subsamples were placed in distilled water for 20 min. to rinse off any excess preservative. Daphnia were selected individually (n=20) and included a range of body lengths so as not to limit the applicability of my results. Diaptomus were placed in groups of five similar-sized animals (within 0.02 mm; n=20 groups). Individuals or groups of animals were transferred to small pre-weighed 7 mm boats that had been punched from aluminum foil. The weighing boats were placed in a partially closed petri plate, oven-dried at 60°C for 24 h, cooled and weighed to the nearest 0.5  $\mu$ g with a Cahn 25 Electrobalance.

### **Comparison of preserved and unpreserved dry weight**

A comparison of the dry weight of preserved and unpreserved animals was performed with animals that had been collected on the same

day from a culture maintained for approximately 30 days in a laboratory aquarium. I followed the field protocol to preserve animals with the two chemical preservatives and dry-ice. To correct for any possible effects of duration of preservation, I preserved all animals for 14 d since preliminary investigations indicated that changes in the length of zooplankton and the weight of Diaptomus stabilized within the first two weeks of preservation. A parallel group of animals was sorted, measured (n=20) and dried immediately. This treatment provided information on the dry weight of unpreserved animals.

#### **Relationship between wet and dry weight of Daphnia**

Previously frozen animals were thawed and rinsed with distilled water. Individual animals were randomly selected and picked up with fine forceps. Each animal was blotted twice on each side of its carapace with Kimwipe, then transferred with dry forceps onto small pieces of aluminum foil which were pinched closed on the edges to form a half circle with the animal inside. The wet weights were determined with the Cahn 25 Electrobalance. The wet weight was defined as that value which was maintained for 5 sec. Following this, animals were dried for 24 h at 60°C and weighed again. I assumed that the initial rapid drop in wet weight was indicative of any external water that was present on the animal or weighing pan.

### **Statistical Analyses**

The statistical program SAS Jmp (Cary, N. Carolina) was used to test the differences in length over time and weight over time (ANOVA, repeated measures). This program was also employed to determine the differences in mean dry weights of Diaptomus in the various preservatives. Analysis of covariance (Zar 1984) was used to determine the homogeneity of the slopes and differences between the elevations for the regression equations developed for Daphnia in the various preservatives and weight loss over time.

## RESULTS AND DISCUSSION

### Effect of preservative on length over time

The length of Daphnia did not change significantly over time in either of the chemical preservatives for the duration of the 40 d (ANOVA Repeated Measures;  $P < 0.05$ ; Fig 1.3a and b). By comparison, the length of Diaptomus preserved in both ethanol (Fig 1.4a) and formalin (Fig 1.4b) decreased significantly over the first 7 d of observation (Tukey-Kramer HSD test;  $P < 0.05$ ), with an average decrease of 8 and 6%, respectively. Since none of the measurements taken after 40 d was statistically different from those taken on the 7th day, there was probably no further shrinkage in the size of Diaptomus after the first 7 days of preservation.

I conducted tests to determine the effect of freezing on length measurements because animals in the above experiments had been previously frozen for up to 30 d. For both Daphnia and Diaptomus, there were no significant differences between length measurements ( $n=15$ ) for animals that had been frozen for 8 or 30 d (t-tests,  $P > 0.20$  in both cases), which suggests that the duration of freezing was not an important factor. Although I could not determine if freezing prior to preserving had a confounding effect, an independent study in which animals from Ranger L. were preserved without any freezing confirmed the extent of shrinkage that I observed within the first 7 days of experimentation (D. McQueen, York University, Biology Department,



Figure 1.3      Change in length (mm;  $\pm$  1 S.D.) of  
Daphnia catawba preserved in a) 70%  
ethanol and b) 4% formalin

Figure 1.3a

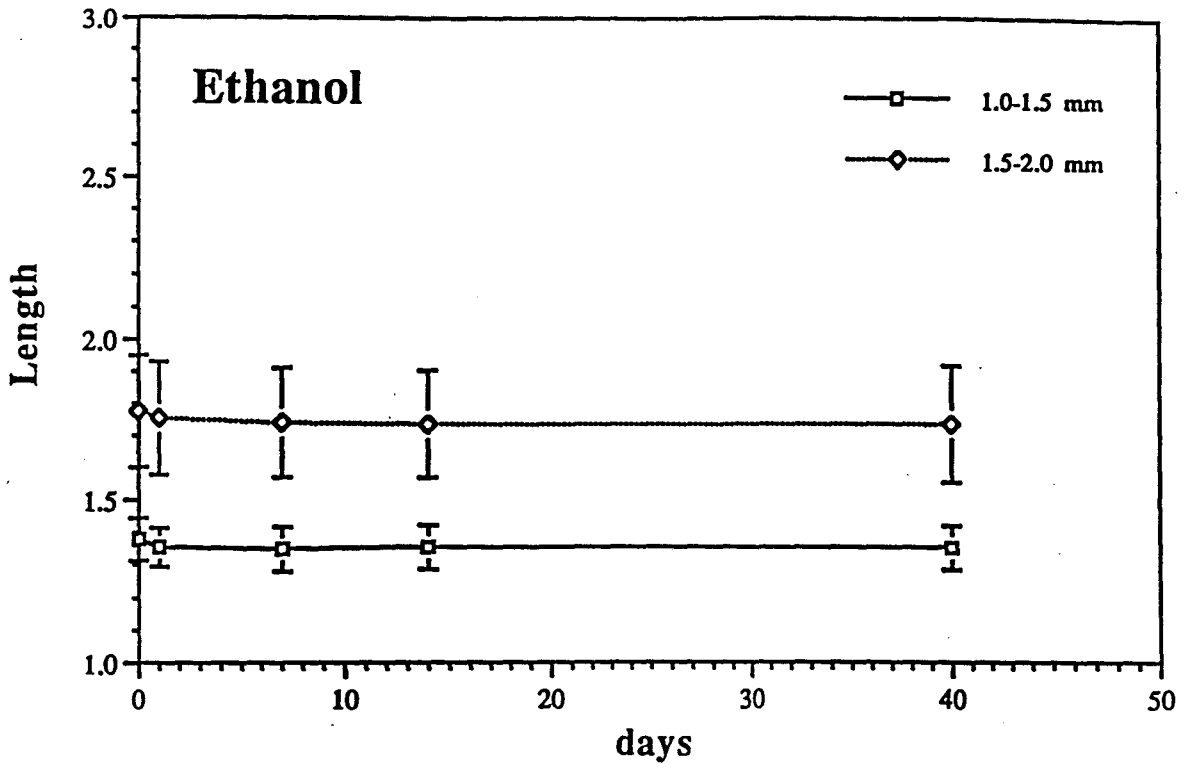


Figure 1.3b

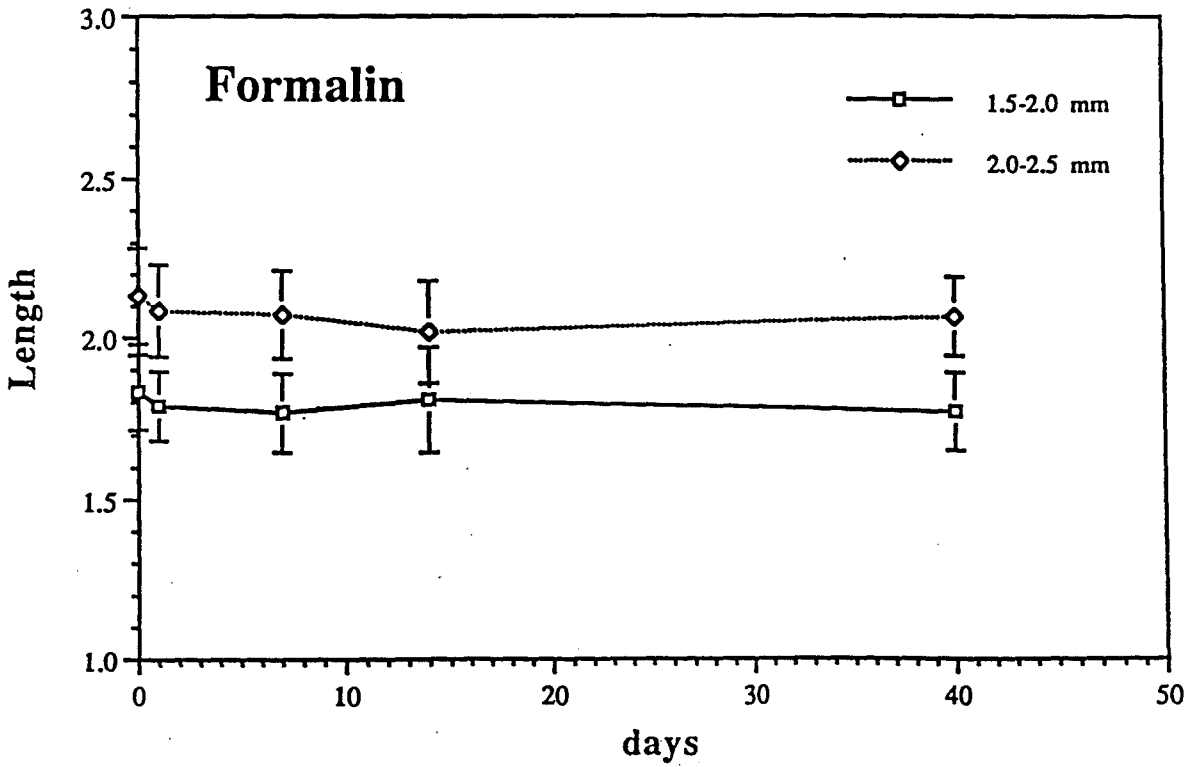


Figure 1.4      Change in length (mm;  $\pm$  1 S.D.) of  
Diaptmous minutus preserved in a) 70%  
ethanol and b) 4% formalin

Figure 1.4a

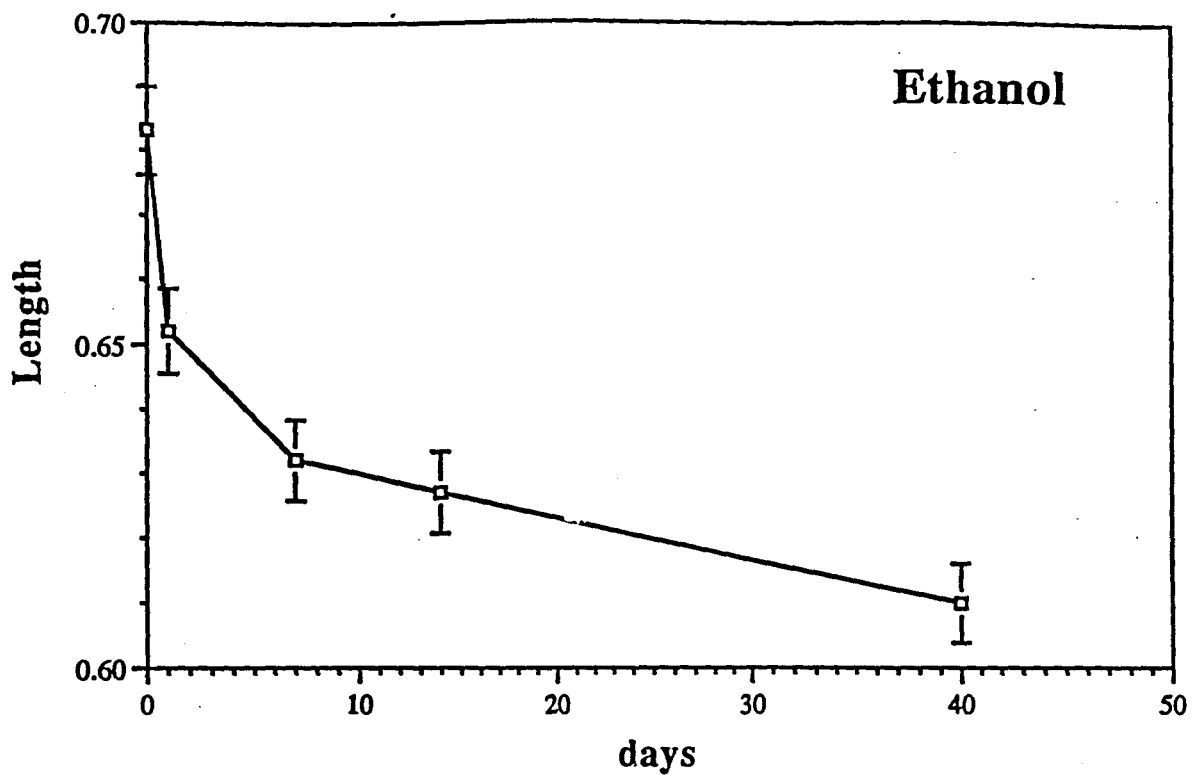
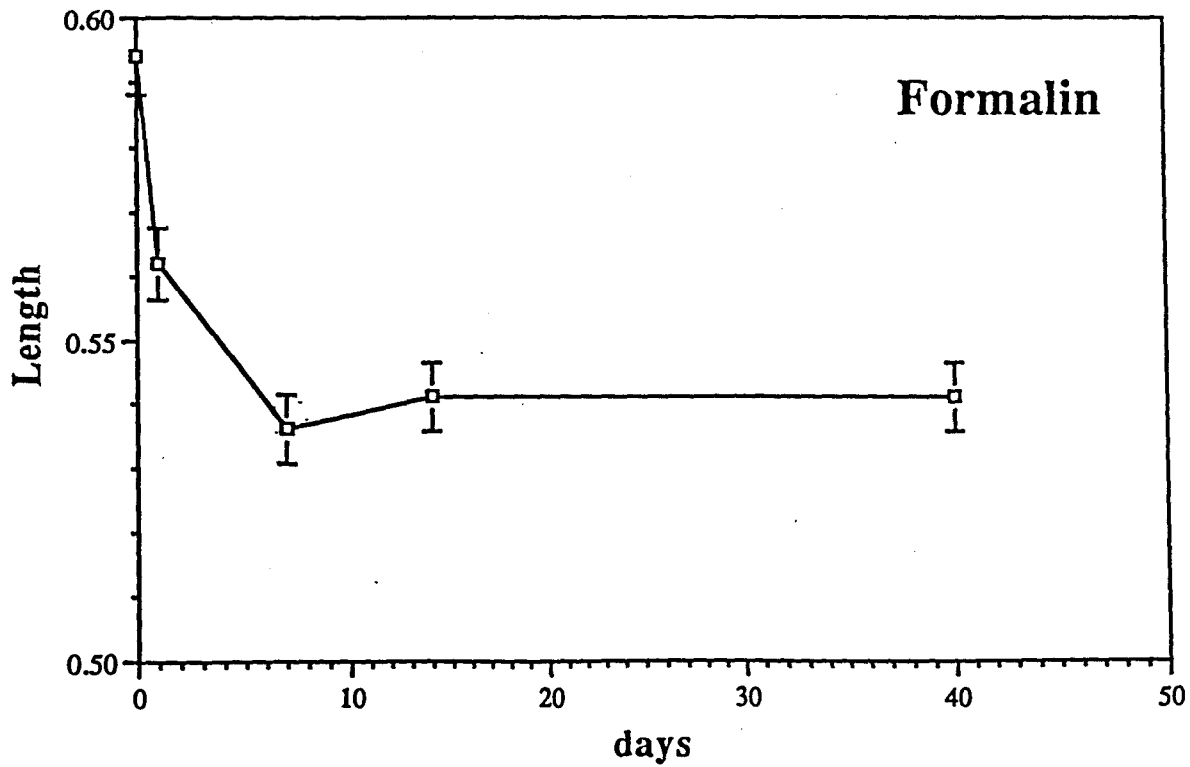


Figure 1.4b



unpub. data). Therefore, I concluded that freezing prior to the addition of chemical preservatives did not confound the effects of preservatives on length measurements. Further research using parallel experiments with animals frozen prior to preservation and animals preserved without freezing would provide a means of verifying this conclusion.

### **Effect of preservative on weight over time**

I determined the effect of 70% ethanol and 4% sugar-formalin on the dry weight of Daphnia individuals by comparing animals that had been preserved for 9 and 21 days (Fig. 1.5a and b). Because of the well-documented allometric relationship between weight and length for Daphnia (Downing and Rigler 1984, Chapter 7), it is appropriate to compare the slopes and intercepts of the length-weight regression lines corresponding to the two preservation durations for each of the chemical preservatives. Analysis of covariance indicated that slopes of 9- and 21-d data were homogeneous for both preservatives ( $P > 0.05$ ); however, their corresponding elevations were significantly different ( $P < 0.02$ ). For a given size of Daphnia, the 21-d preservation period resulted in statistically lower dry weight compared with the 9-d preservation for both chemicals, indicating that the length of time in preservative has a significant effect on dry weight measurements. Further tests should be performed to determine if and when the effect of either preservative will stabilize over time.

Figure 1.5

Effect of preservation on the dry weight ( $\mu\text{g}$ ) of Daphnia catawba in a) 70% ethanol and b) 4% formalin over time. Lines are the least-squares regression equations.

Figure 1.5a

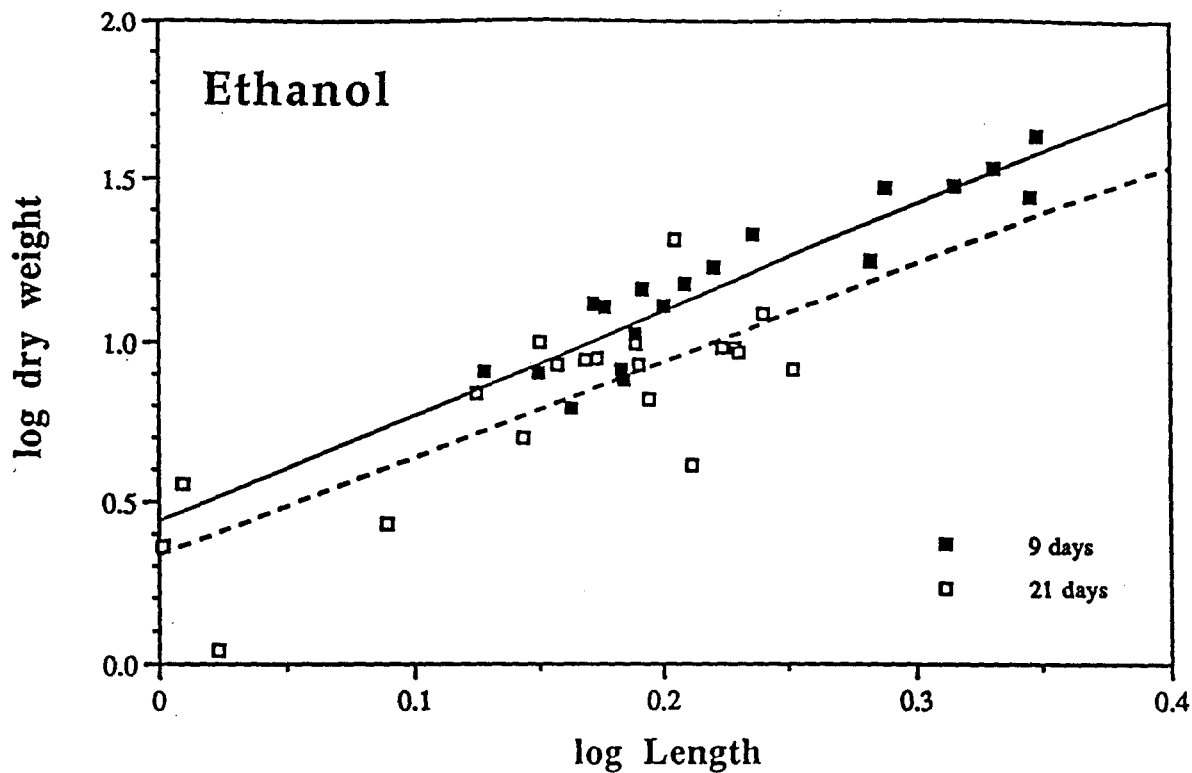


Figure 1.5b

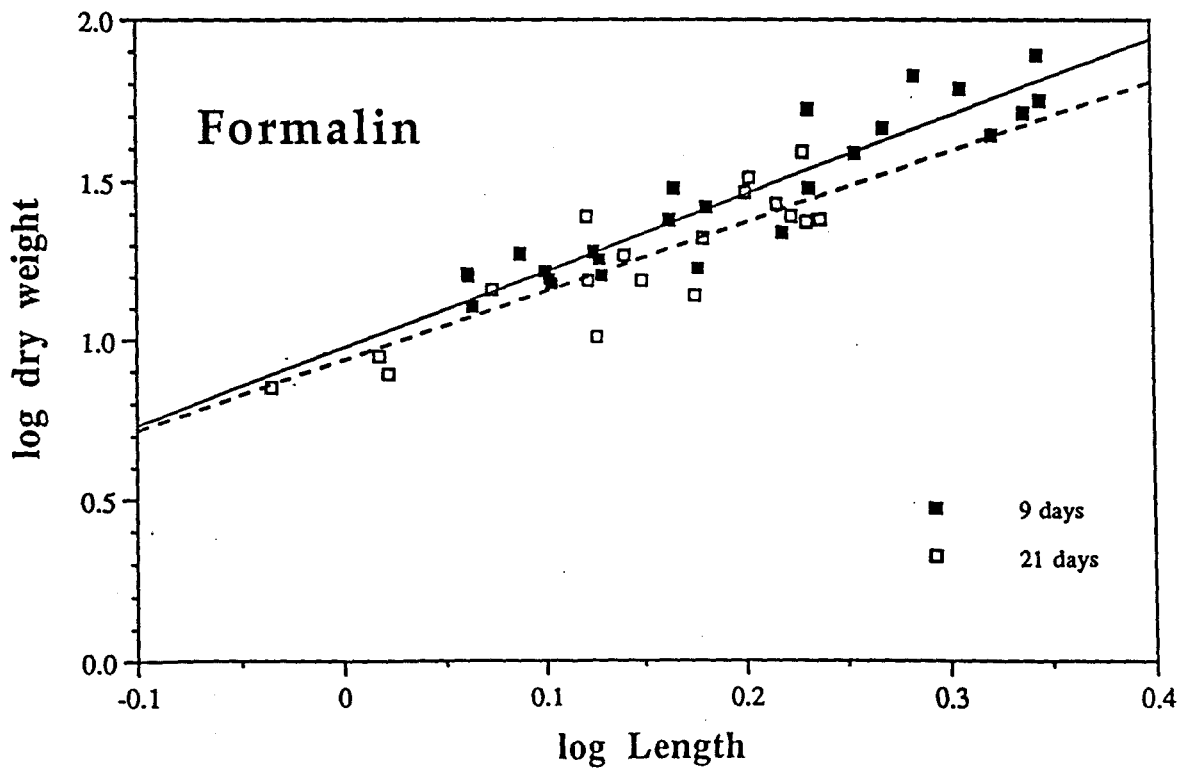
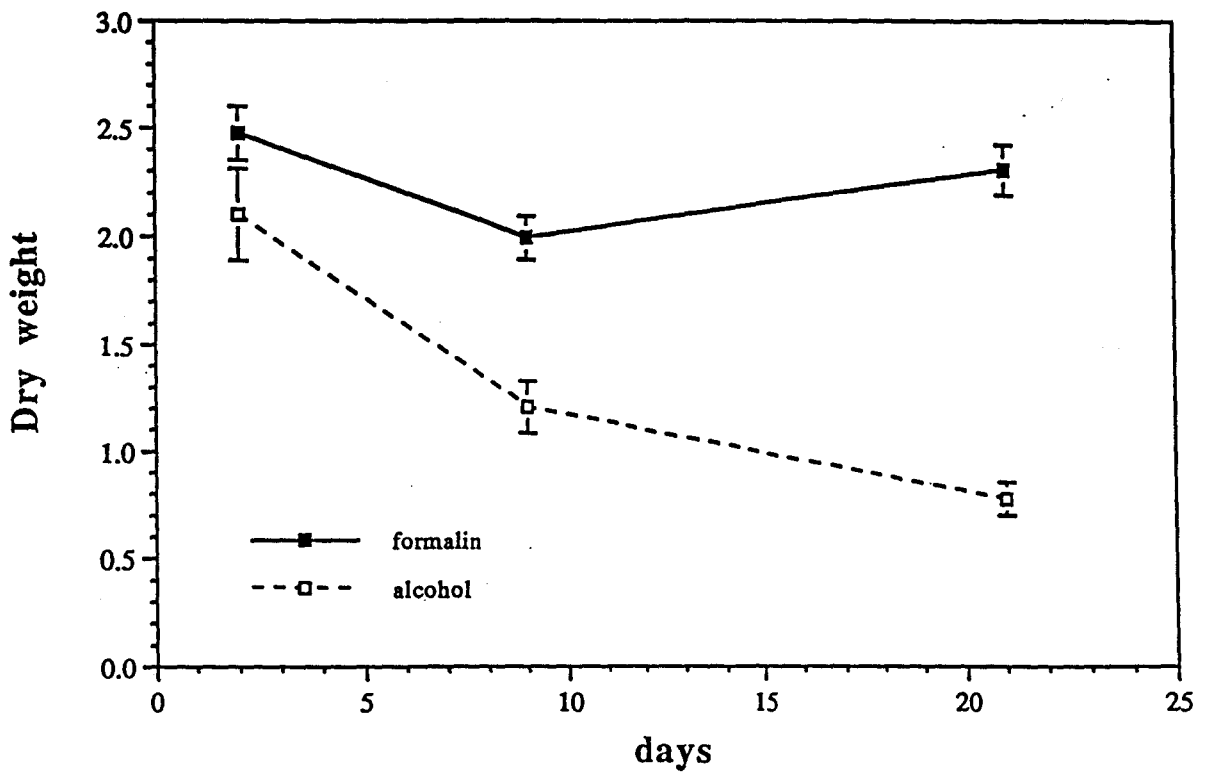


Figure 1.6

Dry weight ( $\mu\text{g}$ ;  $\pm 1$  S.D.) of Diaptomus minutus preserved for different durations in ethanol and formalin



Figure 1.6



I determined the effect of preservation duration on the dry weight of Diaptomus by comparing measurements taken after 2, 9 and 21 d of preservation in ethanol and formalin (Fig. 1.6). For both chemicals, there were significant differences in dry weight among the three preservation durations (2-way ANOVA,  $P < 0.05$ ). Since there was a significant drop in dry weight of Diaptomus after 2 d of preservation, but not beyond 9 d, Diaptomus probably reached a stabilized weight within the first two weeks of preservation in both chemical preservatives.

