AN ANALYSIS OF SEASONAL SESTONIC-MERCURY AND THE EFFECT OF BIOMANIPULATION ON THE PHYTOPLANKTON OF TWO PRECAMBRIAN SHIELD LAKES

AN ANALYSIS OF SEASONAL SESTONIC-MERCURY AND THE EFFECT OF BIOMANIPULATION ON THE PHYTOPLANKTON OF TWO PRECAMBRIAN SHIELD LAKES

by

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TITLE: An Analysis of Seasonal Sestonic-Mercury and the Effect of Biomanipulation on the Phytoplankton of Two Precambrian Shield Lakes

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ABSTRACT

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As part of the collaborative Dorset Research Project investigating mercury and energy fluxes in fresh-water lakes, I measured mercury in the seston (Chapter 1) and studied the biomanipulation impacts on the phytoplankton (Chapter 2) of two Precambrian Shield lakes. Sestonic-mercury (HgT) was measured in the metalimnion and hypolimnion of each lake throughout the summer of 1995 to determine seasonal fluctuations and the relationship with algal productivity. In each lake, sestonic-HgT (pg Hg/L) did not significantly change in the metalimnion but significantly increased in the hypolimnion by season's end. Combined influences of external HgT inputs, seston sedimentation and increased methylmercury production in the hypolimnia over the season may have contributed to these trends. In comparison to other variables measured, algal productivity was highly correlated with sestonic mercury concentrations in both lakes at each limnetic depth. Although there were no significant differences between lakes with respect to average weight-specific HgT (pg HgT/mg D.W.), chlorophyll *a* exhibited the best correlations with HgT in Mouse L. whereas algal biomass was more highly correlated with HgT in Ranger L. This disparity between lakes may be the result of apparent inter-lake differences in light availability and algal community structure. It was also apparent that changes in the proportions of large and small cells over the season affected the magnitude of sestonic mercury measured. With respect to the potential for trophic transfer of mercury, I suggest that small edible algal cells may bioconcentrate more mercury per unit weight than larger, inedible ones. The data also

indicate that seston samples should be collected throughout the season at discrete depths if sestonic-mercury measurements are to be used in trophic transfer models.

I also examined the effects of fish biomanipulation on the phytoplankton community of these study lakes. Prior to the biomanipulation, Ranger L. had a top-piscivore community whereas Mouse L. had a top-planktivore community. The biomanipulation involved the removal of top-piscivores from Ranger L. and adding top-piscivores to Mouse L. Trophic Cascade theory predicts that algal biomass in these lakes, with their similar morphometries and resource characteristics, should be ultimately controlled by top-consumer abundance. In addition, model predictions expect "edible" algal size-classes and groups in the community to experience the greatest changes in abundance. Therefore in Ranger L., it was expected that the removal of piscivores would result in higher algal biomass (particularly edible algae), whereas the addition of piscivores in Mouse L. would result in lower algal biomass (particularly edible algae). However, for those years following the biomanipulation, algal biomass significant increased in both lakes compared to pre-manipulation years. This suggests that variables other than direct trophic forces were controlling algal biomass from year to year, regardless of changes in the fish communities. When algal size-classes were tested, only edible cells varying from 10 - 30 μm increased in Mouse L., contrary to what was predicted. In Ranger L., large cells and colonies > 30 μm unexpectedly increased when all other size-classes did not significantly change. With respect to algal group composition, both Greens and Cryptomonads significantly increased in Mouse L. whereas only Greens significantly increased in Ranger L.. Both of these groups were considered to be edible and thus these results were not consistent with the model predictions. As such, I suggested that "bottom-up" influences were important in controlling both size-class and taxonomic abundances. However, when individual size-classes of representative algal genera were compared between pre- and post-

manipulation years, there were some effects which may be attributed to the biomanipulation. In particular, large Green colonies became prevalent in Mouse L. during post-manipulation years as a probable response to increased grazing pressure. Conversely, "edible" Greens became prevalent in Ranger L. after the biomanipulation, supporting the prediction of reduced zooplankton grazing pressure. These results have revealed the necessity to test specific algal genera of varying size-classes in order to detect the effects of biomanipulation. They also showed that the majority of algal genera, regardless of size, were not affected by the biomanipulation. Limitations to my interpretation of the data are discussed and vary from time-scale issues to consumer and resource availability unknowns.

Along with recommendations for further studies in this area, I hypothesized that the trophic transfer of sestonic-mercury to zooplankton could be intensified if small, edible algal genera (shown to be impacted by Top-Down forces), have relatively higher weight-specific mercury concentrations. However, considering that the phytoplankton community as a whole has shown resilience to herbivory, I also suggest that the majority of mercury measured in the seston is not available for trophic transfer to zooplankton consumers.