#### **Comparison of dry weights of preserved and unpreserved animals**

I determined the length-dry weight relationship of unpreserved Daphnia and those preserved in the two chemicals and in dry-ice (Table 1.1; Fig. 1.7). Since the slopes of the respective length-weight regressions were statistically homogeneous (ANCOVA;  $P > 0.50$ ), I compared the elevations and found significant differences among the four treatments ( $P < 0.0005$ ). Subsequent pairwise comparisons between elevations indicated that for a given length interval, the dry weights of preserved animals were uniformly lower than those of unpreserved animals ( $P < 0.05$ ). These results also confirmed preliminary data which suggested that the dry weight of given sizes of animals preserved in 70% ethanol were significantly lower than those preserved in 4% formalin ( $P < 0.001$ ). Although the effects of freezing and preservation in formalin were similar ( $P > 0.50$ ), there was a substantial residual variation around the best fit line for animals

TABLE 1.1

Summary of regression Equations for Daphnia catawba (preserved for 14 days)

Preservative	Equation	n	r <sup>2</sup>	S.E.	P
No preservative	Log W=0.913+2.285 LogL	26	0.83	0.10	<.0001
4% formalin	Log W=0.581+3.023 LogL	25	0.59	0.16	<.0001
frozen	Log W=0.804+2.260 LogL	25	0.54	0.17	<.0001
70% ethanol	Log W=0.776+2.576 LogL	30	0.82	0.12	<.0001

frozen ( $r^2=0.543$ ), indicating that freezing may have differentially affected the dry weight.

To illustrate the extent to which the dry weight of preserved Daphnia may underestimate the actual unpreserved dry weight, the dry weights of Daphnia preserved by the three methods were compared to unpreserved dry weights for a range of Daphnia lengths (Table 1.2). The range of weight loss for ethanol-preserved animals and frozen animals was quite large, ranging from 5% to 70% dry weight loss depending on the length of the animal and the preservative used. Formalin-preserved animals maintained a dry-weight loss of approximately 20-25% regardless of length.

I hypothesized that the drying time (24 h) used in this study may have been inadequate since formaldehyde precipitates proteins and blocks body pores (Dumont et al. 1975). To address this possibility, I repeated the experiment but increased the drying time to 48 and 72 h. Doubling and tripling the drying time resulted in an additional 10% and 20% weight loss for animals preserved in 4% sugar-formalin, but this weight loss could not account for the substantial dry weight difference for Daphnia preserved in the two chemical preservatives.

I also determined the relationship between the dry weight of unpreserved and preserved Diaptomus. There were no significant differences between the dry weight of unpreserved animals and those that were frozen on dry-ice, although both were significantly higher

TABLE 1.2

Dry Weight Measurements of Preserved *Daphnia catawba* Using Various Preservatives (values expressed as percent of unpreserved dry weight)

Preservative	Length (mm)				
	0.5	1.0	1.5	2.0	2.5
4% formalin	79.2	77.6	76.9	76.3	75.9
freezing	59.5	72.8	81.9	89.0	95.0
70% ethanol	27.9	46.5	62.7	77.5	91.3

than animals preserved in either chemical preservative (Tukey-Kramer HSD multiple comparison after ANOVA;  $P < 0.001$ ; Table 1.3). Unfortunately, these results contradict those obtained previously which show that ethanol-preserved animals weighed less than formalin-preserved ones (Fig. 1.6). The apparent inconsistency may be attributed to the fact that animals were collected from the lake at different times for the two series of experiments. The animals used in the second set of experiments had been maintained in a laboratory culture prior to the experiment which may also have contributed to the difference in length-weight comparisons. If the effect of preservatives on dry weight of Diaptomus is dependent on the storage products in the animals then it is necessary to take into account the time of year that the samples were collected because the weight of Diaptomus change through the ice-free season (Chapter 3). The samples analysed for this research were collected in June and July when Diaptomus weighed slightly less than later in the season (Chapter 3, Fig. 3.4a). Therefore, future studies must take into account the possible interactive effect of animal condition and time of the year with the type of preservative used.

#### **Relationship between wet weight and dry weight of Daphnia**

Few investigators have attempted to directly measure the wet weight of animals (Giguere et al. 1989). Instead, ecologists tend to estimate wet weight from dry-weight data by assuming that a single conversion factor can be applied over a range of different taxa.

TABLE 1.3

The Average Dry Weight of *Diaptomus minutus* (n=5, preserved for 14 days)

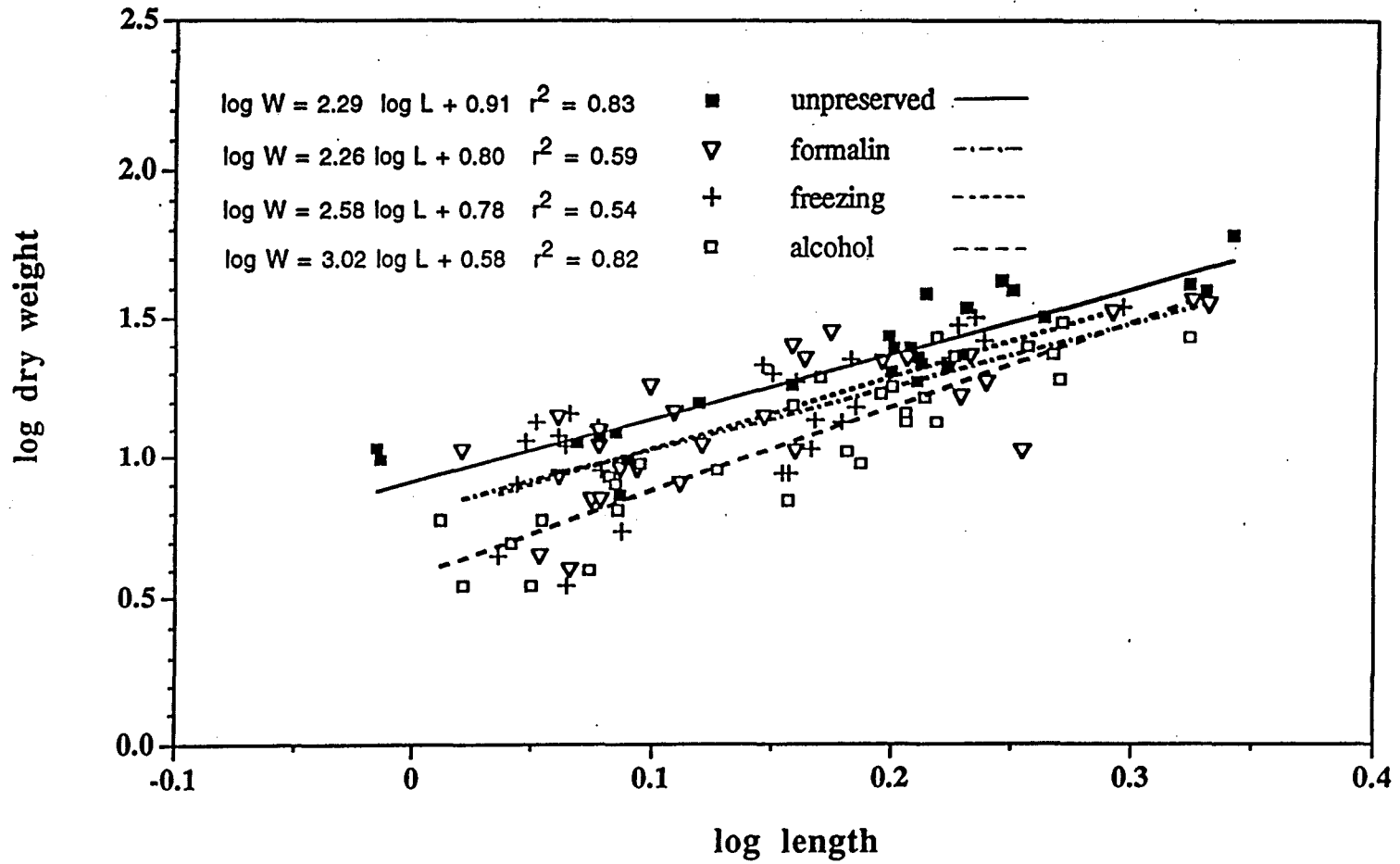
Preservative	n	Dry Weight ( $\mu\text{g}$ )	S.E.
No preservative	15	1.765	0.128
4% formalin	20	1.515	0.111
freezing	17	2.109	0.120
70% ethanol	19	1.463	0.114

Figure 1.7

Length-weight relationships for Daphnia  
catawba corresponding to different  
preservation treatments. All animals  
were preserved for 14 d. Lines are the  
least-squares regression equations.



Figure 1.7

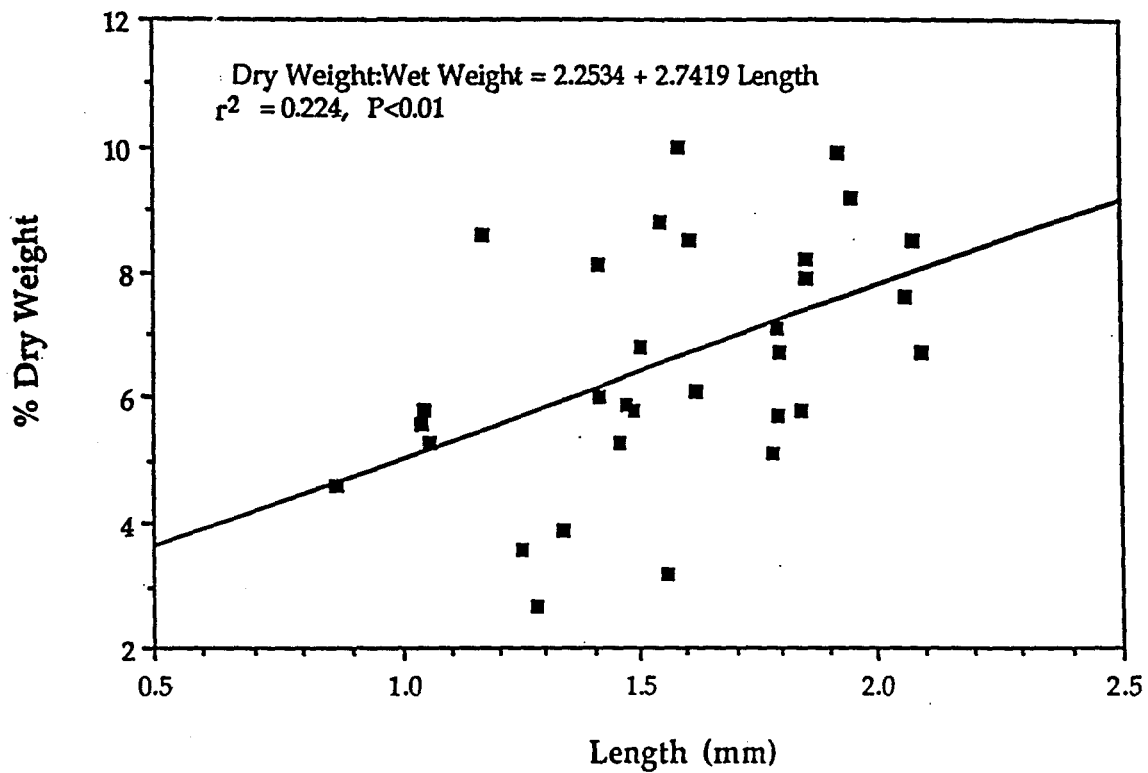


Despite reports that caution against this practice (Bottrell et al. 1976), there are too few direct comparisons of dry and wet weights for the assumption to be properly challenged.

My results suggest that for Daphnia catawba, a constant conversion factor should not be applied across the entire size range (Fig. 1.8). Although there is considerable scatter in the relationship, the percent dry weight of Daphnia increases significantly with size of animal ( $P < 0.01$ ). These results contrast with those of Bottrell et al. (1976) who suggested that the percent dry weight of taxa such as Bosmina, Heterocope and Leptodora decreased with body size. Since the proportion of dry weight varied from 0.02 to 0.10, the recommendation of Dumont et al. (1975) to apply a general dry to fresh-weight ratio of 0.1 may lead to considerable error. The possible taxa-specific and length-specific relationships indicate that investigators should use reported wet-weight-dry-weight conversions cautiously, and whenever practical, conduct wet-dry comparisons for each taxon in the study.

Figure 1.8      Percent dry weight of Daphnia catawba  
versus carapace length (mm). Line is  
the least-squares linear regression  
through data.

Figure 1.8



## GENERAL DISCUSSION

Length-weight relationships of zooplankton seem to vary significantly across published studies. This variation could be due to differences in the biochemical composition of the zooplankton and lake specific characteristics, or it may be the result of methodological differences such as type of preservation, length of preservation and weighing methods (Giguere et al. 1989). Although the former sources of variation are inevitable, the latter can be controlled and standardized. The fact that chemical preservation of freshwater zooplankton alters the resulting dry weight measurements is an issue that should not be ignored if researchers intend to draw comparisons across studies (Bird and Prairie 1983; Giguere et al. 1989; Schram et al. 1981). Acknowledging and accounting for the effects caused by preservation technique will significantly increase the accuracy and allow more meaningful comparisons across studies.

I have shown that the dry weight of Daphnia catawba preserved in the most commonly used preservatives differ significantly from unpreserved Daphnia of the same size. Our results contrast with those reported by Bottrell et al. (1976) and Dumont et al. (1975) who suggested that formalin preservation did not seriously affect body weight, or that weight loss over a long storage period in 4% formalin would not likely exceed 5 to 10%. Our results bracket those of Giguere et al (1989) who observed losses in the range of 37 to 43%. The application of a single factor to correct for all types of

preservatives should be used with caution since the dry-weight loss for D. catawba varies according to the preservative employed.

At present there is little information available regarding the biochemical basis of how the preservatives actually alter the zooplankton size and weight. Storage in both formalin and alcohol solutions lead to lipid breakdown and dissolution of oil (Steedman 1976); neither is a good preservative for lipids over time. As well, alcohol preservatives have a dehydrating effect (Dumont et al. 1975) and formalin preservatives have been reported to reduce dry weight (Pace and Orcutt 1981). These preservative properties may also confound dry weight results because the extent and the rate at which the chemicals leach out the lipids is not known.

The results of this study support the notion that the commonly used preservatives do alter zooplankton dry weight as a function of preservation time. In a study concerning the dry weight loss in Ceriodaphnia lacustris, maximum dry weight loss was found to occur in the first 30 days of preservation when 3% formalin was used (Schram et al. 1981). Giguere et al. (1989) have recommended that for small and large zooplankton, the minimum standard length of time in preservative should be 1 month and 6 months, respectively, to ensure dry weight stabilization. Since the effects were taxa-specific, the length of time required for weight stabilization for each taxon should be determined so that consistent procedures for measuring dry weights of preserved samples can be established.

Further research is necessary to determine the extent to which preservatives affect the length measurements of all freshwater zooplankton, especially since length measurements are often the only measurements taken when equations borrowed from the literature are employed for dry weight estimates. The results of this study indicated that length shrinkage was significant in Diaptomus, although apparently not in Daphnia. Since any change in length represents a change in the carapace, not necessarily the internal composition, these changes in carapace may be a function of the amount of calcium present in the carapace. Yan et al. (1989) have suggested that the calcium of Daphnia is approximately 50 times that of copepods. Acid materials leach out of specimens preserved in 75% ethanol, thus causing the acid alcohol to decalcify calcareous shells (Steedman 1976) which may be a source of shrinkage. Formalin also progressively dissolves skeletal calcium (Leslie and Moore 1986). Hence, the carapace of Diaptomus may have been more susceptible to decalcification due to preservation since there was less calcium in its carapace to begin with.

The differences in dry weight estimates and length-weight relationships across studies may be comparable if the techniques used to determine these estimates and relationships were standardized. Acknowledging and accounting for the effects of preservatives on zooplankton length and weight may establish more accurate and comparable dry weight estimates and potentially reduce the error presently incurred if these factors are ignored.

## CHAPTER 2

### Dietary differences among herbivorous zooplankton in two softwater lakes

#### INTRODUCTION

Zooplankton are often subjected to changes in the quantity and quality of their food resources (Kerfoot et al. 1988, Lynch 1989) and seasonal shifts in food quality in natural systems have been reported (Gaedke 1992; Sterner et al 1993). However, defining and measuring the food resources available for utilization in natural environments is difficult. Food availability in aquatic environments has been defined by a number of measures which include total phytoplankton biomass based on the wet weight of algal cells (McCauley and Kalff 1981; Berquist et al. 1985), the amount of chlorophyll a in the cells (McQueen et al. 1989; Elser and Goldman 1991), and availability based on algal sizes (Chow-Fraser and Knoechel 1985; Watson et al. 1992). Although all of these methods represent measures of the resources that occur naturally, there are disadvantages in each case. Both the total phytoplankton biomass in a system and chlorophyll a fail to distinguish between the edible and inedible phytoplankton available. Assigning an edibility criteria to each algal species based only on algal size will indicate the food items that may be ingested but provides no information on the actual diet items preferred by



herbivores, nor does this method identify any dietary differences that may occur among zooplankton taxa of similar size. Stomach content analyses provide an alternative method of assessing the food available to herbivorous zooplankton (Kerfoot et al. 1985). This method yields meaningful information which may indicate differences in the diets of various herbivores (Kerfoot et al. 1985; Chow-Fraser and Wong 1986; Chow-Fraser and Maly 1992). A common criticism of this method is that phytoplankton species which can be easily digested may not be detected or in some cases may be underestimated, while those with resistant walls may be overrepresented (Knisely and Geller 1986). Despite this drawback, stomach content analyses is the most convenient method that identifies seasonal shifts in herbivore diet items and provide important information regarding the utilization of shared, and possibly limited, resources.

This study examines the diets of herbivorous zooplankton in two softwater lakes with different food-web structures to determine whether the preferred diet items of each herbivore change over the ice-free season and whether dietary differences are prominent among herbivores. If the phytoplankton species preferred and ingested by herbivorous zooplankton differ among taxa, then the proportion of phytoplankton that is "edible" may differ for each species. The herbivores chosen for this study were Diaptomus minutus and Holopedium gibberum which are present in both Mouse and Ranger Lakes, and Daphnia catawba which co-occurs with Holopedium and D. minutus in Ranger Lake.

Stomach-content analyses will be used to identify the diet items of the various herbivores across the ice-free season. Electivities ( $\epsilon$ ) will be calculated in order to determine if the preferred food items change through the season and differ among the zooplankton taxa. An index of "edible" phytoplankton will be developed and used to calculate the amount of food available to each herbivore. This quantity which is operationally defined as "edible" algae will then be compared to other more traditional measures of available food such as the biomass of all phytoplankton <30 m, total phytoplankton biomass and chlorophyll a.

## METHODS

### Study Sites

A description of the study sites has been provided in the general introduction of this thesis. Phytoplankton samples were collected at approximately 3-week intervals (n=5) from June to September in 1992 in each lake. Integrated phytoplankton samples were collected by lowering a weighted tygon tubing (5/8" diameter) through the euphotic zone (approximately 6 m) at a deep station (Station 3) in both lakes.

### Phytoplankton Sampling and Processing

Five-ml subsamples were settled for 24 hours in phytoplankton sedimentation chambers. All algae were identified to genus (and species, if possible); dimensions of algae were taken and cells were enumerated in 2 transects at 200X magnification and three transects at 400X magnification. The entire slide was scanned for large dinoflagellates and colonies (eg. Dinobryon). The biomass of each phytoplankton was estimated by volumetric approximation to geometric shapes and assuming a specific gravity of one. Biomasses were subsequently expressed as  $\mu\text{g/L}$ . Chlorophyll a values were interpolated from Figure 12 in Ramcharan et al. (1993, unpub). The method used to measure Chl a involved extraction in 90% acetone and photometric analyses. reported Chl a were calculated by subtracting the corrected Chl a from total Chl a.

### **Zooplankton Stomach Content Analyses**

Adult zooplankton of each species were randomly selected and processed for stomach content analysis on five sampling dates from June to September in each lake. Animals were collected by vertical hauls at the deep station (Station 3) from the euphotic zone (approximately top 6 m) and preserved immediately with Lugol's iodine. In the lab individual animals were isolated with a Pasteur pipette and transferred onto a depression slide where they were rinsed with distilled water. Each animal was then transferred onto a clean glass slide with a drop of distilled water. Whole guts were dissected out using mounted No. 000 insect pin. Once removed, the gut was placed in a drop of glycerin, covered with a glass cover slip, and gently squashed with a blunt instrument. The slide was sealed with three coats of nail polish applied to the edge of the coverslip which allowed the guts to be examined later. In this study only those dissections in which at least 80% of the gut was removed in tact were enumerated for contents. The process was continued until ten intact guts were processed for each zooplankton taxon for each sampling occasion.

### **Index of Diet Preference**

Selectivity ( $\alpha$ ) (Confer and Moore, 1987) and electivity indices ( $\epsilon$ ) (Chesson, 1978) were calculated for all zooplankton taxa on each of the sampling dates to determine the food preferences over the season. The indices were calculated with biomass estimates rather

than densities since the latter fails to account for the size of the prey items.

The selectivity for each prey item was calculated as

$$\alpha_i = \frac{(p_i/a_i)}{\sum p_i/a_i}$$

where  $p_i$  is the proportion of diet item  $i$  in stomachs and  $a_i$  is the proportion of diet item  $i$  in the lake.

The corresponding electivity was calculated as

$$\epsilon = (n-1)/(n-2)\alpha+1$$

where  $\alpha$  is as defined above and  $n$  is the number of diet items in the lake.  $\epsilon$ -values are the normalized  $\alpha$ -values which range between -1 and +1. Negative values indicate avoidance and positive values indicate preference for a prey item (Strauss, 1979).  $\alpha$ -values are directly comparable when the food base is constant; however, when numbers of prey types vary,  $\epsilon$ -values are more comparable (Confer and Moore, 1987). Since the food base varied substantially over the season and differed between lakes in this study,  $\epsilon$ -values were used to compare food preferences among species and between lakes.

### Index of "Edible" Phytoplankton

The selectivity values ( $\alpha$ ) were also used to provide an index of "edible" phytoplankton for each animal in the two lakes. The index of edible phytoplankton biomass based on stomach content analyses (Ed-SCA) was calculated as follows:

$$\text{Ed-SCA} = n * [\sum (\alpha * m_i)]$$

where  $m$  is the biomass of each algal diet item. Original data for these calculations have been included in Appendix B.

To estimate the edible phytoplankton biomass based on algal size criterion (Ed-SIZE), I used the results of the stomach content analyses and categorized the ingested algae by size for each of the herbivores in the two lakes. For Diaptomus, all algae with the longest dimension  $<10 \mu\text{m}$  was considered "edible" and these algal biomass were summed to produce an estimate of Ed-SIZE for each sampling occasion. Traditionally the size criterion applied for cladocerans, such as Daphnia and Holopedium, included all unicellular algae  $<30 \mu\text{m}$  (eg. Chow-Fraser and Knoechel 1985); however, in this study I have included all unicellular algae  $<40 \mu\text{m}$  since stomach content analyses indicated that both Daphnia and Holopedium were ingesting large cryptomonads  $>30 \mu\text{m}$  but  $<40 \mu\text{m}$  in length.

## RESULTS AND DISCUSSION

### Total Phytoplankton Biomass

At the deep station (Station 3, max depth was 13 m and 9m in Ranger Lake and in Mouse Lake, respectively) in both lakes, total phytoplankton biomass peaked in mid-summer; however, the peak biomass in Ranger Lake in mid-summer was almost double that in Mouse Lake (Fig. 2.1a and 2.1b). I categorized the total phytoplankton biomass in Ranger and Mouse Lakes by size (Fig. 2.1a and 2.1b, respectively) and by taxonomic group (Fig. 2.2a and 2.2b) to evaluate the potential food resources. Large colonial algae (eg. Dinobryon, Uroglena) were dominant throughout the season in both lakes, as were large unicells (>30  $\mu\text{m}$ ) such as cryptomonads and diatoms. When the data were sorted by algal taxonomic group, chrysophytes dominated throughout the summer while cryptomonads were common; chlorophytes were only prominent in mid-summer in Mouse Lake. Such a distribution of algal taxa and functional size categories are characteristic of unproductive lakes in Canada (Chow-Fraser et al. in press)

### Dietary Preferences

The electivities of the dominant herbivores in Mouse and Ranger Lakes (summarized in Tables 2.1 through 2.5) clearly varied over the summer. For example, Diaptomus minutus in both lakes appeared to prefer a relatively constant diet consisting primarily of unicells (<10 $\mu\text{m}$ ) and small colonies. In Ranger Lake, this functional

size group included chrysophytes such as Ochromonas and Chrysidiastrum and cryptophytes such as Rhodomonas and Cryptomonas (Table 2.1). By comparison, algae of this size category that were preferred in Mouse Lake included only Ochromonas and Rhodomonas (Table 2.2). Another difference in preference was evident for colonial taxa; in Ranger Lake, Aphanocapsa and Chroococcus were preferred in mid-season, while Aphanocapsa and Gleocapsa were preferred at the beginning and end of the season in Mouse Lake. In general, diaptomids appeared to select against large colonies such as Dinobryon and Uroglena, the dominant algae in the two lakes.

In both lakes, Holopedium preferred diet items that varied in size, ranging from small unicells (<10  $\mu\text{m}$ ) to large colonies (eg. Dinobryon), and exhibited very obvious shifts in diet item preferences through the season. While large colonies such as Dinobryon and Chryso-sphaerella were preferred at the beginning and towards the end of the season for Holopedium in Ranger Lake, those in Mouse Lake showed a much higher preference for Dinobryon colonies in June and July but not later in the season (Tables 2.3 and 2.4, respectively). This mid-season preference of Holopedium in Mouse Lake for colonial algae (eg. Dinobryon and Gleocapsa) marked a switch from the preferred individual cells (eg. Ochromonas, Cryptomonas) at the beginning of the season. In Ranger Lake the preference for small unicells (eg. Chlorella) fluctuated through the season.



Figure 2.1 Total phytoplankton biomass categorized by algal size in a) Ranger Lake and b) Mouse Lake

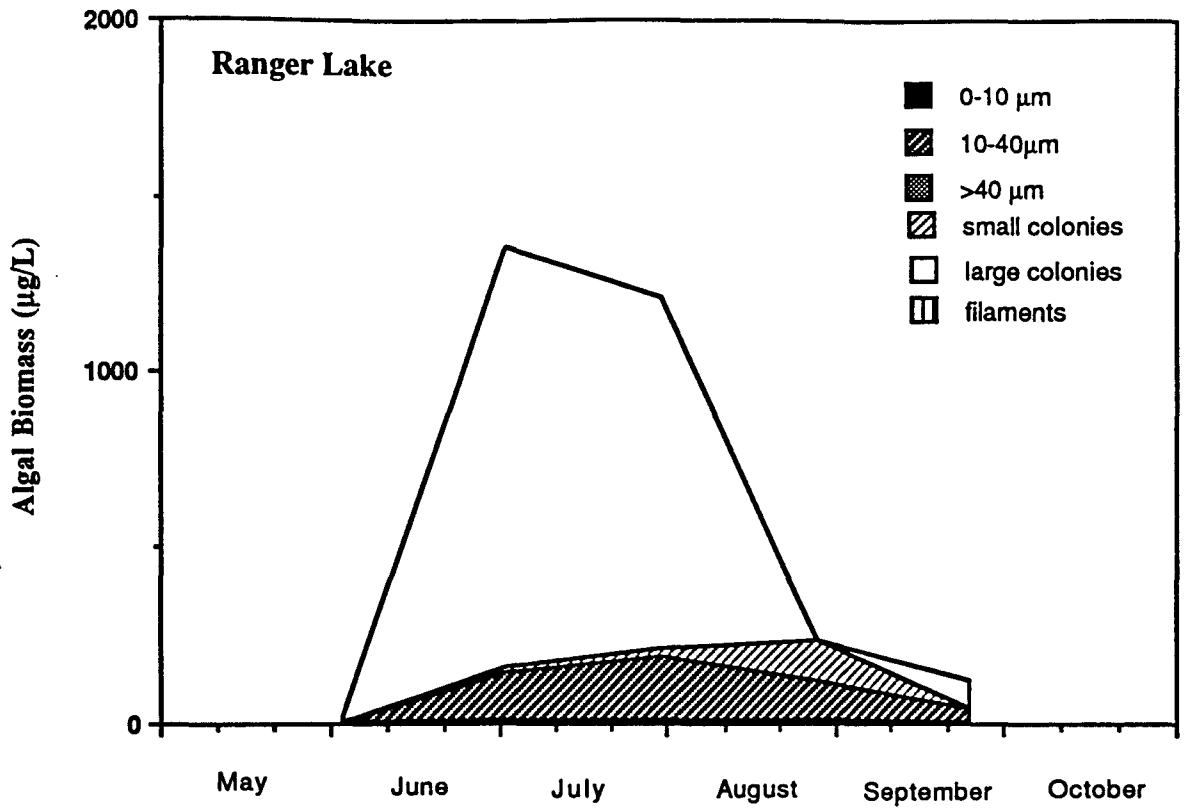


Figure 2.1b

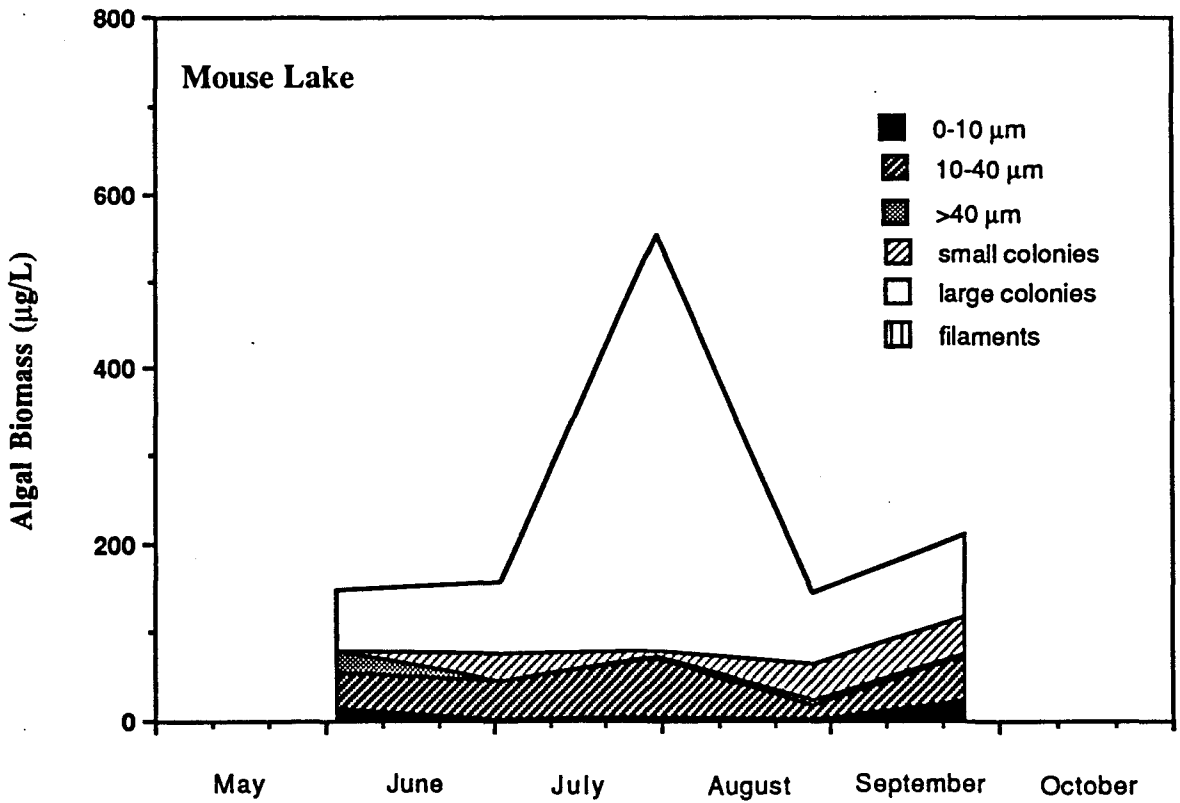


Figure 2.2 Total phytoplankton biomass categorized by algal taxonomic groups in a) Ranger Lake and b) Mouse Lake

Figure 2.2a

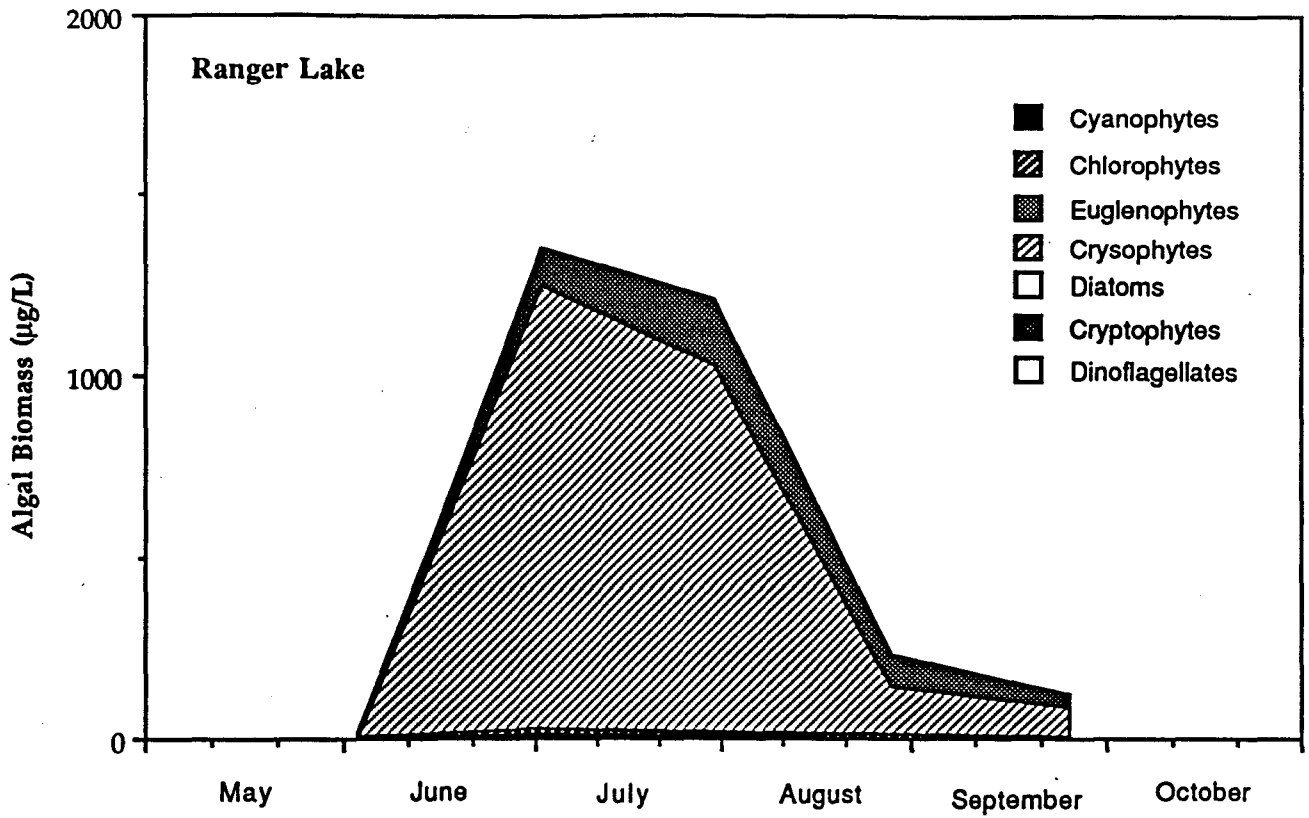


Figure 2.2b

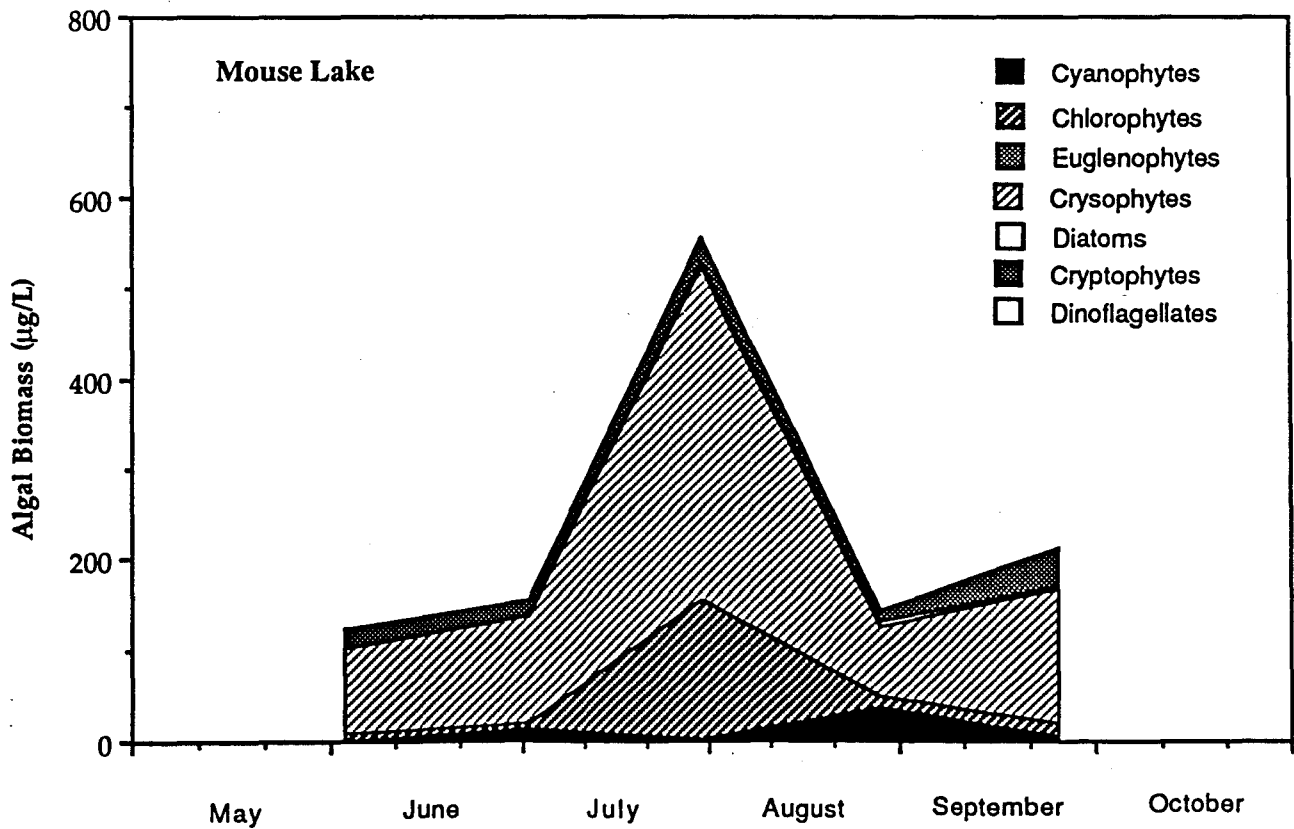


TABLE 2.1 Seasonal Electivities of Diaptomus minutus in Ranger Lake

Algal Species	June 1	June 30	July 28	Aug 25	Sept 21
Dinobryon	0.24	-0.98	---	---	---
Uroglena sp.	---	---	-0.89	-0.93	-0.85
Cryptophyta	0.42	---	---	---	---
Ochromonas	0.90	0.66	---	0.19	0.77
Crypt small	0.47	0.40	0.36	-0.23	0.47
Chlorella	0.01	0.86	-0.44	-0.08	0.55
Rhodomonas	0.05	0.53	0.09	0.76	0.29
Chrysidiastrum	---	0.64	0.56	0.89	---
Scenedesmus	---	0.79	---	---	---
Merismopedia	---	-0.80	-0.67	-0.52	---
Stichoglea	0.84	0.27	---	0.86	---
Aphanocapsa	---	---	0.94	---	0.22
Chroococcus	---	---	0.72	---	---
Gleocapsa	---	---	---	---	0.92

TABLE 2.2 Seasonal Electivities of Diaptomus minutus in Mouse Lake

Algal Species	June 1	June 30	July 28	Aug 25	Sept 21
Dinobryon	-0.84	-0.90	---	---	---
Crypt medium	0.54	---	---	0.55	0.59
Aphanocapsa	0.93	-0.81	0.37	0.45	0.64
Chlorella	0.07	0.21	-0.12	0.47	0.40
Rhodomonas	0.37	0.67	0.78	0.77	0.79
Ochromonas	0.59	0.94	0.59	0.41	-0.01
Chrysidiastrum	0.58	---	0.79	---	-0.24
Crypt small	-0.71	0.66	0.83	---	---
Chroococcus	---	0.38	0.20	-0.43	0.73
Gleocapsa	---	---	0.25	0.91	0.80
Merismopedia	---	---	-0.38	---	---
Crypt large	---	---	---	---	0.09

TABLE 2.3 Seasonal Electivities of Holopedium gibberum in Ranger Lake

Algal Species	June 1	June 30	July 28	Aug 25	Sept 21
Dinobryon	0.92	-0.66	-0.16	0.91	0.91
Chrysochaerella	0.86	---	---	---	---
Uroglena sp.	---	-0.18	-0.69	-0.92	-0.64
Stichoglea	-0.28	0.40	---	0.88	---
Ochromonas	0.52	0.57	0.09	0.36	0.71
Crypt medium	---	---	-0.28	---	0.19
Crypt small	0.07	0.32	0.30	-0.35	0.04
Chlorella	-0.50	0.84	0.60	-0.22	0.12
Rhodomonas	-0.69	0.04	-0.51	0.02	0.06
Aphanotheca	---	-0.24	0.87	---	---
Aphanocapsa	---	0.74	0.55	-0.79	0.44
Gleocapsa	---	0.45	---	---	---
Chroococcus	---	---	0.73	---	---
Chrysidiastrum	---	0.11	0.52	---	---
Crypt large	---	0.02	-0.10	-0.42	0.50
Merismopedia	---	-0.71	-0.08	-0.03	0.48

TABLE 2.4 Seasonal Electivities of Holopedium gibberum in Mouse Lake

Algal Species	June 1	June 30	July 28	Aug 25	Sept 21
Dinobryon	0.64	0.49	0.25	-0.33	-0.30
Crypt large	-0.01	-0.68	0.29	0.77	0.62
Crypt medium	0.82	0.83	---	-0.14	0.77
Anthrodesmus	0.24	---	---	-0.52	0.37
Chrysamoeba	0.80	-0.32	0.48	---	---
Aphanocapsa	0.57	-0.35	-0.42	-0.08	0.18
Chlorella	0.31	-0.06	0.36	-0.23	0.28
Rhodomonas	-0.03	-0.41	0.29	-0.41	-0.05
Ochromonas	0.41	0.77	0.24	-0.54	-0.68
Chrysidiastrum	0.24	---	-0.34	---	---
Uroglena small	---	-0.38	-0.75	-0.60	-0.39
Chroococcus	---	-0.26	0.19	-0.87	0.57
Uroglena large	---	-0.44	---	---	-0.66
Gleocapsa	---	0.70	0.73	0.95	0.88
Merismopedia	---	-0.66	0.35	---	---
Crypt small	---	-0.32	0.88	---	---



TABLE 2.5 Seasonal Electivities of Daphnia catawba in Ranger Lake

Algal Species	June 1	June 30	July 28	Aug 25	Sept 21
Dinobryon sp.	0.96	-0.31	-0.61	0.97	0.82
Chryso-sphaerella	0.17	---	---	---	---
Uroglena sp.	---	---	-0.96	---	-0.95
Ochromonas	0.14	0.55	-0.22	-0.24	0.83
Crypt small	-0.37	0.48	0.80	-0.58	0.43
Chlorella	-0.86	0.68	-0.12	-0.56	0.55
Rhodomonas	-0.75	0.47	0.74	0.19	0.33
Chrysamoeba	---	0.12	---	---	---
Crypt large	---	0.69	0.52	-0.60	0.70
Aphanocapsa	---	0.45	0.88	---	0.11
Gleocapsa	---	0.81	---	---	---
Stichoglea	0.01	0.25	---	---	---

Daphnia in Ranger Lake appeared to be a much more generalist feeder. For example, Daphnia preferred unicells of varying sizes (eg. Ochromonas, small and large Cryptomonas and Rhodomonas) throughout the season. However, Dinobryon colonies were highly preferred at the beginning and end of the season when they were less abundant (Table 2.5). Mid-season there was a shift in food preference to the numerous gelatinous greens and blue-greens (eg. Gleocapsa and Aphanocapsa). The shifts in food preference by Daphnia appear to be a function of strictly what is available which suggests that Daphnia feeds opportunistically on a large number of diet items.

#### **Index of "Edible" Phytoplankton**

It is clear from the above analysis that the type of algae that is preferred by zooplankton in their natural environment varies from lake to lake and from species to species. For example, what is ingested by Holopedium is not necessarily ingested by Diaptomus. This fact limits the usefulness of applying a single size criterion to define "edible" phytoplankton for all taxa as is often done in the literature. For example, the broad size range of diet items (ranging from small unicells <10  $\mu\text{m}$  to large colonies) preferred by both Holopedium and Daphnia did not conform to the size criterion used in previous studies to define algae that are edible (eg. Chow-Fraser and Knoechel 1985; Watson et al. 1992; Wainman et al. 1993). Even so, Diaptomus in both lakes generally preferred items that were < 10  $\mu\text{m}$  and this is entirely consistent with the assumption made by Chow-

Fraser (1986), there were obvious departures through the season. To make this study more accurately reflect the food that is actually edible to the respective herbivores, I have used the information from the SCA to calculate a new index of "edible" algae for each zooplankton on each sampling occasion (Table 2.6a and 2.6b). This index weights the importance of diet items according to their corresponding "alpha" values and accounts for the number of diet items of each herbivore (see Method).

In both lakes the food available to Diaptomus dropped to low levels in July and August, but increased again in September (Figure 2.3a and 2.3b). In Ranger Lake, small unicells and small colonies accounted for most of the edible phytoplankton biomass throughout the season, with large colonies contributing notably mid-season (Figure 2.3a). The edible phytoplankton biomass of Diaptomus in Mouse Lake consisted primarily of small ( $<10 \mu\text{m}$ ) and medium ( $10\text{-}30 \mu\text{m}$ ) unicells throughout the season (Figure 2.3b), although large unicells became prominent towards the end of the season.

Total food available to Holopedium in Ranger Lake peaked in July (Table 2.6), while that in Mouse Lake was relatively constant from June to August and declined towards September (Table 2.7). The biomass of unicellular algae and small colonies was relatively constant throughout the season in both lakes, while the biomass of large colonial algae defined the shape of the algal distributions (Figure 2.4a).