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GENERAL INTRODUCTION

Contaminant fate in aquatic ecosystems has become a growing concern as increases in global industrialization proliferate the distribution of pollutants. One contaminant in particular, mercury, has warranted particular attention for it is readily emitted into the air from a number of anthropogenic sources and is transported long distances in the atmosphere (Watras and Huckabee, 1994). Commonly, this particulate mercury is deposited over pristine sites, far away from original (point) sources (Fitzgerald et al., 1991) . Once this inorganic mercury enters lakes, it can potentially be converted into the highly lipophilic mercurial species methyl-mercury (MeHg) (Ramlal et. al., 1985; Korthals and Winfrey, 1987; Xun et. al., 1987; Gilmour and Henry, 1991). It is this organic form of mercury that is of greatest concern as it can be taken up and accumulated by aquatic organisms (Jernelov and Lann, 1971; Huckabee et. al., 1979; Boudou et. al., 1991; Bloom, 1992).

In fact, mercury accumulation in top-predator fish from a number of lakes in Ontario have been deemed unsafe to eat by the provincial government. However, a few lakes in the same area with similar limnological characteristics, do not have fish consumption advisories. Why some lakes have contaminated fish where others don't, forms the basic research question of the Dorset Research Project. The Dorset Research Project involves the collaboration of researchers from a number of universities and the provincial government to assess and model the impacts of between-lake differences in food-web structure, water chemistry and geochemistry on mercury biomagnification (D. McQueen, Principal Investigator). One of the main objectives of this project was to study the path-way of mercury in the food-webs of two soft-water lakes located near the town of Dorset, Ontario.

These lakes share similar physico-chemical and morphometric characteristics but had different food-web hierarchies. The plan was to alter the top-predator fish communities of these lakes to bring about changes in the lower food-web. Mercury was measured in the water and biota of each trophic level to ascertain the effects of food-web changes to mercury bioaccumulation. In addition, the biomanipulation experiment provided a good opportunity to test conventional theories about consumer-related controls on community abundances at each trophic level.

My contribution to this project focused on the lowest trophic level of these lakes, namely the phytoplankton community. In Chapter 1, I investigated the seasonal sestonic-mercury dynamics in seston (which mostly consisted of living and dead phytoplankton) from each lake to gain a better understanding of mercury fate at discrete depths in the water column (metalimnion and hypolimnion, respectively). In addition to obtaining sestonic-mercury concentrations, I wanted to examine the relationship between algal productivity and the amount of mercury measured. In Chapter 2, I examined four years of phytoplankton community data to test the effects of fish biomanipulation in each lake. Biomanipulation theory (as well as the Trophic Cascade and Top-Down:Bottom-Up hypotheses) predict that algal biomass will change as a result of shifting abundances in higher trophic levels. However, the potential influences of resource (bottom-up) limitations are also included in this investigation. In general, the phytoplankton community was assessed as both an introductory level for mercury movement in the food-web and a trophic level which is particularly dependent on the combined impacts of consumers and resource availability.

Chapter 1:

SEASONAL AND DEPTH DISTRIBUTION OF SESTONIC MERCURY AND THE ROLE OF ALGAL PRODUCTIVITY IN TWO PRECAMBRIAN SHIELD LAKES

ABSTRACT

As part of a study on the movement and fate of mercury in freshwater food-webs, I focused on the seasonal dynamics of Total Mercury (HgT) in the seston (living and dead phytoplankton) of two Precambrian Shield lakes (Mouse and Ranger). Sestonic-HgT samples (filtered through 63-μm Nitex mesh) from metalimnetic and hypolimnetic depths in the euphotic zone, were collected and analyzed using 'ultra-clean' techniques. In both lakes, sestonic-mercury (pg HgT/L) did not significantly change among dates over the season (ANOVA, $p > 0.05$), although Ranger L. exhibited significant differences between mercury values measured at the beginning and end of the season (Student's t-test, $P < 0.05$). In contrast, sestonic-HgT significantly increased in the hypolimnia of both lakes by seasons end. Combined influences of external HgT inputs, seston sedimentation and increased methylmercury production in the hypolimnia over the season may have contributed to these trends.

In comparison to other variables measured, algal productivity was highly correlated with sestonic mercury concentrations in both lakes at each limnetic depth. Although there were no significant differences between lakes with respect to average weight-specific HgT (pg/mg D.W.), chlorophyll *a* exhibited the best correlations with HgT in Mouse L. whereas algal biomass was more highly correlated with HgT in Ranger L. This disparity between lakes may be explained by the inter-lake differences in light availability and algal community structure. It was also apparent that changes in the proportions of large and small cells over the season had an effect on the magnitude of sestonic mercury measured. With respect to the potential for trophic transfer of mercury, these results imply that small edible algal cells bioconcentrate more mercury per unit weight than larger, inedible ones.