Figure 2.3      Edible phytoplankton biomass of  
Diaptomus categorized by algal size in  
a) Ranger Lake and b) Mouse Lake

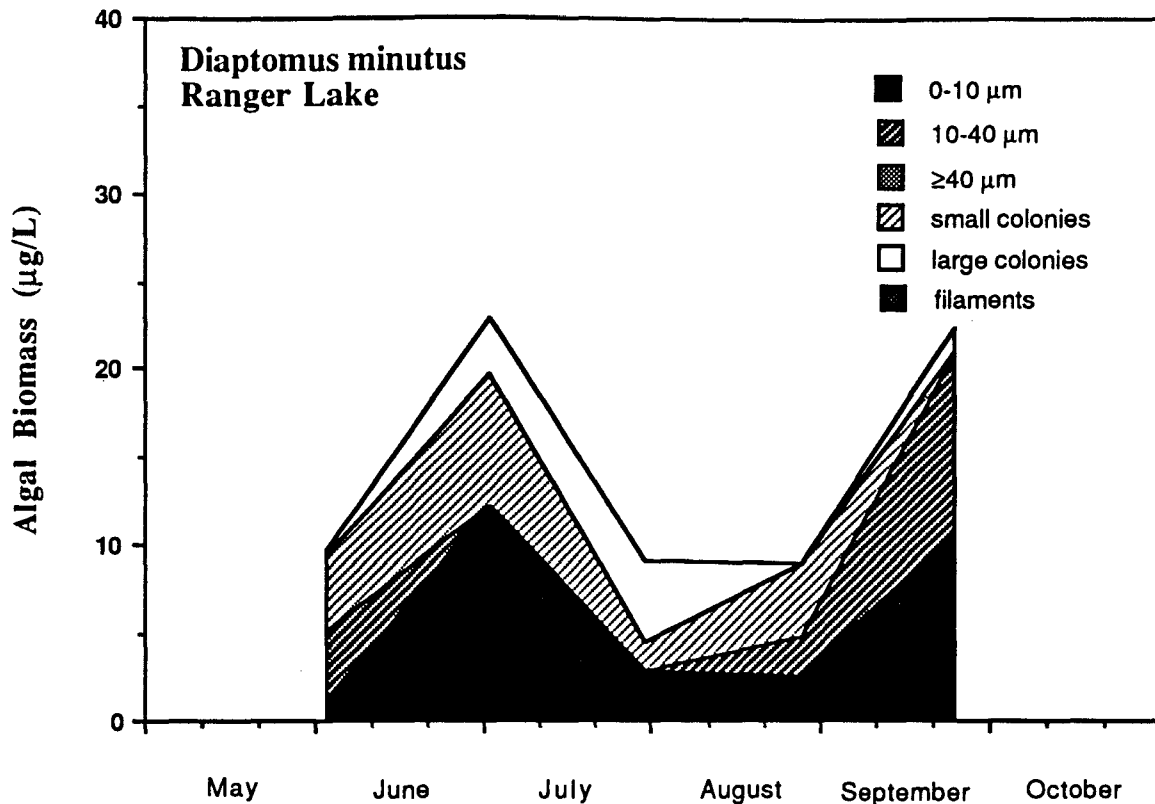


Figure 2.3b

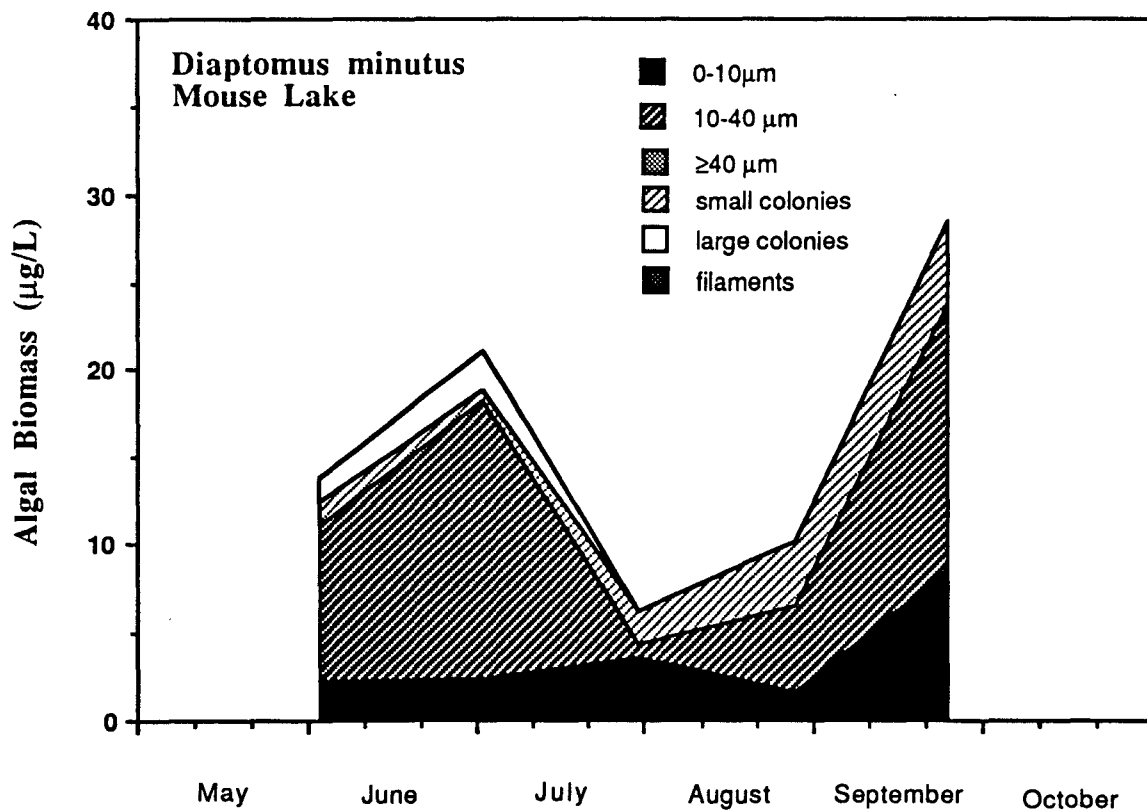


Figure 2.4

Edible phytoplankton biomass of  
Holopedium categorized by algal size in  
a) Ranger Lake and b) Mouse Lake

Figure 2.4a

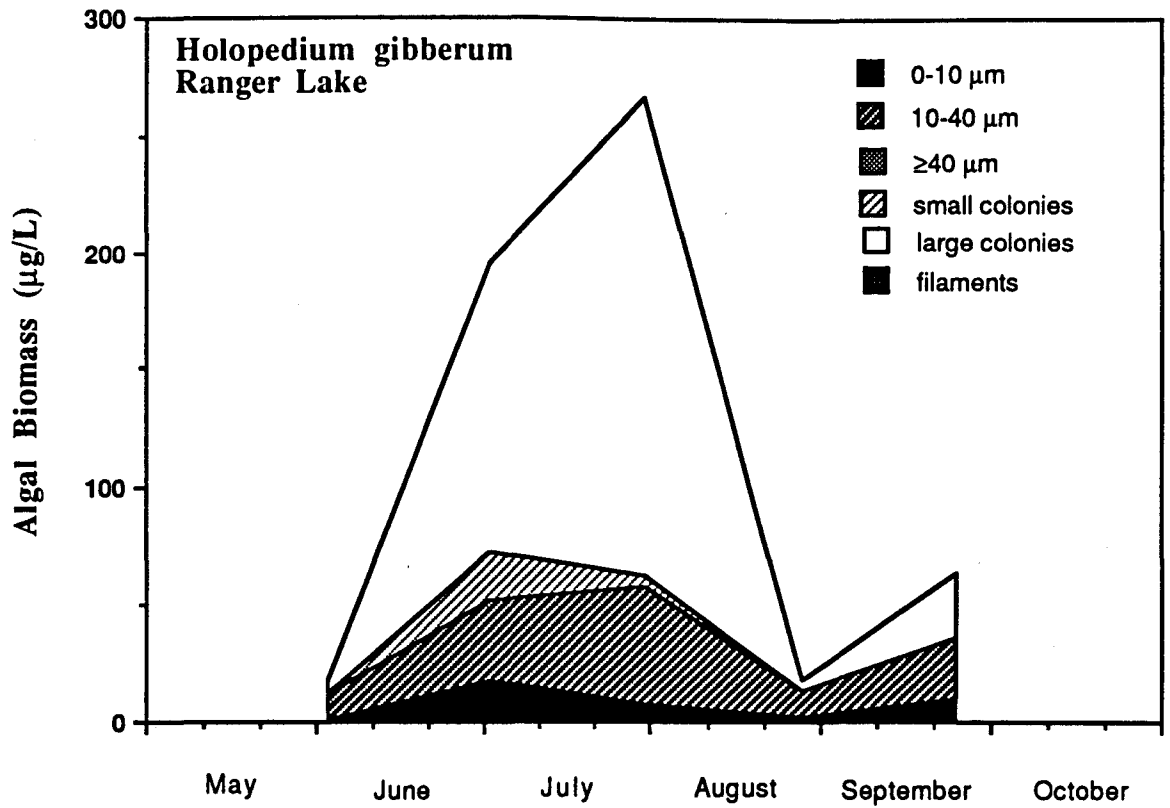


Figure 2.4b

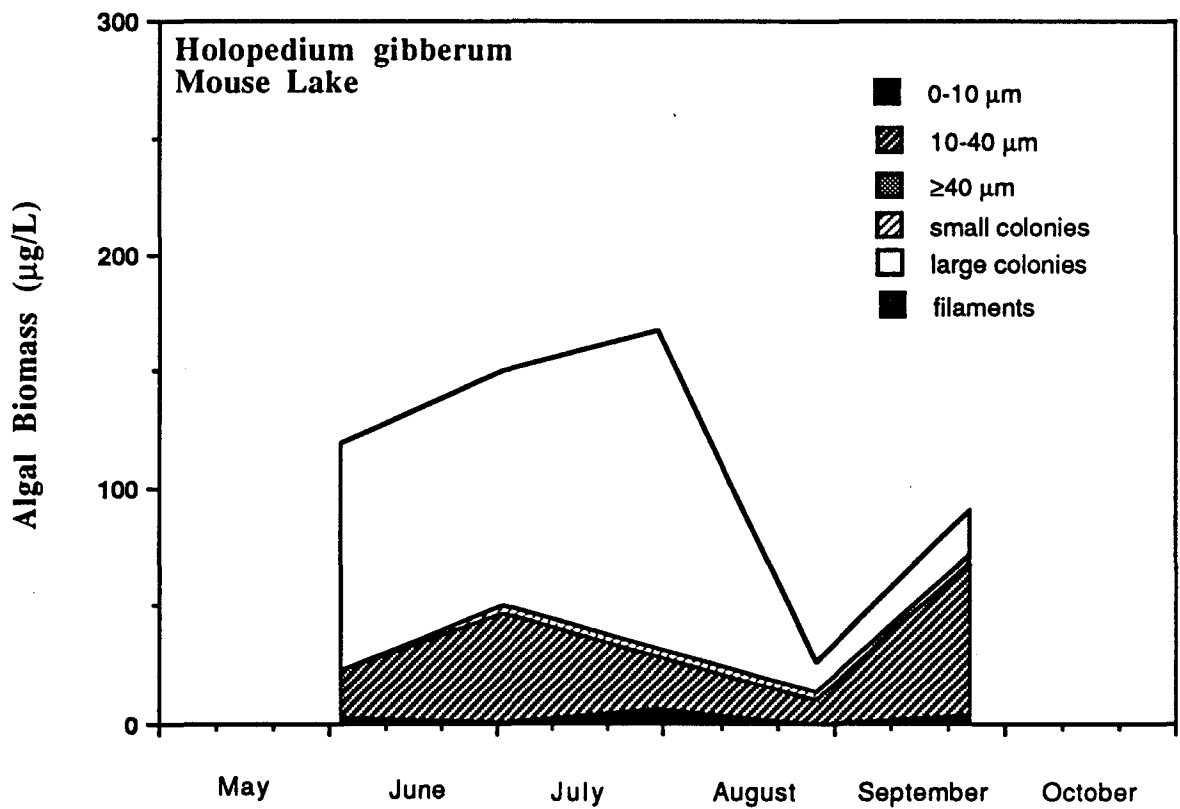


Figure 2.5 Edible phytoplankton biomass of Daphnia  
categorized by algal size



Figure 2.5

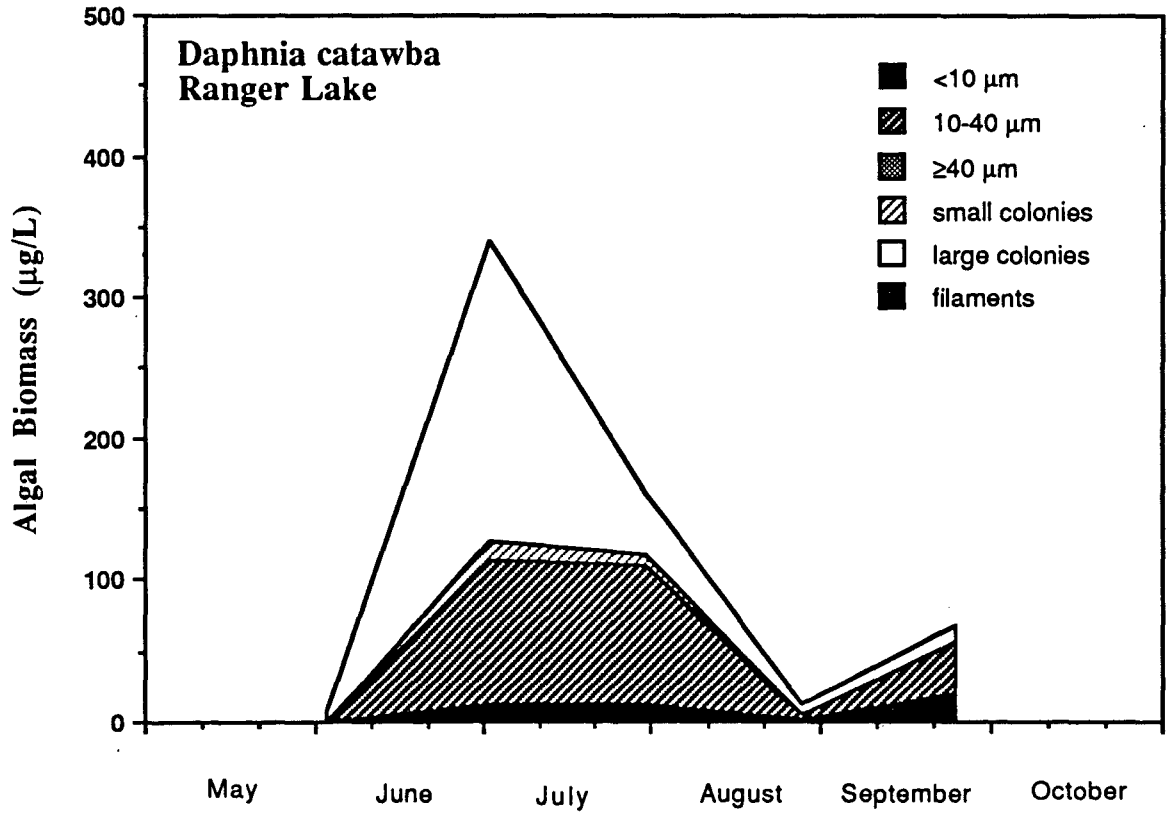


Table 2.6

Summary of total phytoplankton biomass, chlorophyll a and edible phytoplankton biomass as determined by algal sizes (ED<sub>SIZE</sub>) and stomach content analyses (ED<sub>SCA</sub>) for Diaptomus, Holopedium and Daphnia in Ranger Lake. (All measurements are in µg/L)

Date	Total	Chl a	ED <sub>SCA</sub>			ED <sub>SIZE</sub>	
			<i>Diaptomus</i>	<i>Holopedium</i>	<i>Daphnia</i>	Cladoceran	<i>Diaptomus</i>
June 01	11.60	1.7	9.8	13.6	7.7	8.9	4.5
June 30	1315.50	2.1	22.7	196.4	339.7	141.2	14.8
July 28	1210.04	4.2	9.1	267.5	162.5	188.8	12.5
Aug 25	235.93	3.1	9.0	18.2	11.0	121.5	13.2
Sept 21	124.14	2.6	22.4	63.6	68.9	46.5	7.7

Table 2.7

Summary of total phytoplankton biomass, chlorophyll a and edible phytoplankton biomass as determined by algal sizes (ED<sub>SIZE</sub>) and stomach content analyses (ED<sub>SCA</sub>) for Diaptomus and Holopedium in Mouse Lake. (All measurements are in µg/L)

Date	Total	Chl a	ED <sub>SCA</sub>		ED <sub>SIZE</sub>	
			<i>Diaptomus</i>	<i>Holopedium</i>	<i>Holopedium</i>	<i>Diaptomus</i>
June 01	124.70	2.8	13.9	119.7	54.6	16.3
June 30	157.70	1.5	20.5	150.2	44.9	3.6
July 28	554.90	5.5	6.4	167.9	73.3	4.8
Aug 25	144.70	3.8	10.2	26.7	23.5	3.0
Sept 21	212.48	2.4	28.4	91.4	77.3	23.7

For Daphnia in Ranger Lake, the edible phytoplankton biomass followed trends similar to Holopedium in that lake (Table 2.6), however, edible phytoplankton biomass (Ed-SCA) peaked at the end of June for Daphnia and at the end of July for Holopedium. Daphnia had a higher mean edible phytoplankton biomass than Holopedium in Ranger Lake which may be the result of Daphnia's generalist feeding strategy.

#### **A Comparison of the Estimates of Available Food**

The notable differences between the edible phytoplankton biomass determined from SCA (Ed-SCA) and the edible phytoplankton biomass determined by algal size (Ed-SIZE) were evident for all of the herbivores (Table 2.6 and 2.7). Although both Daphnia and Holopedium were ingesting unicellular algae <40  $\mu$ m in length (observed from SCA), the edible phytoplankton biomass estimated based on this size criterion produced estimates of edible algae that were less than the estimates based on SCA. This trend was also apparent for Diaptomus in both lakes. Also, as indicated in Table 2.6, the edible phytoplankton biomass based on size was assumed to be the same for both Holopedium and Daphnia in Ranger Lake since these two species were of similar body size. However, the edible phytoplankton biomass determined in this study (Ed-SCA) indicated differences in the available food for these two taxa. Assigning an algal size criterion to estimate the algae available for consumption assumes that all food in one size category may be edible. As indicated from the stomach content analyses (See Appendix A) and the electivity tables, this

assumption is not always valid. The SCA approach has demonstrated that for both Holopedium and Daphnia, not all food in one size category was edible nor did all edible food fall into one size category.

The food available to herbivorous zooplankton has historically been defined by a number of measures which include total phytoplankton biomass based on the wet weight of algal cells (McCauley and Kalff 1981), the amount of chlorophyll a in the cells (McQueen et al. 1989; Elser and Goldman 1991), and availability based on algal sizes (Chow-Fraser and Knoechel 1985; Watson et al. 1992). To determine if the edible phytoplankton biomass based on stomach-content analyses was significantly related to the other common measures of food, I regressed the seasonal values of edible phytoplankton biomass (Ed-SCA) against corresponding values of total phytoplankton, chlorophyll a and edible phytoplankton biomass based on algal size (Ed-SIZE) for each animal in the two lakes. The edible phytoplankton biomass (Ed-SCA) was not significantly related to the other measures of food for Holopedium or Diaptomus in either lake ( $P > 0.05$ ). The only significant relationship was between the edible phytoplankton biomass (Ed-SCA) and total phytoplankton biomass for Daphnia in Ranger Lake ( $P = 0.038$ ).

## GENERAL DISCUSSION

Total phytoplankton biomass, chlorophyll a, edible phytoplankton biomass based on algal size criterion (ED-SIZE) and edible phytoplankton biomass based on SCA (ED-SCA) all represent some measure of the food available to herbivorous zooplankton in their natural environment. The primary difference between these measures, however, is the extent to which each accurately describes the food that is available and edible to these herbivores. While total phytoplankton biomass and chlorophyll a are quite frequently measured, these measures provided only a generalized measure of the food available to all herbivores. By assuming that all available algae are the same to all zooplankton, these measures of food ignored differences in diets that existed among taxa in the two study sites. Nevertheless, for a generalist feeder such as Daphnia, total phytoplankton or edible phytoplankton biomass based on size criterion (ED-SIZE) was shown to be a good indicator of available food.

The major limitation to using stomach-content analyses is misrepresentation and misidentification of the gut contents. For example, fragile forms (eg. flagellates) may be completely destroyed by the mandibles or may appear as an unidentifiable mass, while particles resistant to digestion may be overrepresented. Another limitation is that one cannot say with certainty that a particular food is not eaten because of its absence from the gut (Lampert 1987). Nevertheless, it is clear that all identifiable particles in the gut

have been ingested; in this sense, stomach-content analyses provides useful information on the size of particles ingested and on the degree of fragmentation and utilization of colonies or cells (Lampert 1987). This technique also provides information about differences in herbivore preference for certain diet items and identifies shifts in preference through the season.

The pattern of selection for algae has been studied in some detail in published laboratory studies. Freshwater herbivores are known to discriminate among algae on the basis of cell size, cell shape, taste and nutritional quality (Wilson 1973; Knisely and Geller 1986; Demott 1988; Butler et al. 1989; Vanderploeg 1990). The degree of selection seems to vary with the zooplankton taxa (Vanderploeg 1990) and with lake origin (ie. presence of interfering bluegreen algae, Richman and Dodson 1983). Despite these demonstrated differences, there is still a tendency for investigators in field studies to assume that the same edibility criterion should be applied equally to all zooplankton taxa throughout the season. In this study, I have shown that the diets of herbivores are taxon-specific, and can change from month to month and from lake to lake. An estimate of edible algae that recognizes such differences should thus be more appropriate than one which ignores taxon-specific and season-specific differences for natural assemblages of herbivorous zooplankton.

## CHAPTER 3

### Factors contributing to dry weight differences among herbivorous zooplankton in two softwater lakes with contrasting food-web structures

#### INTRODUCTION

Zooplankton weight is an important parameter that is routinely used to estimate community biomass and secondary production (Giguere et al. 1989). Dry weight is seldom measured directly because of the labour-intensive processing involved and expensive equipment required; instead, body length is more conveniently measured and then is used to estimate dry weight from length-weight relationships previously developed in other studies (Bottrell et al. 1976). This practice, however, does not account for any differences in length-specific dry weight of zooplankton which is known to vary significantly across studies.

In all aquatic ecosystems there are potential top-down and bottom-up forces that influence the zooplankton community structure (see review by Vanni 1987). There is some evidence that predation by planktivores may affect zooplankton biomass (see review by McQueen et al. 1989; Tessier et al. 1992). However, it is not known whether increased predation contributes to changes in the length-specific dry weight of herbivorous zooplankton, although there is indirect



evidence that predation by fish can cause a reduction in the clutch size, egg size and the relative fat content of eggs for Holopedium gibberum in 25 lakes of Algonquin Park (Arts and Sprules 1988). If predation forces cause animals of a certain length to weigh less than those not subjected to predation, then I would expect the length-specific weights of herbivorous zooplankton to be lower in an environment with increased predation such as Mouse Lake. Therefore, the first testable hypothesis for the study is that weight at length will be less for herbivores in Mouse Lake than in Ranger Lake.

Considerably less is known, or reported, about possible bottom-up forces. The quality and quantity of food available to these herbivores tend to vary seasonally (eg. Geller and Muller 1985; Kerfoot et al. 1988; Lynch 1989; McQueen et al. 1989; Gaedke 1992; Sterner et al. 1993). Researchers have therefore suggested that changes in food quality and availability may account for variations in weight at length of herbivorous zooplankton (Schindler 1971; Goulden et al. 1982; Williamson and Butler 1987; Lynch 1989; Sterner et al. 1993). If bottom-up forces (ie. food) are responsible for differences in weight of a given length of herbivore in the two lakes, then I would expect a correspondence between changes in length-specific dry-weight and changes in food. Therefore, a second testable hypothesis is that herbivores will weigh more in the lake with more food available.

Most studies that address the relationship between food and

zooplankton weight are based on laboratory experiments where the food base is known and manipulated (Elmore 1983; Sterner et al. 1993; Lynch 1989). In nature, however, the food available to these animals change in quality and quantity throughout the season and is difficult to quantify. Available food can be estimated in a variety of ways which include the biomass of the total phytoplankton community (estimated by either direct cell counts or chlorophyll a) or some fraction of the phytoplankton (eg. <30  $\mu\text{m}$ , Chow-Fraser and Knoechel 1985); <60  $\mu\text{m}$ , Wainman et al. 1993). This latter approach has been deemed to be a more accurate estimate of available food and has been referred to as the "edible" fraction in the literature. Past investigators have tended to use size as the sole criteria of "edibility", but this is problematic because not all algae of a certain size are "edible" and not all "edible" algae are of a certain size (see Chapter 2). In Chapter 2, I used SCA to develop an index of "edible" phytoplankton so that the algal biomass available to each of the herbivores could be estimated. This approach indicated that the algal size restrictions suggested by Chow-Fraser and Knoechel (1985) were not always appropriate for determining the available food of the dominant herbivores in Mouse and Ranger Lakes. In this chapter I evaluate the extent to which total phytoplankton biomass, chlorophyll a and "edible" phytoplankton biomass (as determined in Chapter 2) are related to herbivore dry weight changes as this relationship has not yet been documented in the literature.

Herbivore reproduction and population densities also change

through the season. The contribution of eggs or ephippia to female herbivore biomass are known to affect length-weight regressions (Dumont et al. 1975; Bottrell et al. 1976). Therefore, in addition to changes in available food, bottom-up effects may also be tested by correlating variations in weight to changes in clutch size and animal density since these are both known to be influenced by food quality and quantity (Maly 1973; Tessier and Goulden 1982; Elmore 1983; Williamson and Butler 1987)

This chapter examines the seasonal changes in the length-specific weight of several herbivorous zooplankton in the two softwater lakes and evaluates the relative impacts of lake-specific characteristics on herbivore weight at length in Mouse and Ranger Lakes. First, length-weight relationships will be developed for each of the herbivores throughout the ice-free season to determine the changes in weight at length between lakes. Since animals used for these measurements had to be preserved when collected, the results of Chapter 1 will be used to correct for preservation. To determine bottom-up effects, herbivore weights will be regressed against various measures of food (as discussed in Chapter 2), as well as other indirect indicators of resource competition such as clutch size and population density. On the other hand, the effect of predation will be considered by determining if the dry-weight differences between lakes are consistent with the presence or absence of planktivores. Empirical models that estimate dry weight of each herbivore in the two lakes will be developed using stepwise regression analyses.

## METHODS

### Study Sites

A description of the study sites has been provided in the general introduction of this thesis. Tables 1 in Appendix A summarizes the physical and chemical characteristics of Mouse Lake and Ranger Lake in 1992.

### Phytoplankton

The total phytoplankton biomass, chlorophyll a and edible phytoplankton biomass based on stomach content analyses were determined as indicated in Chapter 2.

### Zooplankton

#### Length and Weight

Zooplankton were collected by vertical haul (80  $\mu\text{m}$  net) at approximately 3-week intervals ( $n=5$ ) from June to September in 1992 in each lake. Net hauls through the euphotic zone (6 m) were taken at a deep station (approximately 13 m in Ranger Lake and 9 m in Mouse Lake) in each lake. Zooplankton that were to be used for determination of seasonal length-weight relationships were rinsed with filtered lake water and immediately preserved with a 4% sugar-formalin solution (Prepas, 1978).

Due to the volume of work required to process the zooplankton, it was necessary to preserve the samples at the time of collection. Chemical preservatives alter the length-specific dry weight of herbivorous zooplankton and, in some taxa, the length is altered as well (see Chapter 1). To account for the effects of preservation, Daphnia dry weights were increased by 23% which represented the mean dry weight loss for animals preserved in 4% sugar-formalin ranging from 1.0 mm to 2.5 mm (Table 1.3, Chapter 1). I did not alter the length measurements of Daphnia because preservation in 4% sugar-formalin did not change the length (Fig. 1.3a and 1.3b, Chapter 1). For Diaptomus preserved in 4% sugar-formalin, experiments indicated that a length shrinkage of 6% and a dry weight loss of 14% occurred as a result of preservation (Chapter 1). These correction factors were applied to Diaptomus in this study. Since I did not investigate the effects of preserving Holopedium in 4% sugar-formalin and no such information exists in the literature, I have assumed that the effects of 4% sugar-formalin on length and weight of Holopedium are negligible for purposes of this study.

To formulate length-weight relationships, I randomly selected Holopedium, Daphnia and Diaptomus from each of the samples of interest. Zooplankton body lengths were measured individually with the Optimus Image Analysis System (Bioscan Inc., Edmonds, Washington). Daphnia were measured from the top of the carapace to the base of the tail spine. Diaptomus were measured from the top of the head to the base of the caudal rami (Figure 1.1 and 1.2, Chapter

1). The contracted body length of individual Holopedium was measured since I was unable to measure claw length on many of the animals. The contracted body measurements were converted to relaxed body length using the equations generated by Yan and Mackie (1987). I determined the accuracy of all length measurements by randomly measuring a 10% subsample of animals three times. The repeated measures were always within a range of less than 1.0% of the total body length. In most cases, the animals selected for these analyses represented the size range of animals measured in similar subsamples (Chow-Fraser, unpub.); however, for an unknown reason the Holopedium specimens I selected from Ranger Lake tended to be large.

All Daphnia and Holopedium larger than 1.5 mm were weighed individually; however, smaller Holopedium needed to be sorted into groups of 2 to 5 animals depending on the length and clutch size in order to achieve an accurate dry weight estimate. I tried to ensure that animals with similar length (within 0.2 mm) and equal clutch sizes were grouped together. Diaptomus of similar size (within 0.05mm) were weighed in groups of five.

After measurement, individuals or groups of animals were transferred to pre-weighed aluminum boats that had been constructed by punching holes through foil. The weighing boats were placed in a partially closed petri plate and dried in the oven at 60°C for 24 hours. The boats were then cooled for 30 minutes and then weighed to the nearest 0.5  $\mu\text{g}$  with a Cahn 25 Electrobalance.

### **Clutch Size**

Holopedium clutch size was determined as the number of eggs per adult female. Eggs were enumerated when the length measurements were taken. Diaptomus clutches dropped off due to preservation and only Daphnia without eggs were considered in this study.

### **Density**

Zooplankton densities were determined by counting the number of individual animals of each taxon in a 10% subsample of the original samples used for determination of the length-weight relationships. Densities were reported as the number of animals per litre of water sampled.

### **Temperature**

The mean water temperature of the top 6 m in each lake was calculated from data provided by Ramcharan et al. (1993, unpub.) for each sampling date. If temperature data was not available on the specific sampling dates used in this study then an average was calculated based on the data collected on the week preceding and the week following the sampling dates used in this study.

## Data Analyses

Log<sub>10</sub> transformations were applied to the lengths and dry weights of Holopedium and Daphnia prior to performing the length-weight regression analyses (Model I regression). Log transformation was not necessary for Diaptomus. For Daphnia and Holopedium, data were grouped according to sampling date and lake origin and length-weight regressions were performed (Excel 4.0). Analysis of covariance (Zar 1984) was then used to determine if the slopes and intercepts differed for the significant length-weight regression equations. SAS Jmp was used to do a two-factor ANOVA (lake and season) for Diaptomus.

For each of the herbivores in the two lakes, dry weight, length, density and clutch size data, total phytoplankton biomass, edible phytoplankton biomass (ED-SCA) and chlorophyll a were pooled for the season and entered into a stepwise regression analyses for each species in the two lakes to determine the order in which the variables contributed to predicting dry weight. These variables were then used to generate multiple regression models for each of the zooplankton.



## RESULTS AND DISCUSSION

### **Length-Weight Relationships**

For each herbivore in the two lakes the data were initially pooled for the entire season to generate length-weight regression models. In each case the relationship between length and dry weight was significant ( $P < 0.05$ , Tables 3.1a, 3.1b, 3.2a, 3.2b and 3.3). For all taxa there was considerable scatter in the pooled data, although much of the observed variation in the data could be explained by the month-to-month differences in dry weight.

### **Diaptomus**

Model I regression statistics indicated that the individual (monthly) relationships between length and dry weight for Diaptomus were significant only at the beginning of the season for both lakes (Regression analyses  $P < 0.05$ , Tables 3.1a and 3.1b). A two-factor ANOVA was used to determine if the dry-weight estimates differed through the season within each lake or between lakes. Within each lake, the dry weights were significantly different only for the end of June and September (two-factor ANOVA  $P < 0.001$ ). Between lakes the dry weights were significantly higher in September in Mouse Lake ( $P = 0.035$ ).

Table 3.1a

Summary of Model I seasonal regression statistics for Diaptomus minutus dry weight in Ranger Lake ( $W = a + b L$ ;  $L = 0.51-0.76$  mm)

Date	b	a	n	r <sup>2</sup>	P
June 01	16.53	-7.16	13	0.63	0.001
June 30	11.17	-4.10	19	0.27	0.024
July 28	14.90	-6.54	20	0.19	0.054
Aug. 25	5.30	-0.28	19	0.03	0.474
Sept 21	7.47	-1.42	19	0.03	0.453
Pooled	12.08	-4.56	90	0.25	<0.001

Table 3.1b

Summary of Model I seasonal regression equations for Diaptomus minutus dry weight in Mouse Lake ( $W = a + b L$ ;  $L = 0.52-0.72$  mm)

Date	b	a	n	r <sup>2</sup>	P
June 01	18.44	-7.93	17	0.75	<0.001
June 30	12.41	-4.56	16	0.22	0.063
July 28	-4.68	5.58	20	0.02	0.579
Aug. 25	3.07	1.64	20	0.01	0.669
Sept 21	-8.66	10.11	20	0.01	0.613
Pooled	15.76	-6.26	93	0.29	<0.001

### Holopedium

Much of the variation in the pooled dry weight data for Holopedium in both lakes was explained by month-to-month differences (Fig. 3.2a and 3.2b; 3.3a and 3.3b). However, not all of the individual length-weight relationships were significant (Table 3.2a and 3.2b). The lack of statistical significance on certain dates was likely the result of the small sample size ( $n \leq 20$ ). In both lakes the length-weight regression equations were significant at the beginning and end of the sampling season (June 1 and September 21, respectively) and on one date mid-season (July 28 in Ranger Lake and June 30 in Mouse Lake). The slopes of the significant regression equations (Model I) for animals in both Ranger and Mouse Lakes were tested and the analyses indicated that the slopes were significantly different (ANCOVA  $P < 0.01$  and  $P < 0.05$ , respectively).

Model II regression statistics for Holopedium in Ranger Lake indicated that the functional relationship between weight and length varied across the season. The slopes of the individual regression equations varied from 2.25-2.87. The slope of the pooled regression equation was substantially higher than the individual equations (Model II regression, slope= 3.64). For Holopedium in Mouse Lake, the Model II regression statistics indicated that the functional relationship between length and weight was extremely variable through the season with slopes ranging from 0.34 to 7.59. This degree of variability may be attributed to clutch size which ranged from 0-7 eggs.

Table 3.2a

Summary of Model I and Model II regression statistics for Holopedium gibberum in Ranger Lake ( $\log W = a + b \log L$ ;  $L = 0.42 - 2.08 \text{ mm}$ )

Date	Model	b	S.E.	a	S.E.	n	r <sup>2</sup>	P
June 01	I	2.36	0.63	1.49	0.073	13	0.56	0.003
	II	2.87		1.44				
June 30	I	1.85	0.90	2.04	1.650	20	0.19	0.054
	II	2.25		1.93				
July 28	I	2.34	0.95	1.65	0.290	17	0.29	0.270
	II	2.85		1.48				
Aug. 25	I	2.07	0.13	0.81	0.480	20	0.14	0.115
	II	2.52		1.63				
Sept 21	I	1.96	0.58	1.59	0.070	20	0.39	0.003
	II	2.39		1.54				
Pooled	I	2.99	0.22	1.54	0.050	90	0.67	0.194
	II	3.64		1.40				

Table 3.2b

Summary of Model I and Model II regression statistics for Holopedium gibberum in Mouse Lake (Log W = a + b Log L; L = 0.42 - 2.32 mm)

Date	Model	b	S.E.	a	S.E.	n	r <sup>2</sup>	P
June 01	I	2.73	1.01	1.28	0.05	19	0.30	0.022
	II	4.28		1.29				
June 30	I	1.12	0.49	1.84	0.05	17	0.25	0.036
	II	1.76		1.82				
July 28	I	0.97	0.83	1.59	0.14	20	0.07	0.257
	II	1.52		1.50				
Aug. 25	I	0.22	0.34	1.80	0.05	20	0.02	0.529
	II	0.34		1.78				
Sept 21	I	4.84	1.85	1.16	0.52	20	0.28	0.018
	II	7.59		0.94				
Pooled	I	2.59	0.32	1.43	0.04	96	0.41	<0.001
	II	4.06		1.31				

Figure 3.1

a) Pooled length-weight regression relationship using all seasonal data for Holopedium gibberum in Ranger Lake  
b) Individual length-weight relationships of Holopedium gibberum in Ranger Lake. Lines are the least-squares regression equations.

Figure 3.1a

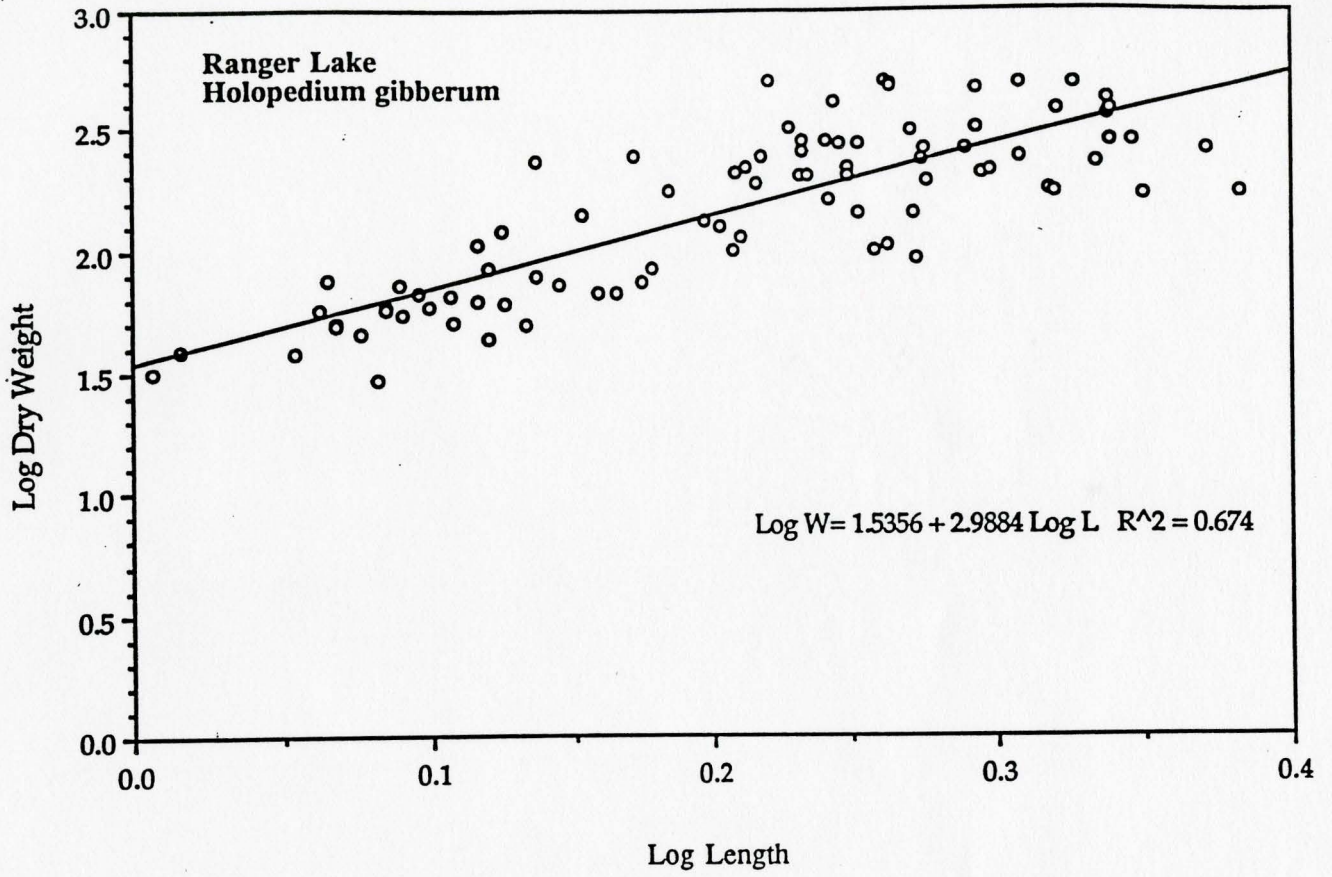


Figure 3.1b

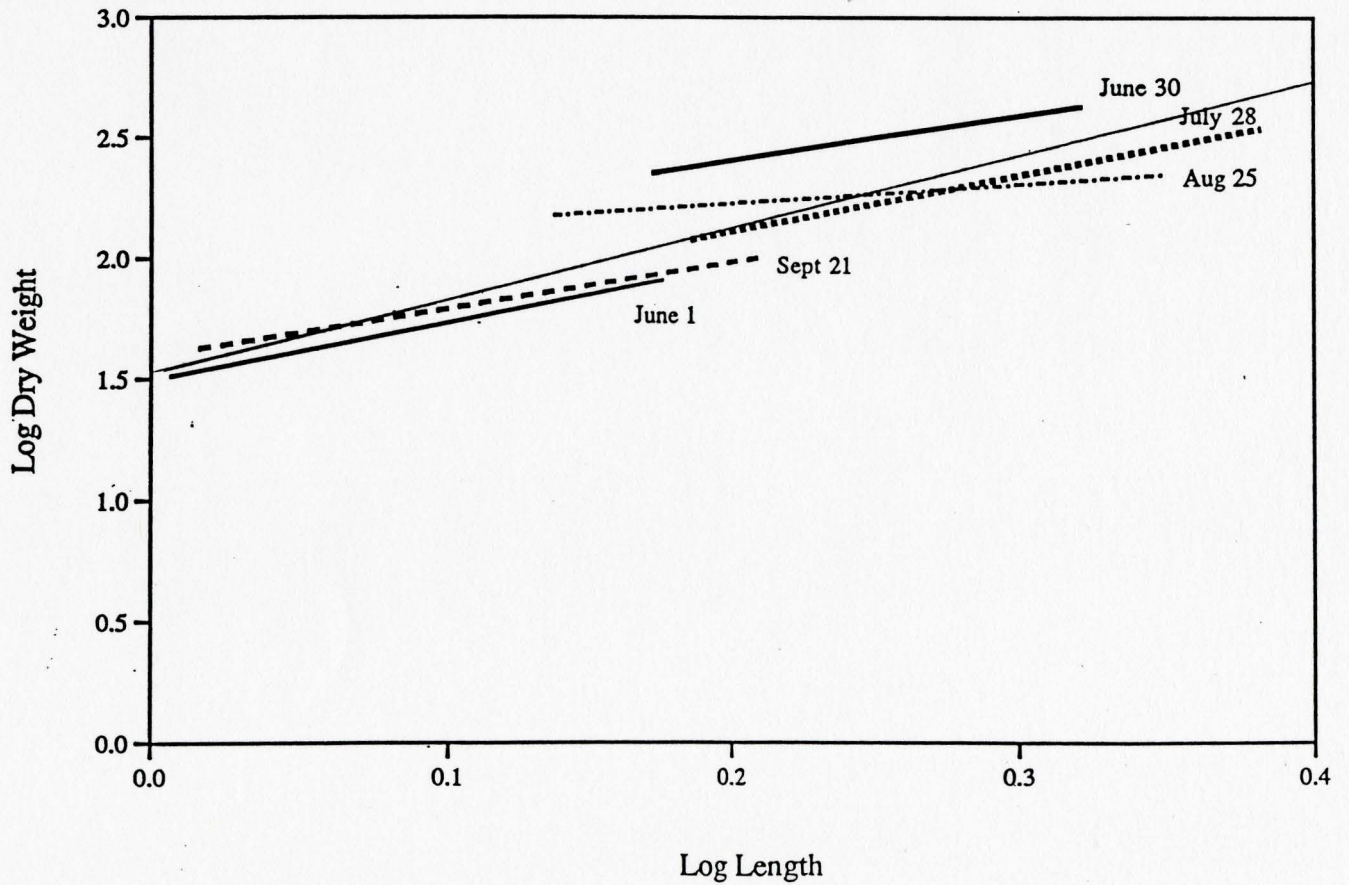




Figure 3.2

a) Pooled length-weight regression relationship using all seasonal data for Holopedium gibberum in Mouse Lake  
b) Individual length-weight relationships of Holopedium gibberum in Mouse Lake. Lines are the least-squares regression equations.

Figure 3.2a

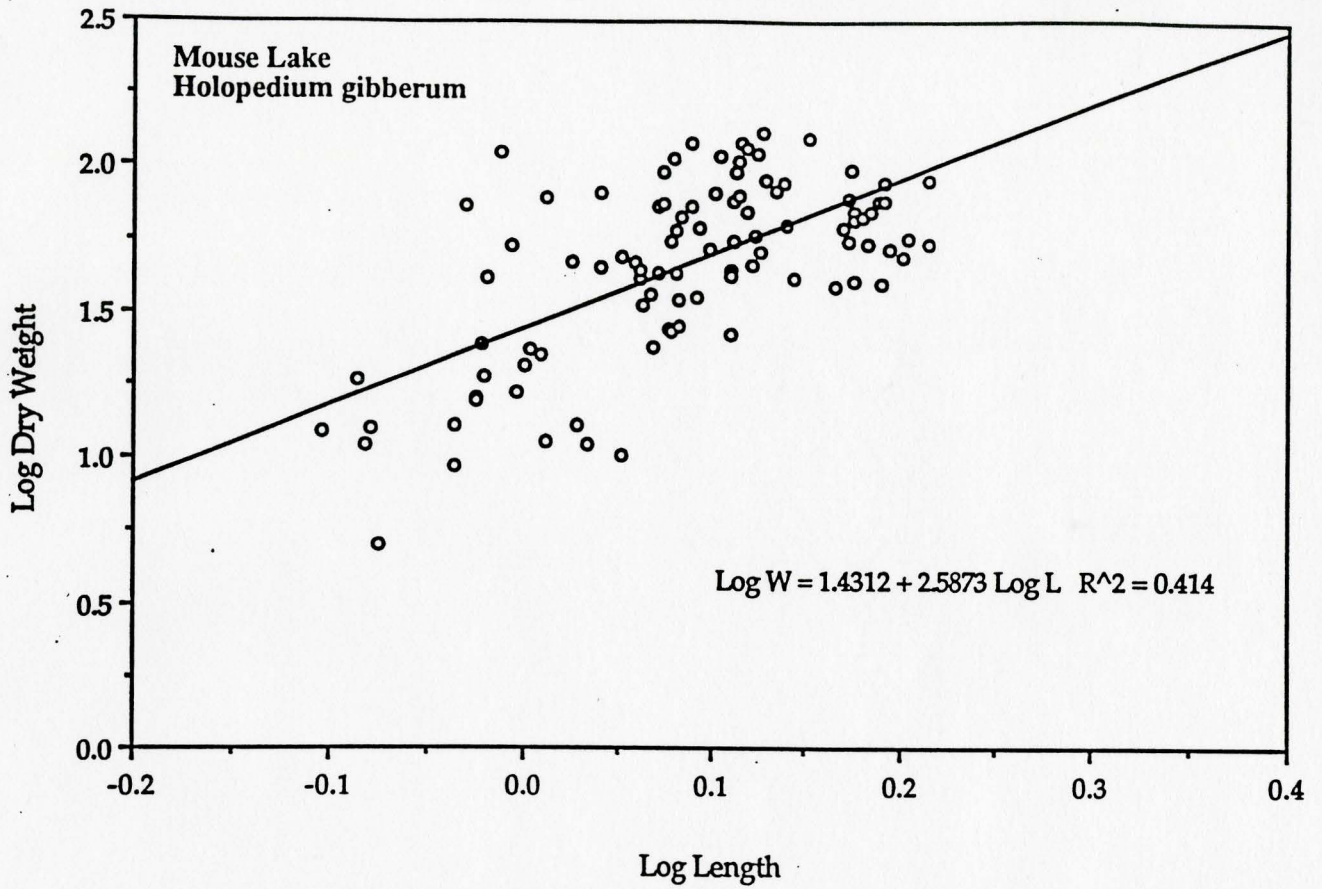
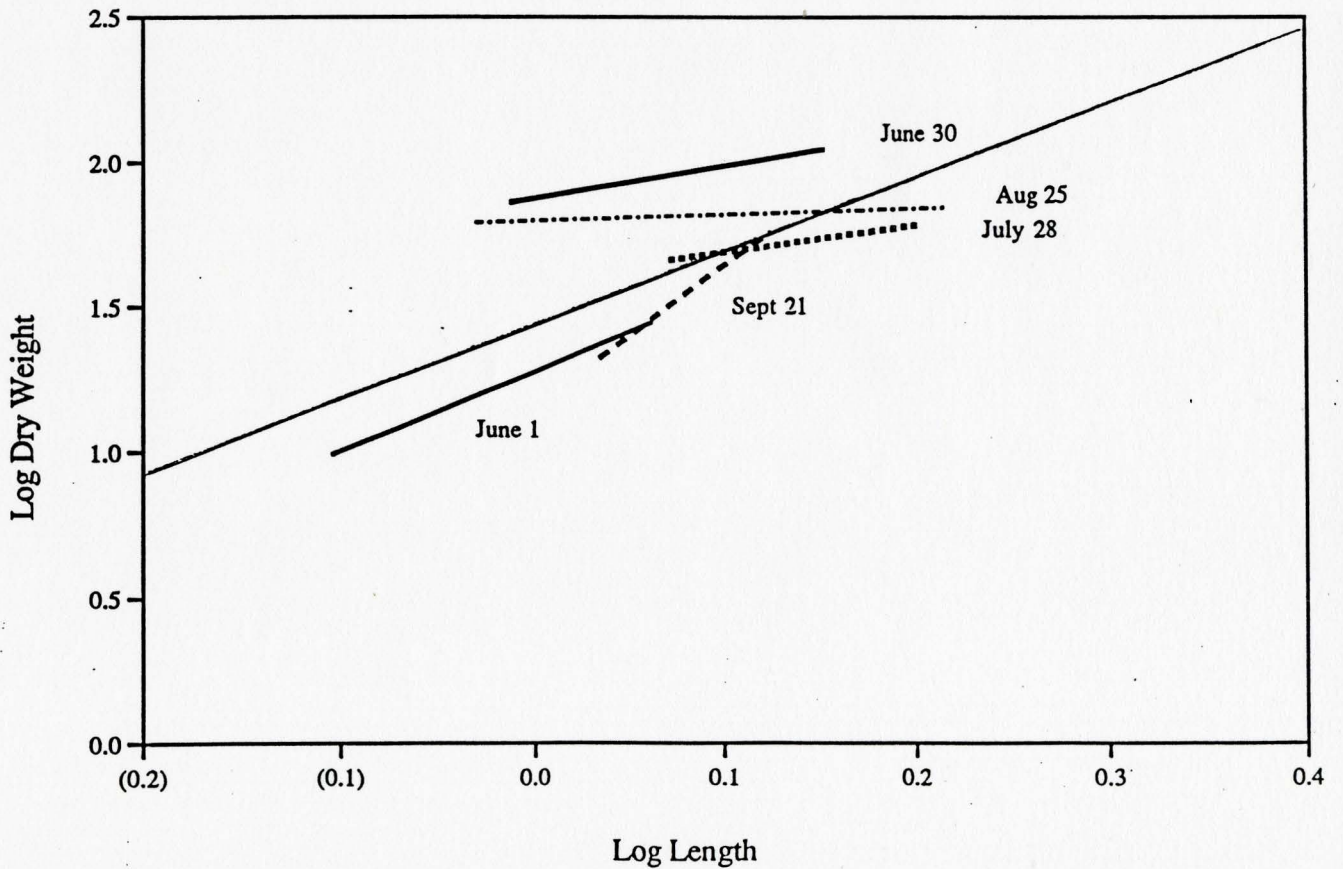