For improved estimation of sestonic-mercury, these data indicate that seston samples be collected throughout the season at discrete depths if sestonic-mercury measurements are to be used in trophic transfer models.

INTRODUCTION

During the last decade, advancements in ultra-trace mercury detection in remote aquatic systems has fostered our understanding of mercury as a global contaminant. It has been established that increasing mercury burdens in fresh-waters are the result of anthropogenic inputs (Lindqvist, 1991a; Watras and Huckabee, 1994). Greater than 50% of mercury entering lakes comes from atmospheric deposition and is mostly in the form of inorganic mercury (Fitzgerald and Watras, 1989; Mierle, 1990; Johansson et. al., 1991, Fitzgerald et. al., 1991). Once inorganic mercury has entered the water column, it has an increased potential to be transformed via methylation into methylmercury (MeHg), particularly in the hypolimnion (Ramlal et. al., 1985; Korthals and Winfrey, 1987; Xun et. al., 1987; Gilmour and Henry, 1991). MeHg, a highly lipophilic and relatively toxic compound, has been implicated as the predominant mercurial species of concern in bioaccumulation studies (Jernelov and Lann, 1971; Huckabee et. al., 1979; Boudou et. al., 1991; Bloom, 1992).

For a number of pristine lakes surveyed in the Precambrian Shield, top-predator fish were observed to have mercury concentrations (>0.5 ppm) exceeding levels considered safe for human consumption (OMOE and OMNR, 1989). The majority (> 90%) of this mercury is in the form of MeHg (Bloom, 1992). Trophic transfer of MeHg has been implicated as the main cause of mercury bioaccumulation in fish and the proportion of MeHg in Total mercury (HgT) tends to increase with each trophic level (Watras and Bloom, 1992; Watras et. al., 1994). To improve our understanding of this trophic transfer of mercury, it is necessary to assess mercury dynamics and concentrations within each compartment of the food-web.

In this study, I focused on the lowest trophic level, namely the phytoplankton community. As the primary producers in pelagic freshwater systems, the phytoplankton serve mainly as a food source for herbivorous zooplankton but may also sustain omnivorous invertebrates and larval fish species (Moss, 1988; Horne & Goldman, 1994). Due in part to their relatively small size, the phytoplankton have the potential to accumulate HgT directly from the water column. Algae have been found to exhibit a number of metabolism-dependent and independent mechanisms for heavy metal uptake and accumulation (Vymazal, 1984; Gadd, 1990; Harris and Ramelow, 1990; Majidi et. al., 1990). Both dead and living algal cells have been found to accumulate heavy metals although mechanistic differences probably exist (Gadd, 1990). Past studies have shown that a small proportion (13-30%) of HgT in phytoplankton is MeHg, indicating that algae have an affinity to accumulate more than one type of mercurial species (Watras and Bloom, 1992). Therefore, the measurement of *in-situ* HgT in phytoplankton provides novel information on the amount of all mercurial species ad/absorbed to algal cells.

The phytoplankton communities from two dystrophic lakes (Mouse and Ranger) on the Precambrian Shield near Dorset, Ontario, Canada were assessed monthly in parallel from June to September in 1995 for the analyses of sestonic-HgT, algal productivity and algal community structure. Although samples were collected from all limnetic depths in the euphotic zone, I decided to limit our sample analyses to metalimnetic and hypolimnetic samples only. This decision was based on both logistical limitations and the extremely low seston dry-weight, chlorophyll *a* and algal biomass estimates determined for the epilimnion over the season. I was concerned that contamination error could markedly affect HgT measured for epilimnetic samples. As such, I focused on the prevalent plankton layers of the lower depths, where sample HgT measured was always more than twice the

background HgT measured. This approach is in accordance with the results found by Watras and Bloom (1994), where high HgT concentrations in lake water were mainly associated with plankton layers found in the metalimnia and hypolimnia.

Both Ranger and Mouse lakes have been intensively studied over five years as part of a whole-lake biomanipulation experiment (D. McQueen, Principal Investigator, York University). Among other important food-web characteristics, Sebalj (1995) has documented the diel seasonal grazing rates for herbivorous zooplankton in both of these lakes at various depths in the water column. In conjunction with this knowledge, the determination of sestonic-HgT dynamics at discrete depths will provide us with a better understanding of sestonic-HgT transfer to the next trophic level.