Figure 3.2b



### Daphnia

For Daphnia both the pooled length-weight regression equation and the regression equation generated for each date were statistically significant ( $P < 0.001$ , Table 3.3; Fig 3.3a). Analysis of covariance indicated no significant difference in the slopes of the individual regression lines ( $P > 0.50$ ). However, the elevations of the lines were significantly different (ANCOVA  $P < 0.025$ ; Fig. 3.3b) which indicated that the length-specific weights of animals collected in September were greater than the length-specific weights of animals collected earlier in the season, especially in July. Based on the Model II regression statistics, the slopes of the length-weight relationship ranged from 2.47 to 2.97 for the individual sampling dates.

### Seasonal Changes in Weight at Length

#### Diaptomus

To compare the dry weight differences across the season and between lakes, the mean lengths and dry weights were calculated (Tables 3.4a and 3.4b). Diaptomus in both lakes experienced a drop in mean dry weight at the end of June (Fig. 3.4a and 3.4b). Animals in Mouse Lake continued to increase in weight for the remainder of the season, while those in Ranger Lake remained relatively constant. Based on the weighted average length and dry weight, Diaptomus in Mouse Lake were heavier than those in Ranger Lake despite having a smaller average body length.

Table 3.3

Summary of Model I and Model II regression statistics for Daphnia catawba in Ranger Lake (Log W = a + b Log L; L = 0.51 - 2.3 mm)

Date	Model	b	S.E.	a	S.E.	n	r <sup>2</sup>	P
June 01	I	2.50	0.350	0.807	0.058	19	0.75	<0.001
	II	2.97		0.786				
June 30	I	2.23	0.360	0.914	0.075	20	0.68	<0.001
	II	2.65		0.832				
July 28	I	2.29	0.191	0.794	0.045	20	0.89	<0.001
	II	2.72		0.705				
Aug. 25	I	2.42	0.351	0.877	0.083	20	0.73	<0.001
	II	2.87		0.775				
Sept 21	I	2.08	0.376	1.058	0.081	20	0.63	<0.001
	II	2.47		0.981				
Pooled	I	2.36	0.153	0.877	0.033	99	0.71	<0.001
	II	3.80		0.793				

Figure 3.3

a) Pooled length-weight regression relationship using all seasonal data for Daphnia catawba in Ranger Lake.

b) Individual length-weight relationships of Daphnia catawba in Ranger Lake. Lines are the least-squares regression equations.

Figure 3.3a

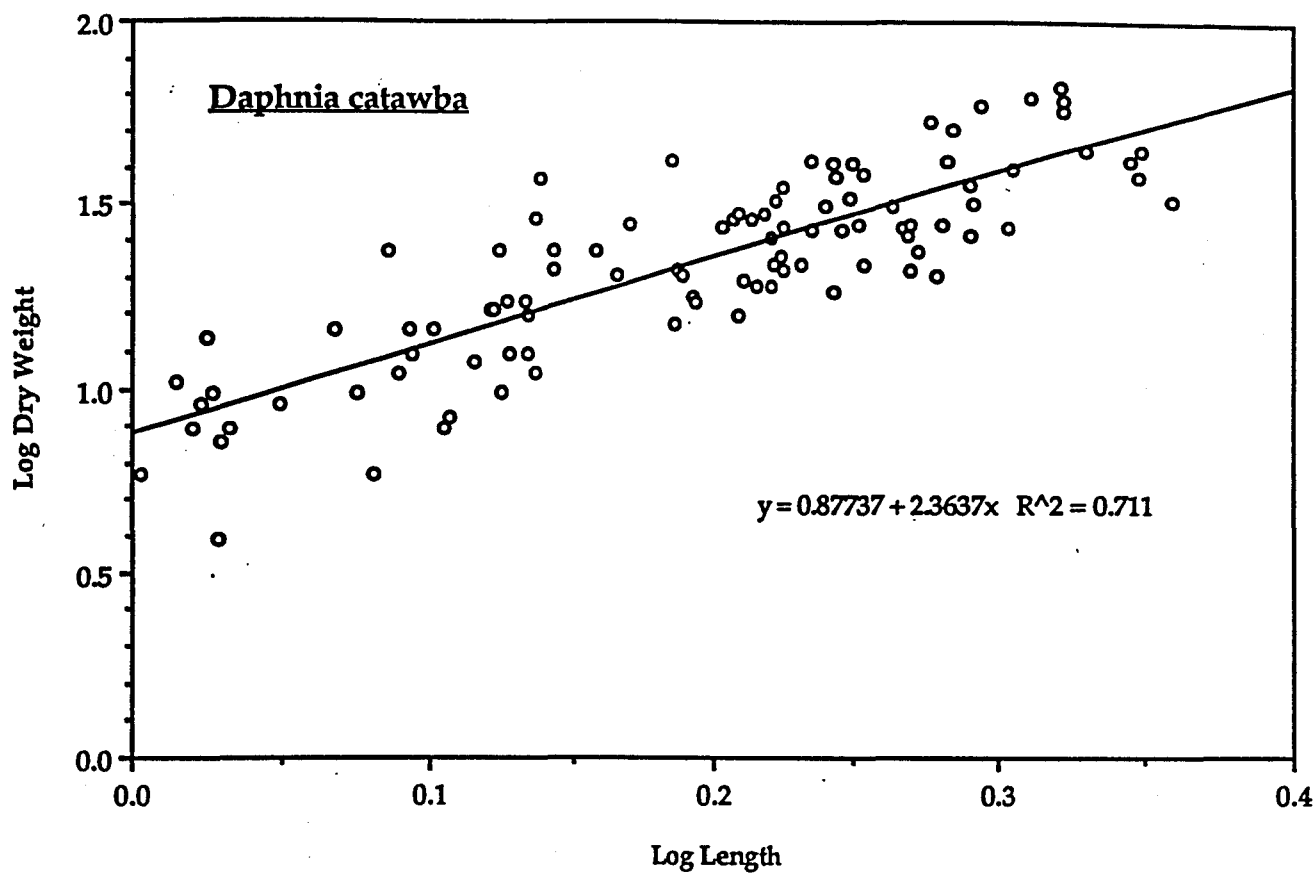


Figure 3.3b

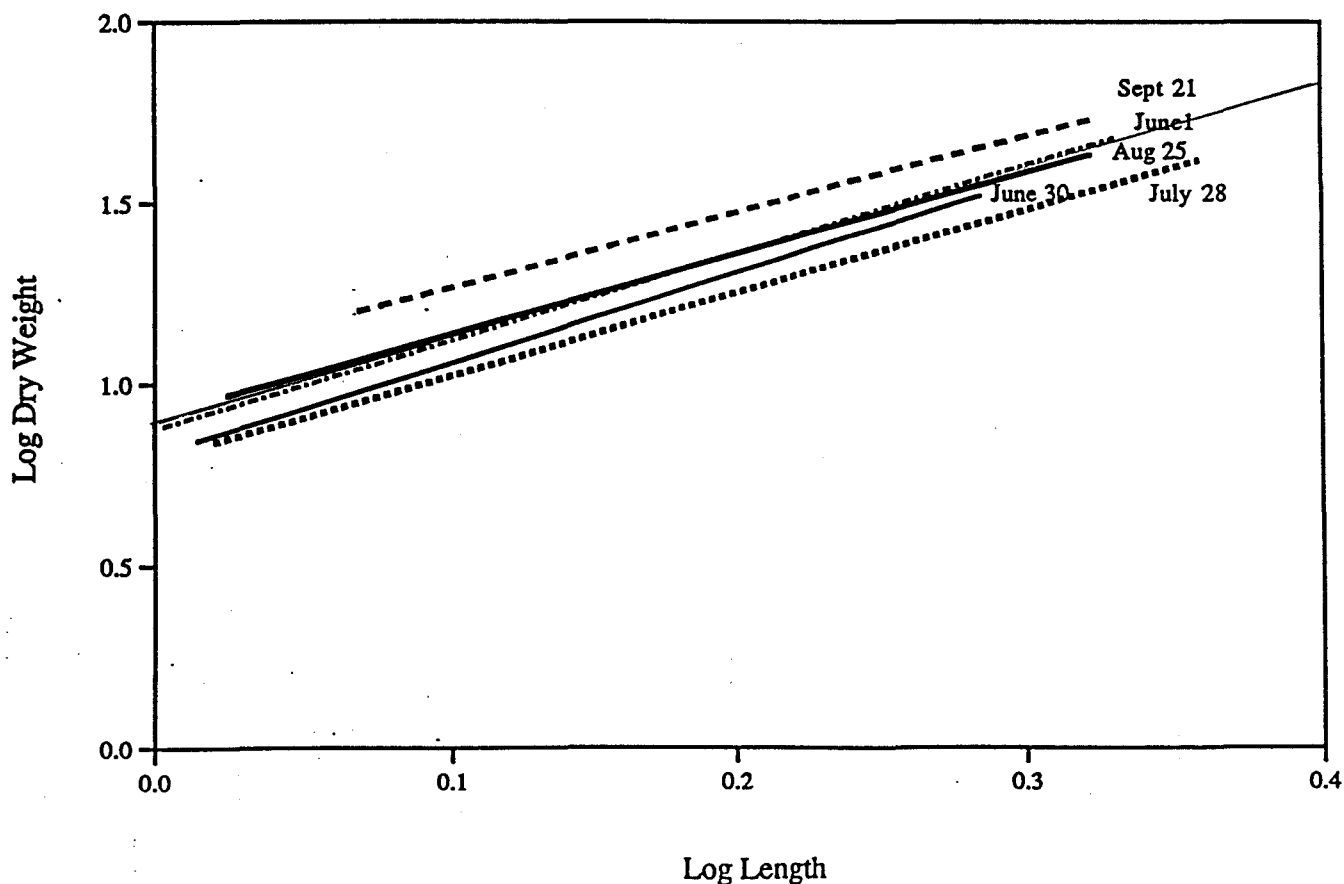


TABLE 3.4a Summary of average seasonal lengths and dry weights of Diaptomus minutus in Ranger Lake

Date	n	Average Length (mm)	S.E.	Average Dry Weight ( $\mu\text{g}$ )	S.E.
June 1	13	0.62	0.006	3.10	0.12
June 30	19	0.61	0.003	2.69	0.06
July 28	20	0.66	0.002	3.29	0.06
August 25	19	0.65	0.002	3.18	0.06
Sept 21	<u>19</u>	<u>0.62</u>	0.001	3.24	0.06
	90				
Weighted Averages:		0.633		3.10	

TABLE 3.4b Summary of average seasonal dry weights of Diaptomus minutus in Mouse Lake

Date	n	Average Length (mm)	S.E.	Average Dry Weight ( $\mu\text{g}$ )	S.E.
June 1	17	0.60	0.004	3.15	0.09
June 30	16	0.59	0.002	2.76	0.06
July 28	20	0.59	0.001	2.81	0.04
August 25	20	0.63	0.002	3.59	0.06
Sept 21	<u>20</u>	0.64	0.001	4.53	0.07
	93				
Weighted Averages:		0.611		3.40	

### Holopedium

The seasonal changes in the length-specific dry weights of Holopedium were estimated from a body length that was common to both lakes and present on all sampling dates (1.41 mm). The corresponding dry weights were averaged from raw data corresponding to  $\pm 0.20$  mm of the body length (Table 3.5). Holopedium in both lakes exhibited a dry weight peak in June that was followed by a substantial drop in dry weight in July, increasing only slightly in August; dry weight was lowest at the beginning and the end of the summer for Holopedium in both lakes.

The length-specific dry weight of Holopedium in each lake was interpolated using the pooled regression equations in order to compare these estimates with the individual monthly dry weight estimates (Table 3.5). The pooled length-weight regression produced quite different estimates than the month-to-month models (Table 3.5). In Ranger Lake the dry weight estimated using the general regression equation overestimated dry weight at the beginning and end of the summer by approximately 30%, while underestimating the dry weights mid-summer by as much as 40%. In Mouse Lake, the dry weight estimate for the beginning of the summer was overestimated (approximately 35%) when the general equation was applied, while July, August and September dry weight estimates fell within 20% of the dry weight estimated from the general equation.



TABLE 3.5 Mean dry weight estimates for 1.41 mm Holopedium gibberum in Ranger and Mouse Lakes calculated from the raw data for animals between 1.21 mm and 1.61 mm (A) and the dry weight estimate interpolated from the pooled regression equation with length = 1.41 mm (I)

Date	Ranger Lake	Mouse Lake
	Holopedium Dry Weight ( $\mu\text{g}$ )	Holopedium Dry Weight ( $\mu\text{g}$ )
June 1	65.3 (A)	43.1 (A)
June 30	242.3 (A)	103.5 (A)
July 28	153.4 (A)	59.0 (A)
Aug 25	163.7 (A)	70.5 (A)
Sept 21	65.7 (A)	51.7 (A)
Average	88.1 (A)	68.8 (A)
Pooled	95.8 (I)	65.7 (I)

## Daphnia

Since all monthly regression equations were found to be significant for Daphnia, I compared dry-weight estimates interpolated from the regression equations with the mean dry weight averaged from the raw data on each date to determine the accuracy of the developed individual length-weight models. The individual regression equations estimated the dry weights within 2% to 7% of the calculated mean dry weight for 1.5 mm animals (Table 3.6). While the monthly regression equations provided weight estimates that were comparable with the raw data, the pooled regression equation generated a dry weight estimate which deviated substantially from the individual monthly dry weight estimates, overestimating the dry weight by as much as 20% in July and underestimating the dry weight by approximately 25% in September.

## **Seasonal Changes in Phytoplankton**

Both lakes experienced a mid-summer peak in total phytoplankton biomass; however, the biomass in Ranger Lake in mid-summer far exceeded that in Mouse Lake (Fig. 3.4a). The seasonal changes in chlorophyll a (Ramcharan et al. 1993, unpub.) mirrored the trends in total phytoplankton for both lakes (Fig. 3.4b). Although the edible phytoplankton biomass based on stomach content analyses for Holopedium and Daphnia appeared to graphically resemble the trends observed for total phytoplankton biomass (Fig 3.4a; Fig. 3.5a and 3.5b), the actual percent edible phytoplankton fluctuated considerably. Diaptomus in both lakes appeared to have available a

TABLE 3.6 Dry weight estimates for 1.5 mm Daphnia catawba. Estimates were interpolated from the length-weight regression equations for each date and using the pooled regression equation. Mean dry weight estimates were also calculated from the raw data for 1.5 mm animals (mean dry weight were based on animals between 1.3 mm and 1.7 mm).

Date	Interpolated Dry Weight Estimate ( $\mu\text{g}$ )	Mean Dry Weight ( $\mu\text{g}$ )	S.E.
June 1	17.7	18.0	0.74
June 30	20.2	18.7	0.57
July 28	15.7	16.7	2.92
Aug 25	20.1	21.6	1.11
Sept 21	26.6	25.6	0.83
Pooled	19.7	20.6	0.21

Figure 3.4

- a) Seasonal changes in total phytoplankton biomass in Ranger Lake and Mouse Lake
- b) Seasonal changes in chlorophyll a in Ranger Lake and Mouse Lake

Figure 3.4a

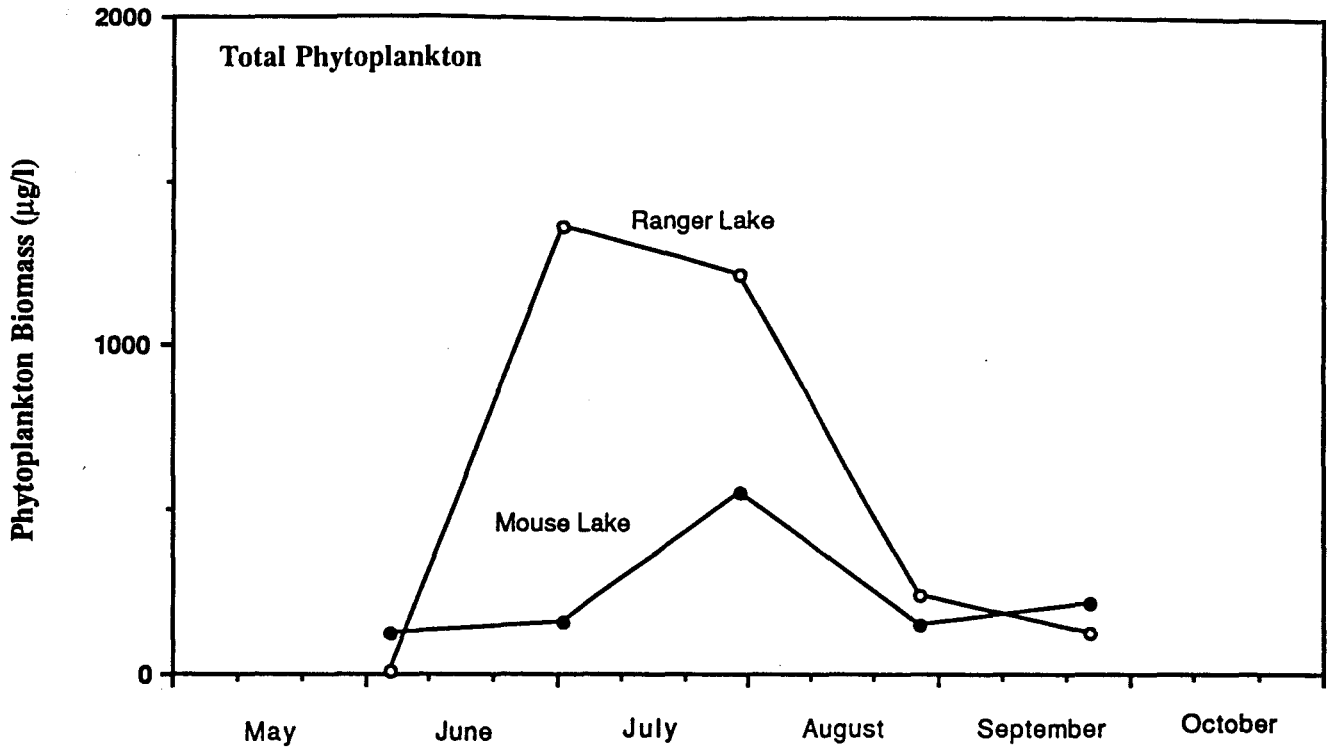


Figure 3.4b

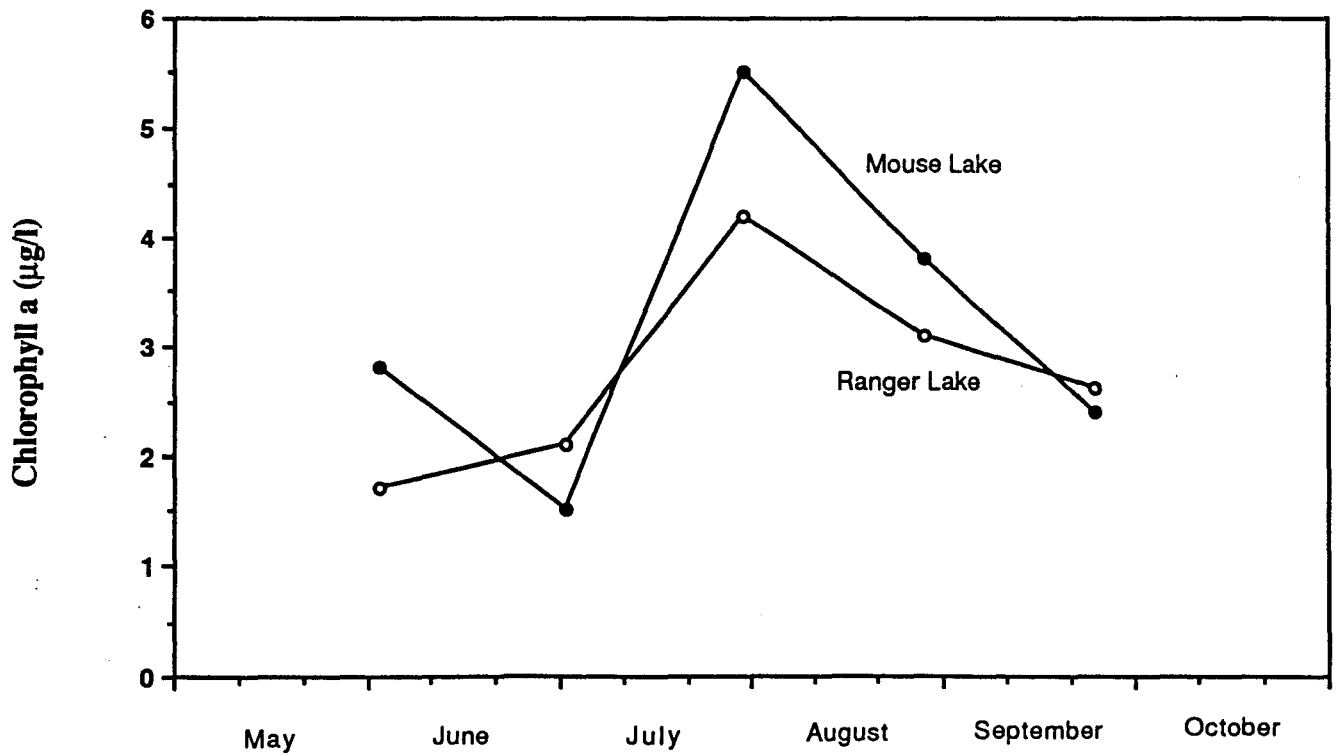


Figure 3.5

Seasonal changes in edible phytoplankton biomass determined from stomach content analyses for a) Holopedium, Daphnia and Diaptomus in Ranger Lake. b) Holopedium and Diaptomus in Mouse Lake

Figure 3.5a

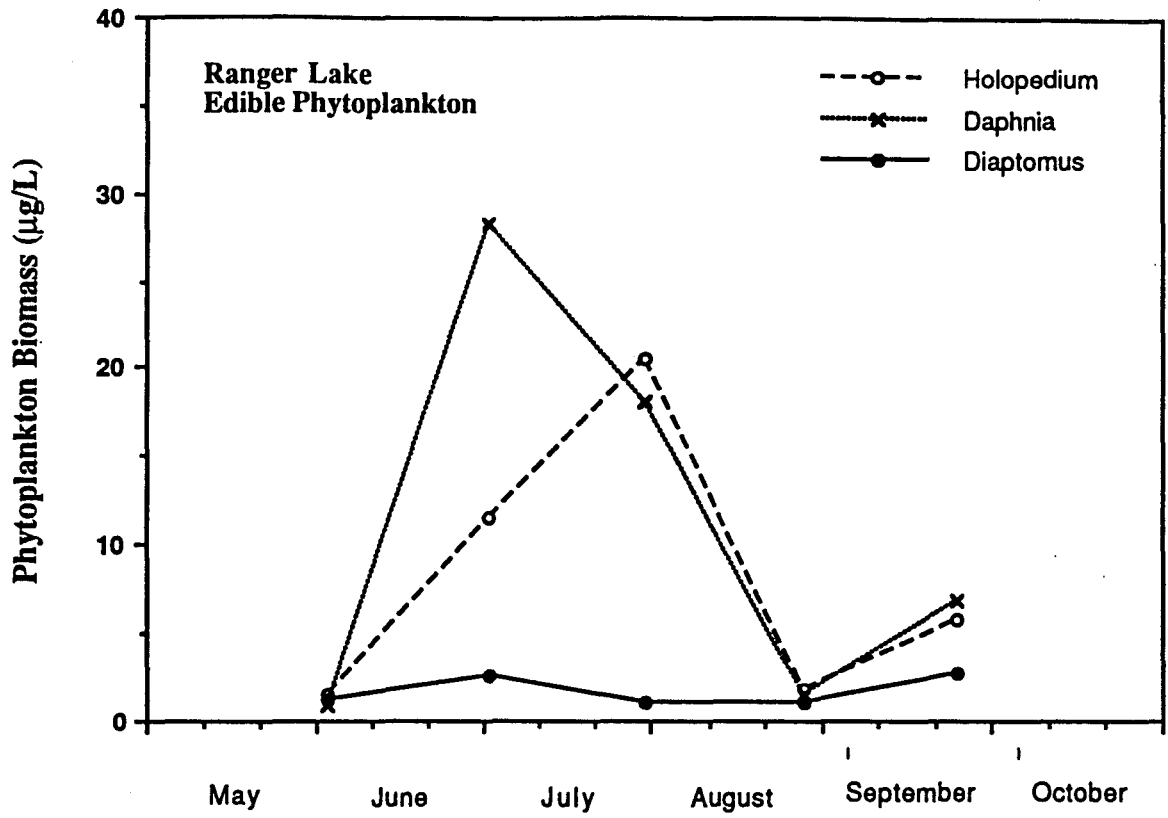
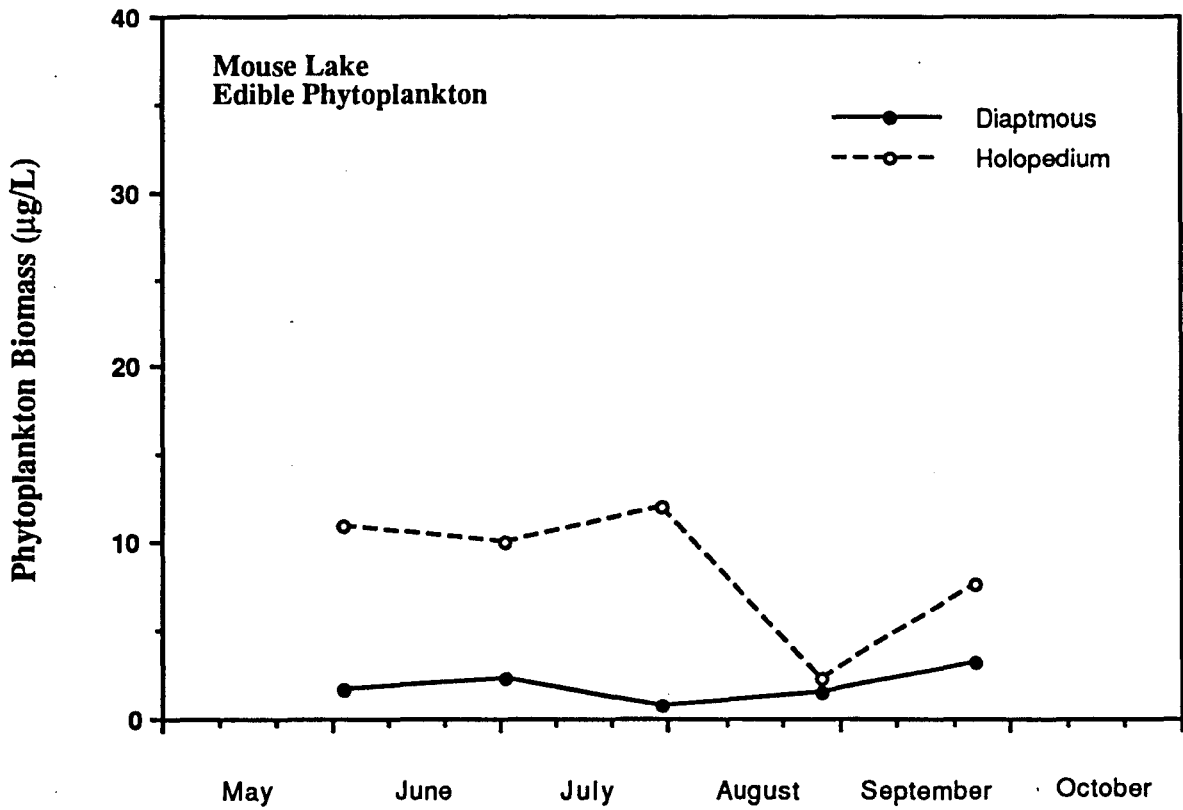


Figure 3.5b



relatively constant biomass of "edible" food; however, the actual percent edible phytoplankton represented less than 10% of the total phytoplankton in both lakes mid-season.

### **Seasonal Changes in Zooplankton Density**

The abundance of Diaptomus were higher in Ranger Lake than Mouse Lake throughout the season with the highest densities at the end of the season in both lakes (Fig. 3.6a and b). Holopedium in Ranger Lake were far less abundant for most of the season (Fig. 3.6a and b) except for September which marked a drastic increase in densities of both Holopedium and Daphnia. The density of Holopedium in Mouse Lake was highest at the end of June; however, towards the end of the season the density dropped substantially.

### **Length, Food, Clutch Size, Density and Temperature as Predictors of Dry Weight**

Stepwise regression analyses were employed to determine which variables should be included as predictors in the multiple regression models for each herbivore in the two lakes. The variables included in each model for Diaptomus, Holopedium and Daphnia have been summarized in Table 3.7.

#### **Diaptomus**

Length was the only significant predictor of Diaptomus dry



Figure 3.6      Seasonal changes in population density  
of various zooplankton taxa in a) Ranger  
Lake and b) Mouse Lake

Figure 3.6a

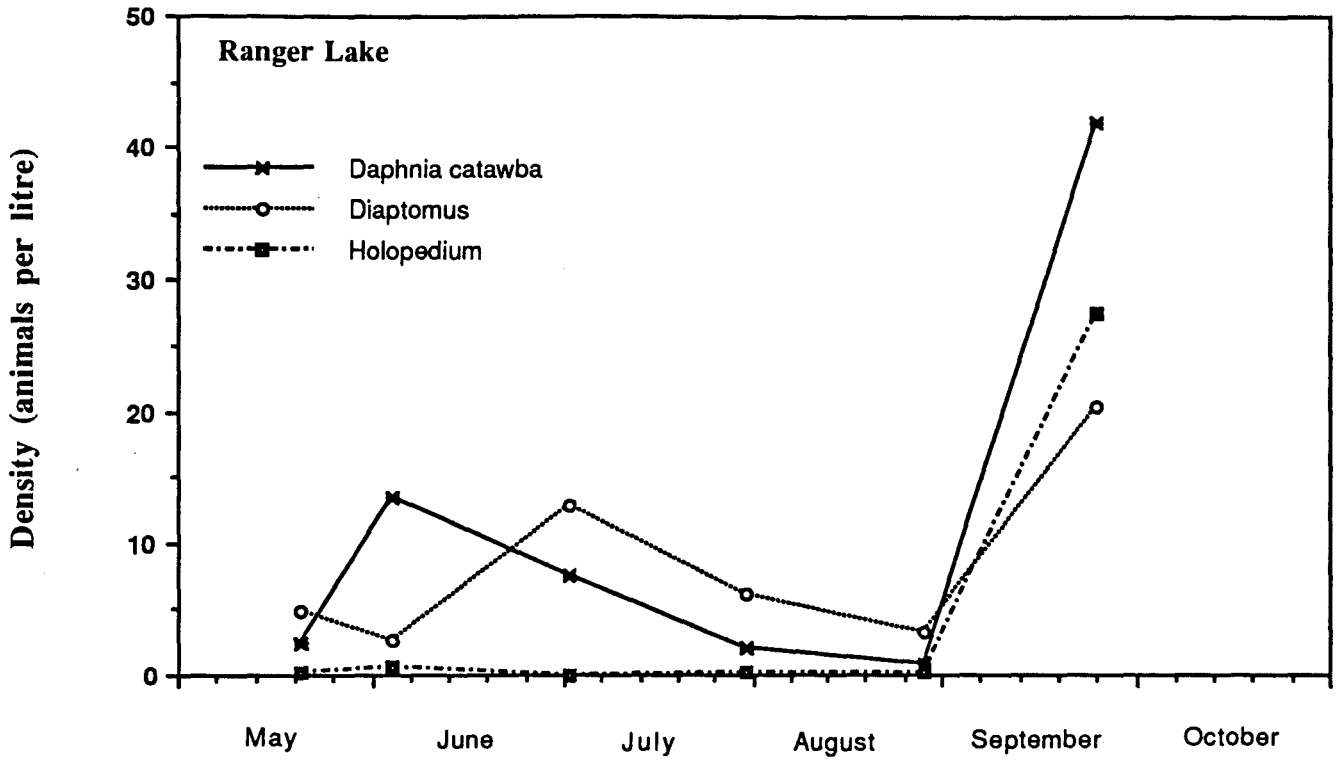


Figure 3.6b

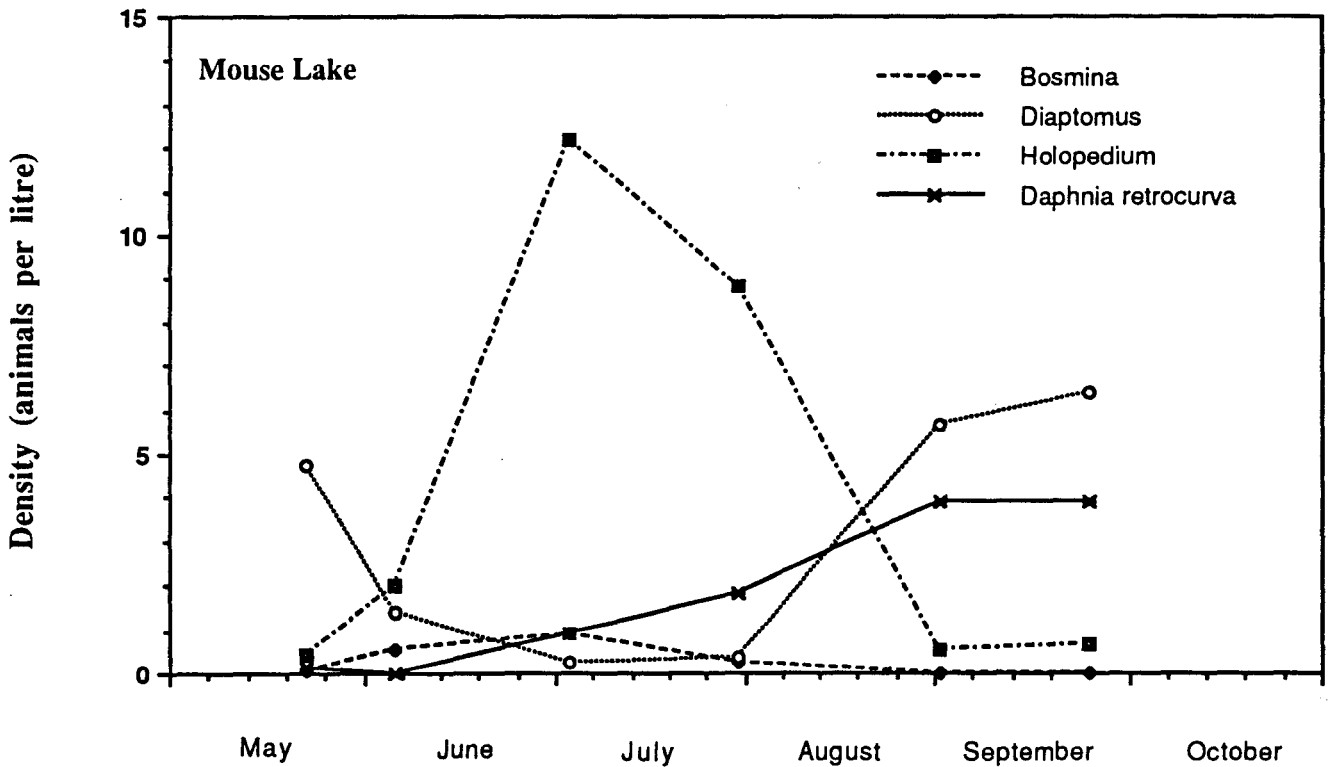


Table 3.7

Summary of multiple regression variables for Diaptomus, Holopedium and Daphnia in Mouse and Ranger Lakes. Total represents the total phytoplankton biomass.

Lake	Animal	Variable	r <sup>2</sup>	P	
Mouse	<i>Diaptomus</i>	length	0.356	<0.001	
		density	0.393	<0.001	
	<i>Holopedium</i>	length	0.420	<0.001	
		density	0.450	0.025	
	Ranger	<i>Diaptomus</i>	length	0.230	<0.001
		<i>Holopedium</i>	length	0.670	<0.001
total			0.800	<0.001	
density			0.830	<0.001	
<i>Daphnia</i>		length	0.710	<0.001	
		density	0.740	<0.001	

weight common to both Ranger and Mouse Lakes (Table 3.7). After length was entered into the regression model for Diaptomus in Ranger Lake, the addition of the remaining variables did not explain any significant amount of the remaining residual variation; therefore the regression model that best predicts dry weight of Diaptomus in Ranger Lake was as follows :

$$(1) \text{ Log W} = 2.432 (\pm 0.48) \text{ Log L} + 0.942 \quad P < 0.001, r^2 = 0.23, n=90$$

Population density was also a significant predictor variable in the regression model for Diaptomus in Mouse Lake which when added to the model explained approximately 40% of the residual variation (Table 3.7). I regressed length and density against weight to obtain the following regression model for Diaptomus in Mouse Lake:

$$(2) \text{ Log W} = 2.521(\pm 0.44) \text{ Log L} + 0.060(\pm 0.03) \text{ Log D} + 1.029$$

$$P < 0.001, r^2 = 0.39, n=94$$

Based on this model, weight is a positive function of length and population density. Clutch size could not be measured as a predictor variable for Diaptomus in this study, but I believe that clutch size would have contributed significantly to the dry weight of females.

### Holopedium

The stepwise regression analyses indicated that several variables could be used as predictors of weight for Holopedium in the

two lakes. Only those variables that were significantly related to weight and able to further explain the residual variation were included in the regression models. In Ranger Lake, length, population density (D) and total phytoplankton biomass (T) were regressed against weight to yield the following regression model for Holopedium:

$$(3) \quad \text{Log } W = 1.65(0.23)\text{Log } L + 0.132(0.03)\text{Log } T - 0.075(0.012)\text{Log } D \\ + 1.445 \quad P < 0.001, r^2 = 0.83, n = 89$$

The weight of Holopedium in Ranger Lake thus appears to be a positive function of length and total phytoplankton biomass and a negative function of population density.

Population density was also a significant predictor variable of Holopedium weight in Mouse Lake. However, in contrast to Holopedium in Ranger Lake, estimates of food were not significantly related to the weight in this lake. Therefore, length and density were regressed against weight to produce the following regression model:

$$(4) \quad \text{Log } W = 2.474(0.315) \text{Log } L + 0.099(0.044) \text{Log } D + 1.405 \quad P < 0.001, \\ r^2 = 0.45, n = 96$$

Clutch size, which ranged from 0 to 7 eggs, was not significantly related to Holopedium dry-weight in either lake. However, length-

weight regressions computed to include ovigerous females often exhibit dramatic seasonal changes in accordance with shifts in the food supply (Geller and Muller 1985). Since the clutch can account for 50% or more of the total mass of a female cladoceran (Lynch 1989), separate regression models with and without ovigerous females may reduce the variation in dry weight and improve dry weight estimates.

### Daphnia

For Daphnia in Ranger Lake factoring population density into the regression model improved predictability of log W, increasing  $r^2$  to 0.74 from 0.71 (Table 3.7). Although Daphnia in Ranger Lake exhibited a generalist feeding pattern (see Chapter 2), the estimates of food were not significantly related to weight. Body length and population density regressed against weight to generate a regression model for Daphnia:

$$(5) \text{ Log W} = 2.445(0.15) \text{ Log L} + 0.072(0.022) \text{ Log D} + 0.807$$

$$P < 0.001, r^2 = 0.74, n = 99$$

For Daphnia in Ranger Lake, weight was a positive function of both length and population density.

### **Bottom-up and Top-down Effects**

The first testable hypothesis for the study was that the weight of a given length will be lower for Mouse Lake than for Ranger

TABLE 3.8 A comparison of the seasonal means of total phytoplankton, chlorophyll a, edible phytoplankton and mean dry weight for Diaptomus and Holopedium in Mouse and Ranger Lakes. The mean dry weight for Holopedium was based on the data for a 1.41 mm animal as indicated in Table 5.

	Mean Total Phytoplankton ( $\mu\text{g/L}$ )	Chl a	Mean Edible Phytoplankton ( $\mu\text{g/L}$ )	Mean Dry Weight ( $\mu\text{g}$ )
<u>Ranger L.</u>				
Diaptomus	579.4	2.7	14.6	3.10
Holopedium	579.4	2.7	111.9	88.06
<u>Mouse L.</u>				
Diaptomus	238.7	3.2	15.9	3.40
Holopedium	238.7	3.2	111.5	68.80

Lake animals if there are any top-down effects of planktivorous fish on herbivore weight. That the weight of Holopedium in Mouse Lake (high planktivore population) was consistently lower than those in Ranger Lake throughout the season (Table 3.5), is consistent with the first hypothesis. However, the seasonal mean dry weight of Diaptomus in Mouse Lake (3.40  $\mu\text{g}$ ) was higher than the mean dry weight of Diaptomus in Ranger Lake (3.10  $\mu\text{g}$ ) and this is inconsistent with this hypothesis.

The second testable hypothesis was that the weight of a given length will be higher for herbivores in the lake with more available food. To test this hypothesis I compared the mean value of each food estimate with the mean dry weight for Holopedium and Diaptomus in the two lakes (Table 3.8). The higher mean weight of Diaptomus in Mouse Lake was consistent with a higher mean biomass of edible phytoplankton based on stomach content analyses. Neither total phytoplankton biomass nor chlorophyll a demonstrated any consistent trends with respect to the correspondence between mean dry weight and available food for either taxa.



## GENERAL DISCUSSION

The dry weights of Diaptomus, Daphnia and Holopedium varied seasonally in both Mouse and Ranger Lakes. These dry weight changes were taxa-specific and unique to each lake and, although comparisons of the animals common to both lakes could be made, it is necessary to consider each lake separately in order to explain the observed differences in dry weight changes.

While length was a good predictor of dry weight on all occasions for Daphnia in Ranger Lake, length measurements alone could not account for the seasonal variation in dry weight for either Diaptomus or Holopedium. In both lakes the length and dry weight of Diaptomus and Holopedium became uncoupled as the season progressed. The subtle dry-weight changes in Daphnia and Diaptomus and the very obvious changes in Holopedium clearly illustrate the need to incorporate factors such as zooplankton density and food abundance.

Zooplankton dry weight is commonly estimated from length measurements and rarely are dry weight measurements taken directly (see review by Downing and Rigler 1984). The fact that dry-weight differences were apparent for the same species in two lakes with very similar morphometry suggests that applying published taxon-specific length-weight regression equations with no consideration of interlake differences and seasonal differences can lead to large errors. For example, if the pooled regression were used to generate weights for Holopedium, the individual estimated dry weight could produce a 30-

40% error. Also, the error incurred would be even higher if the pooled regression equation for Holopedium in Mouse Lake were used to estimate weight of Holopedium in Ranger Lake or vice versa. The results of this study support Lawrence et al.'s (1987) recommendation that estimates of zooplankton dry weight be generated specifically for each study.

Models that include indices of physiological condition and environmental covariates that affect animal weight, in addition to length, are believed to have wider applicability (Yan and Mackie 1987). In this study the quality and quantity of resources available, population density and clutch size were considered as potential predictor variables that may further explain the observed seasonal changes in herbivore dry weight. These variables, however, are clearly not independent. While laboratory experiments allow for controlled environments, the correlations between food, animal density and clutch size makes it difficult to separate the effects of these variables in a natural environment, especially since density and per-capita reproduction are reported to change with food availability (Elmore 1983; Williamson and Butler 1987; Kerfoot et al. 1988).

Population density was an important predictor variable for all of the taxa in Mouse Lake. In each case, weight was a positive function of population density which may have been possible if the food resources available to these animals were not limited. It is

also possible that at high population density the chances of being eaten were reduced and, therefore, adults were able to grow for a longer period of time which may have resulted in a higher weight. Further research is needed to determine if there is a relationship between population size and the effects of predation. In Ranger Lake, the coefficient of population density was positive for Daphnia (Equation 5) but negative for Holopedium (Equation 3). The effects of population density may be different for these two animals due to intraspecific or interspecific competition and the differential ability of the herbivores to exploit the available resources.

Although both Holopedium and Diaptomus were more abundant in Mouse Lake, these animals exhibited smaller mean body lengths than those in Ranger Lake; Holopedium also weighed less on average. Since most planktivorous fish prefer larger bodied prey (Tessier et al. 1992), these herbivores may have reduced predation pressures by maintaining a smaller body length. It is also possible that Holopedium in Mouse Lake weighed less than those in Ranger Lake because they inadvertently fed less in an attempt to avoid being detected by predators. Arts and Sprules (1988) showed that Holopedium exposed to planktivores had proportionately lower lipid reserves in their eggs and this may have resulted if they did not feed as frequently compared with populations that are not subjected to high predation pressure.

The lower weight of Holopedium in Mouse Lake was consistent

with the initial hypothesis that herbivores exposed to predation would have a lower weight at length than those not subject to predation if, in fact, predation affected the weight of the individuals. In contrast, Diaptomus in Mouse Lake had a higher mean weight per unit length than those in Ranger Lake, and this is inconsistent with the hypothesis. Comparing changes in predator density through the season with changes in length-specific weight for herbivores in Mouse Lake may provide further insight into the effects of predation on herbivore weight.

The seasonal dry weight patterns of Daphnia were opposite the trends observed for co-occurring Holopedium. This pattern was most apparent over the last half of the season when food resources were limited and diet overlap between these cladocerans was high (Chapter 2). Kerfoot et al. (1988) have suggested that in communities with few planktivores (ie. Ranger Lake), herbivores are subject to mainly food limitation and competitive dynamics which may explain the opposing dry weight patterns observed in the two cladocerans. The differential ability to exploit the lower quality foods available towards the end of the season may have helped regulate these zooplankton populations (Sterner et al. 1993). It is also possible that Holopedium and Daphnia avoid competition for the same food by segregating their food resources.

The influences of predation and resource availability on the biomass of zooplankton may be equally strong and difficult to

interpret (McQueen et al. 1989). However, research conducted by Smith and Cooper (1982) on cladoceran populations suggests that predation seems to have an effect only after the zooplankton themselves have exhausted their food supply.

Temperature was not an important variable related to herbivore dry weight changes in this study, although it is a closely correlated with food concentrations in nature (Williamson and Butler 1987) and has also been correlated to clutch size (Chow-Fraser and Maly 1991; Elmore 1983). Calculating the mean temperature of a depth which encompasses a broad range in temperatures (eg. 6 m) may not have reflected accurate and appropriate temperature data required for this type of study.

Body lipids may also be an important variable governing seasonal changes in herbivore dry weight (Yan and Mackie 1987; Arts and Sprules 1988). Consideration of the amount of lipid stored by these herbivores may not only improve the models for dry weight estimates, but may also indicate food shortages in natural population since the amount of lipid stored depends on food concentration and quality (Tessier and Goulden 1982).

In summary, this study has shown that seasonal changes in zooplankton body length were significantly related to seasonal dry weight changes in Diaptomus, Holopedium and Daphnia, but that length alone could not precisely predict the seasonal weight changes of

Holopedium and Diaptomus. Population density and total phytoplankton biomass differentially affected the dry weight of these herbivores; effects were both taxa- and lake-specific.

The influences of predation and resource availability on herbivore weight is an area in need of much further research. While Holopedium dry-weight differences were consistent with the presence or absence of a predator population, Diaptomus dry weight differences were not. Because of this inconsistency it is difficult to determine whether the predator effect on herbivore weight is real. It is possible that Diaptomus weight may not be influenced by predation if the planktivores were differentially selecting Holopedium. Since the mean edible phytoplankton biomass (Ed-SCA) for each herbivore was not substantially different between lakes, the effects on food availability of herbivore dry weight were inconclusive. However, the dietary differences among herbivores and seasonal shifts in dietary preference was a real phenomenon that cannot be ignored if future studies are interested in determining the food available to herbivorous zooplankton.

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## **APPENDIX A**

### **Stomach Content Analyses**

Stomach Content Analyses of *Diaptomus minutus* in Ranger Lake

Date	Food Item	Algal Mass ( $\mu\text{m}$ )	Number in gut	Lake Biomass ( $\mu\text{g/L}$ )	Alpha	Electivity
June 1	Chrysospharella	676.8	8	2.68	0.028	-0.016
	Cryptophyta	448.8	8	0.71	0.069	0.425
	Stichoglea	293.0	132	1.86	0.286	0.840
	Ochromonas	555.6	50	0.88	0.433	0.900
	Cryptomonads (S)	86.9	27	0.41	0.078	0.473
	Chlorella	203.7	30	2.91	0.029	0.005
	Rhodomonas	47.6	47	0.98	0.031	0.046
	Dinobryon sp.	1458.7	2	0.87	0.046	0.240
June 30	Dinobryon sp.	1458.6	1	1172.91	0.000	-0.984
	Merismopedia	3.2	16	2.90	0.003	-0.799
	Stichoglea	107.6	20	8.02	0.049	0.268
	Rhodomonas	54.2	11	1.20	0.090	0.531
	Ochromonas	164.6	21	4.70	0.134	0.665
	Cryptomonads (S)	202.0	12	6.73	0.066	0.402
	Chlorella	92.5	11	0.59	0.317	0.857
	Chrysidiastrum	99.0	12	1.73	0.126	0.644
	Scenedesmus	364.3	4	1.24	0.215	0.785
July 28	Merismopedia	3.9	128	10.01	0.006	-0.669
	Aphanocapsa	3.1	144	0.10	0.631	0.939
	Cryptomonads (S)	278.1	9	4.85	0.059	0.356
	Chlorella	172.0	2	3.55	0.011	-0.443
	Rhodomonas	30.8	9	0.93	0.034	0.092
	Uroglena sp.	306.8	16	328.08	0.002	-0.888
	Chrysidiastrum	63.7	4	0.30	0.096	0.555
	Chroococcus	35.6	20	0.51	0.161	0.716
August 25	Cryptomonads (S)	370.0	5	15.85	0.018	-0.230
	Merismopedia	3.1	16	0.84	0.009	-0.518
	Chlorella	190.6	3	3.63	0.024	-0.083
	Rhodomonas	52.3	12	0.50	0.194	0.762
	Ochromonas	284.5	3	3.16	0.042	0.189
	Uroglena sp.	185.0	4	111.63	0.001	-0.932
	Stichoglea	23.6	5	0.06	0.324	0.860
	Chrysidiastrum	256.0	8	0.81	0.388	0.887
Sept 25	Cryptomonads (S)	351.0	8	7.24	0.077	0.467
	Cryptomonads (L)	1788.9	2	23.09	0.031	0.035
	Gleocapsa	17.9	4	0.03	0.498	0.916
	Aphanocapsa	1.9	10	0.08	0.045	0.223
	Chlorella	152.6	10	3.15	0.096	0.553
	Rhodomonas	26.5	18	1.85	0.051	0.287
	Ochromonas	440.4	11	4.77	0.201	0.770
	Uroglena sp.	108.4	8	72.05	0.002	-0.848
	Dinobryon sp.	1458.6	6	4.37	0.261	0.824

Stomach Content Analyses of *Diaptomus minutus* in Mouse Lake

Date	Food Item	Algal Mass ( $\mu\text{g}$ )	Number in gut	Lake Biomass ( $\mu\text{g/L}$ )	Alpha	Electivity
June	Cryptomonads (S)	190.6	1	4.84	0.005	-0.712
	Cryptomonads (M)	302.6	3	1.20	0.093	0.544
	Aphanocapsa	24.4	42	0.21	0.595	0.934
	Chlorella	187.4	8	5.65	0.033	0.070
	Rhodomonas	32.3	21	1.38	0.061	0.367
	Ochromonas	531.3	15	9.27	0.106	0.590
	Chrysidiastrum	42.8	8	0.41	0.104	0.582
	Dinobryon sp.	1458.6	1	69.95	0.003	-0.836
June 30	Dinobryon sp.	1458.6	1	80.49	0.001	-0.897
	Uroglena (S)	205.5	4	13.52	0.005	-0.692
	Chroococcus	9.2	30	0.38	0.062	0.379
	Aphanocapsa	42.8	12	14.52	0.003	-0.809
	Cryptomonads (S)	525.1	11	3.75	0.133	0.663
	Chlorella	105.4	12	2.51	0.044	0.212
	Rhodomonas	19.9	19	0.24	0.138	0.673
	Ochromonas	535.9	27	2.05	0.612	0.936
July 28	Aphanocapsa	8.2	30	0.56	0.062	0.373
	Chroococcus	12.0	18	0.72	0.043	0.203
	Gleocapsa	11.3	24	0.81	0.047	0.255
	Merismopedia	1.6	16	0.27	0.013	-0.375
	Chrysidiastrum	52.3	10	0.33	0.223	0.793
	Ochromonas	120.0	6	0.95	0.107	0.592
	Rhodomonas	14.1	12	0.11	0.214	0.784
	Chlorella	152.6	3	2.91	0.022	-0.124
Cryptomonads (S)	172.2	9	0.82	0.268	0.829	
August 25	Cryptomonads (M)	613.6	8	7.30	0.095	0.550
	Chroococcus	56.1	30	20.95	0.011	-0.435
	Aphanocapsa	15.0	54	1.57	0.073	0.446
	Gleocapsa	11.1	104	0.34	0.475	0.911
	Chlorella	92.5	7	1.17	0.078	0.474
	Rhodomonas	31.4	18	0.40	0.201	0.770
	Ochromonas	171.3	3	1.09	0.067	0.409
Sept 21	Cryptomonads (L)	2817.1	2	36.98	0.034	0.088
	Cryptomonads (M)	483.1	4	4.02	0.107	0.592
	Chroococcus	18.6	20	0.49	0.170	0.731
	Aphanocapsa	23.2	66	2.74	0.125	0.643
	Gleocapsa	6.7	40	0.25	0.234	0.803
	Chlorella	284.5	6	5.87	0.065	0.396
	Ochromonas	440.5	5	17.47	0.028	-0.008
	Rhodomonas	26.3	14	0.38	0.219	0.789
	Chrysidiastrum	76.4	2	1.94	0.018	-0.241

Stomach Content Analyses of *Holopedium gibberum* in Ranger Lake

Date	Food Item	Algal Mass ( $\mu\text{g}$ )	Number in gut	Lake Biomass ( $\mu\text{g/L}$ )	Alpha	Electivity	
June 1	Chrysothrix	676.8	432	2.68	0.320	0.859	
	Selenastrum	15.9	1	0.01	0.004	-0.773	
	Cryptophyta	448.8	4	0.06	0.007	-0.591	
	Stichoglea	293.0	35	1.86	0.016	-0.279	
	Ochromonas	555.6	47	0.88	0.087	0.517	
	Cryptomonads (S)	86.9	53	0.41	0.033	0.069	
	Chlorella	203.7	47	2.91	0.010	-0.497	
	Sphaerocystis	35.6	6	0.23	0.003	-0.825	
	Rhodomonas	47.6	37	0.98	0.005	-0.691	
	Dinobryon sp.	1458.67	104	0.87	0.515	0.920	
	June 30	Chrysamoeba	2026.3	3	11.25	0.017	-0.261
Pseudokephyrion		838.6	1	1.33	0.020	-0.187	
Chrysidiastrum		99.0	20	1.73	0.036	0.113	
Actinomonas		220.9	2	1.23	0.011	-0.439	
Cerodobo draco		1409.0	5	4.47	0.049	0.269	
Uroglena sp.		75.3	168	19.95	0.020	-0.184	
Dinobryon sp.		1458.6	151	1172.91	0.006	-0.663	
Cryptomonads (L)		5171.3	10	54.05	0.030	0.022	
Merismopedia		3.2	144	2.90	0.005	-0.706	
Stichoglea		107.6	155	8.02	0.065	0.396	
Aphanocapsa		69.5	186	2.31	0.174	0.736	
Aphanotheca		76.1	12	1.63	0.017	-0.244	
Gleocapsa		75.4	68	2.15	0.074	0.454	
Rhodomonas		54.2	22	1.20	0.031	0.039	
Ochromonas		164.6	93	4.70	0.102	0.574	
Cryptomonads (S)		202.0	58	6.73	0.054	0.316	
Chlorella		92.5	59	0.59	0.290	0.842	
July 28		Cryptomonads (M)	1456.3	8	50.26	0.016	-0.280
		Chrysidiastrum	63.7	6	0.30	0.088	0.521
	Merismopedia	3.9	896	10.01	0.024	-0.081	
	Cryptomonads (L)	5171.3	8	123.48	0.023	-0.102	
	Aphanotheca	4.0	12	0.01	0.352	0.873	
	Aphanocapsa	3.1	36	0.08	0.096	0.553	
	Chroococcus	35.6	35	0.51	0.171	0.731	
	Ochromonas	42.9	37	3.21	0.034	0.094	
	Cryptomonads (S)	278.1	13	4.85	0.052	0.296	
	Chlorella	172.0	32	3.55	0.108	0.596	
	Rhodomonas	30.8	4	0.93	0.009	-0.514	
	Uroglena sp.	306.8	80	328.08	0.005	-0.694	
	Dinobryon sp.	1458.6	138	671.90	0.021	-0.157	
August 25	Cryptomonads (L)	2724.1	9	73.52	0.012	-0.424	
	Cryptomonads (S)	370.0	17	15.85	0.014	-0.349	
	Merismopedia	3.1	208	0.84	0.027	-0.027	
	Dinobryon sp.	1458.6	8	0.87	0.467	0.909	
	Uroglena sp.	185.0	20	111.63	0.001	-0.923	
	Stichoglea	23.6	25	0.06	0.368	0.879	
	Aphanocapsa	7.2	12	0.90	0.003	-0.790	
	Chlorella	190.6	10	3.63	0.018	-0.219	
	Rhodomonas	52.3	8	0.50	0.029	0.015	
	Ochromonas	284.5	19	3.16	0.060	0.361	
Sept 25	Cryptomonads (S)	351.0	6	7.24	0.031	0.041	
	Cryptomonads (M)	551.8	4	5.28	0.041	0.185	
	Cryptomonads (L)	1788.9	10	23.09	0.082	0.496	
	Gleotila	4.5	2	0.55	0.002	-0.887	
	Merismopedia	2.5	96	0.33	0.079	0.476	
	Aphanocapsa	1.9	30	0.08	0.072	0.441	
	Chlorella	152.6	7	3.15	0.036	0.119	
	Rhodomonas	26.5	21	1.85	0.032	0.058	
	Ochromonas	440.4	16	4.77	0.157	0.709	
	Uroglena sp.	108.4	40	72.05	0.006	-0.637	
	Dinobryon sp.	1458.6	13	4.37	0.461	0.908	



Stomach Content Analyses of *Holopedium gibberum* in Mouse Lake

Date	Food Item	Algal Mass ( $\mu\text{g}$ )	Number in gut	Lake Biomass ( $\mu\text{g/L}$ )	Alpha	Electivity	
June 1	Cryptomonads (L)	1770.1	4	18.26	0.028	-0.007	
	Cryptomonads (M)	302.6	14	1.20	0.256	0.821	
	Anthrodesmus	846.1	1	1.34	0.046	0.235	
	Chrysamoeba	555.6	5	0.88	0.229	0.798	
	Aphanocapsa	24.4	12	0.21	0.100	0.568	
	Chlorella	187.4	22	5.65	0.053	0.305	
	Rhodomonas	32.3	16	1.38	0.027	-0.026	
	Cosmarium	137.6	1	0.44	0.023	-0.112	
	Ochromonas	531.3	16	9.27	0.067	0.408	
	Chrysidiastrum	42.8	6	0.41	0.046	0.235	
	Dinobryon sp.	1458.6	83	69.95	0.126	0.645	
	June 30	Dinobryon sp.	1458.6	125	80.49	0.080	0.486
		Uroglena (S)	205.5	24	13.52	0.013	-0.380
Uroglena (L)		109.3	6	2.08	0.011	-0.441	
Chroococcus		9.2	20	0.38	0.017	-0.255	
Aphanocapsa		42.8	132	14.52	0.014	-0.351	
Gleocapsa		27.5	40	0.26	0.149	0.695	
Merismopedia		2.9	16	0.28	0.006	-0.658	
Chrysamoeba		8181.2	1	19.47	0.015	-0.317	
Cryptomonads (L)		2730.8	16	11.13	0.139	0.676	
Cryptomonads (M)		2051.8	9	2.44	0.269	0.829	
Cryptomonads (S)		525.1	3	3.75	0.015	-0.317	
Chlorella		105.4	17	2.51	0.025	-0.060	
Planktosphaerium		1220.8	2	2.91	0.030	0.022	
Rhodomonas		19.9	4	0.24	0.012	-0.414	
July 28		Cryptomonads (L)	1784.5	16	25.29	0.051	0.289
		Chrysamoeba	2729.9	2	3.25	0.076	0.465
	Aphanocapsa	8.2	18	0.56	0.012	-0.418	
	Chroococcus	12.0	55	0.72	0.042	0.193	
	Gleocapsa	11.3	268	0.81	0.170	0.731	
	Merismopedia	1.6	224	0.27	0.059	0.352	
	Chrysidiastrum	52.3	2	0.33	0.014	-0.336	
	Closterium	138.8	1	1.32	0.005	-0.717	
	Ochromonas	120.0	8	0.95	0.046	0.235	
	Rhodomonas	14.1	9	0.11	0.051	0.292	
	Chlorella	152.6	25	2.91	0.060	0.359	
	Cryptomonads (S)	172.2	38	0.82	0.362	0.877	
	Dinobryon sp.	1458.6	136	190.68	0.047	0.250	
	Uroglena sp.	265.3	60	171.72	0.004	-0.746	
	August 25	Cryptomonads (L)	5569.6	11	3.34	0.198	0.767
		Cryptomonads (M)	613.6	24	7.30	0.022	-0.135
Anthrodesmus		796.4	1	0.95	0.009	-0.520	
Chroococcus		56.1	72	20.95	0.002	-0.866	
Rhabdoderma		21.1	5	10.61	0.001	-0.993	
Aphanocapsa		15.0	235	1.57	0.024	-0.082	
Gleocapsa		11.1	1956	0.34	0.684	0.946	
Chlorella		92.5	21	1.17	0.018	-0.232	
Rhodomonas		31.4	14	0.40	0.012	-0.414	
Ochromonas		171.3	5	1.09	0.009	-0.544	
Dinobryon sp.		1458.6	62	67.66	0.014	-0.331	
Uroglena sp.		480.6	12	8.63	0.007	-0.600	
Sept 21		Cryptomonads (L)	2817.1	21	36.98	0.117	0.623
	Cryptomonads (M)	483.1	23	4.02	0.203	0.772	
	Anthrodesmus	1141.4	2	2.72	0.062	0.374	
	Chroococcus	18.6	36	0.49	0.101	0.571	
	Aphanocapsa	23.2	65	2.74	0.040	0.175	
	Gleocapsa	6.7	188	0.25	0.362	0.877	
	Chlorella	284.5	14	5.87	0.050	0.276	
	Ochromonas	440.5	3	17.47	0.006	-0.678	
	Rhodomonas	26.3	5	0.38	0.026	-0.054	
	Dinobryon sp.	1458.6	13	89.53	0.016	-0.299	
	Uroglena sp. (L)	193.3	12	29.21	0.006	-0.665	
	Uroglena sp. (S)	151.4	8	7.03	0.013	-0.390	

Stomach Content Analyses of *Daphnia catawba* in Ranger Lake

Date	Food Item	Algal Mass ( $\mu\text{m}^3$ )	Number in gut	Lake Biomass ( $\mu\text{g/L}$ )	Alpha	Electivity
June 1	Chrysochlorella	676.8	48	2.68	0.040	0.174
	Stichoglea	293.0	55	1.86	0.029	0.006
	Ochromonas	555.6	18	0.88	0.038	0.142
	Cryptomonads (S)	86.9	19	0.41	0.013	-0.368
	Chlorella	203.7	9	2.91	0.002	-0.865
	Sphaerocystis	35.6	8	0.23	0.004	-0.746
	Rhodomonas	47.6	26	0.98	0.004	-0.746
	Dinobryon sp.	1458.67	155	0.87	0.869	0.963
June 30	Chrysoamoeba	2026.3	2	11.25	0.037	0.124
	Dinobryon sp.	1458.6	120	1172.91	0.015	-0.311
	Cryptomonads (L)	5171.3	15	54.05	0.145	0.688
	Merismopedia	3.2	208	2.90	0.023	-0.101
	Stichoglea	107.6	35	8.02	0.047	0.254
	Aphanocapsa	69.5	24	2.31	0.073	0.447
	Gleocapsa	75.4	68	2.15	0.241	0.809
	Rhodomonas	54.2	17	1.20	0.078	0.472
	Ochromonas	164.6	27	4.70	0.096	0.553
	Cryptomonads (S)	202.0	26	6.73	0.079	0.479
	Chlorella	92.5	9	0.59	0.144	0.685
	Pseudokephyrion	212.2	1	1.01	0.021	-0.148
	July 28	Merismopedia	3.9	1008	10.01	0.091
Cryptomonads (L)		5171.3	9	123.48	0.087	0.518
Aphanocapsa		3.1	42	0.10	0.371	0.880
Ochromonas		42.9	6	3.21	0.018	-0.216
Cryptomonads (S)		278.1	17	4.85	0.226	0.795
Chlorella		172.0	2	3.55	0.022	-0.122
Rhodomonas		30.8	23	0.93	0.177	0.740
Uroglena sp.		306.8	3	328.08	0.001	-0.956
Dinobryon sp.	1458.6	14	671.90	0.007	-0.608	
August 25	Cryptomonads (L)	2724.1	9	73.52	0.007	-0.597
	Cryptomonads (S)	370.0	15	15.85	0.008	-0.581
	Merismopedia	3.1	80	0.84	0.007	-0.633
	Dinobryon sp.	1458.6	25	0.87	0.911	0.966
	Chlorella	190.6	7	3.63	0.008	-0.564
	Rhodomonas	52.3	18	0.50	0.041	0.186
	Ochromonas	284.5	9	3.16	0.018	-0.237
Sept 25	Cryptomonads (S)	351.0	11	7.24	0.070	0.426
	Cryptomonads (L)	1788.9	15	23.09	0.152	0.700
	Gleotila	4.5	2	0.55	0.002	-0.863
	Merismopedia	2.5	64	0.33	0.064	0.391
	Aphanocapsa	1.9	12	0.08	0.035	0.107
	Chlorella	152.6	15	3.15	0.095	0.549
	Rhodomonas	26.5	30	1.85	0.056	0.331
	Ochromonas	440.4	22	4.77	0.265	0.826
	Uroglena sp.	108.4	4	72.05	0.001	-0.947
	Dinobryon sp.	1458.6	6	4.37	0.261	0.824

## **APPENDIX B**

### **Summary of Seasonal Means of Variables Affecting the Dry Weight**

Table C-1

Summary of seasonal means of variables affecting the dry weight (Mean Wt; mg) of *Holopedium* and *Diaptomus* in Ranger Lake. ED<sub>SCA</sub> = edible algal biomass as determined by SCA; ED<sub>SIZE</sub> = edible algal biomass as determined by size (see Methods Chapter 2); Temp = Temperature °C; Density = numbers per litre.

Date	Genus	Mean Wt	ED <sub>SCA</sub>	ED <sub>SIZE</sub>	Chl a	Total	Temp	Density
June 01	<i>Holopedium</i>	65.30	1.5	8.9	1.7	11.61	13.01	0.62
June 30	<i>Holopedium</i>	242.30	11.6	141.2	2.1	1315.49	13.96	0.01
July 28	<i>Holopedium</i>	153.40	20.6	188.8	4.2	1210.04	15.75	0.30
Aug. 25	<i>Holopedium</i>	163.70	1.8	121.5	3.1	235.93	15.25	0.19
Sept 21	<i>Holopedium</i>	65.70	5.8	46.5	2.6	124.14	12.21	27.52
June 01	<i>Diaptomus</i>	3.10	1.2	4.5	1.7	11.61	13.01	2.67
June 30	<i>Diaptomus</i>	2.68	2.5	14.8	2.1	1315.49	13.96	12.78
July 28	<i>Diaptomus</i>	3.29	1.1	12.5	4.2	1210.04	15.75	6.01
Aug. 25	<i>Diaptomus</i>	3.18	1.1	13.2	3.1	235.93	15.25	3.26
Sept 21	<i>Diaptomus</i>	3.24	2.8	7.7	2.6	124.14	12.21	20.31
June 01	<i>Daphnia</i>	18.00	1.0	8.9	1.7	11.61	13.01	13.48
June 30	<i>Daphnia</i>	18.70	28.3	141.2	2.1	1315.49	13.96	7.45
July 28	<i>Daphnia</i>	16.70	18.1	188.8	4.2	1210.04	15.75	2.00
Aug. 25	<i>Daphnia</i>	21.60	1.6	121.5	3.1	235.93	15.25	0.83
Sept 21	<i>Daphnia</i>	25.60	6.9	46.5	2.6	124.14	12.21	41.94

Table C-2

Summary of Seasonal Means of variables affecting the dry weight (Mean Wt;mg) of Holopedium and Diaptomus in Mouse Lake. ED<sub>SCA</sub> = edible algal biomass as determined by SCA; ED<sub>SIZE</sub> = edible algal biomass as determined by size (see Methods Chapter 2); Temp = Temperature °C; Density = numbers per litre.

Date	Genus	Mean Wt	ED <sub>SCA</sub>	ED <sub>SIZE</sub>	Chl a	Total	Temp	Density
June 01	<i>Holopedium</i>	43.10	10.9	54.6	2.8	124.74	11.82	2.01
June 30	<i>Holopedium</i>	103.50	10.0	44.9	1.5	157.07	14.58	12.18
July 28	<i>Holopedium</i>	59.00	12.0	73.3	5.5	554.94	16.30	8.84
Aug. 25	<i>Holopedium</i>	70.50	2.2	23.5	3.8	144.70	15.85	0.53
Sept 21	<i>Holopedium</i>	51.70	7.6	77.3	2.4	212.48	13.77	0.69
June 01	<i>Diaptomus</i>	3.15	1.7	16.3	2.8	124.74	11.82	1.39
June 30	<i>Diaptomus</i>	2.76	2.3	3.6	1.5	157.07	14.58	0.23
July 28	<i>Diaptomus</i>	2.81	0.7	4.8	5.5	554.94	16.30	0.35
Aug. 25	<i>Diaptomus</i>	3.59	1.5	3.0	3.8	144.70	15.85	5.67
Sept 21	<i>Diaptomus</i>	4.53	3.2	23.7	2.4	212.48	13.77	6.39