METHODS

Study Sites

The two study lakes, Mouse and Ranger, are located on the Precambrian Shield in south-central Ontario (45°11'N, 78°51'W and 45°09'N, 78°51'W, respectively) with minimal shoreline development (Figure 1.1 and 1.2). Both lakes are acid-sensitive and dystrophic (Table 1.1) and have similar edaphic and morphological characteristics. Both are single basin lakes and estimated flushing rates are high (> twice per year). Most of this flow is derived from snow-melt in early spring whereas during the summer, flow volume is low (Ramcharan et al., 1995).

Mercury Contamination Protocol

Equipment preparation, HgT extractions and analyses were all performed within the Ontario Ministry of the Environment and Energy (OMEE) designated "Mercury Clean Lab", Dorset Research Centre, Dorset, Ontario. Great care was taken to minimize mercury contamination by using ultra-clean techniques throughout sampling, extraction and analysis protocols. Most equipment used were detergent washed and acid-treated over-night using a strong acid extractant called BES (20% nitric acid, 2% hydrochloric acid and 0.05% potassium dichromate). The exceptions included Nitex mesh (detergent wash only) and GFC filters (20% nitric acid and 5% hydrochloric acid treatment). Lint-free suits and vinyl gloves were worn during cleaning and equipment preparation.

Field Collection

Using an enclosed water collection system consisting of a peristaltic pump with Teflon in-line filters and c-flex tubing, monthly parallel water samples were collected from the

metalimnia and hypolimnia at the deep station of each lake (Figure 1.1 and 1.2) from early June to September of 1995. Whole-lake water samples consisted of non-filtered 1-L replicates (in borosilicate bottles with Teflon-lined lids) and were collected for the measurement of HgT (pg/L). Nitex-filtered (<63 μm) replicate 1-L water samples were collected for sestonic- HgT, chlorophyll *a* and seston dry-weight measurements.

I assumed that the Nitex mesh size of 63-μm would exclude zooplankton in collected water while allowing seston to pass through. Independent One-way ANOVA analyses confirmed that for both chlorophyll *a* and biomass estimates, there were no significant differences between parallel whole-lake water samples and filtered water (Appendix 1). Therefore, I was confident that seston collected for analysis was free of zooplankton but reflected whole-lake seston concentrations. In a preliminary study, I attempted to trap the "edible" size fraction of seston by using 20-μm and 30-μm mesh sizes but this resulted in instances of clogging which caused back-flow prior to the collection of 1-L samples. Clogging of mesh pores was believed to be the combined result of suspended particulates and algal exudates in the water sampled. Filtered water for biomass estimates and algal community composition were collected in 4-oz glass bottles and preserved with acid Lugol's Iodine in the field. Temperature and dissolved oxygen parameters were measured by a YSI 5700 probe and euphotic zones were estimated as twice the Secchi depth transparency (empirically determined in previous years, Chow-Fraser, unpub. data).

Sample Processing

All water samples were transported in ice-packed coolers and taken back to the laboratory for processing within 3-h of collection in the field. Laboratory processing involved the collection of seston onto GF/C filters (0.45 μm pore size) using a vacuum pump system of acid-washed Teflon in-line filters, Teflon tubing and a glass waste flask.

Parallel water samples were filtered onto GF/C filters, wrapped in aluminum foil and then frozen for future chlorophyll *a* and dry weight analyses. Pre-weighed filters used for dry-weight analysis were initially placed in filtering units and treated with distilled water to remove loose fibers.

Gravimetric experiments confirmed that filter weights did not differ significantly (Student's t-test, $p>0.1$) between filters with water run through them once and those with water run through them twice (to mimic lake water filtering effect). Whole-lake water samples remained in borosilicate bottles and were treated with 10-mL of 1% hydrochloric acid and stored at 4°C until analysis. Seston samples on GF/C filters collected for HgT analysis were carefully transferred to Pyrex Petri dishes and injected with 8 mL of BES (20% nitric acid (Optima grade), 2% hydrochloric acid and 0.05% potassium dichromate). This potassium dichromate acid solution destroyed reducing matter in the seston and kept HgT in solution with its high oxidizing potential.

After each injection of acid, Pyrex lids were placed on top of each sample. An extraction period of 24 hours was used as there were no significant (ANOVA, $p>0.1$) differences in HgT extracted for 24-h, 72-h and 120-h extraction periods. After the 24-h extraction period, extractant from each sample was transferred via small volume pipetter to acid-washed borosilicate vials with Teflon-lined screw-caps until analysis could be performed. To account for background contamination, replicate blanks were prepared with each set of seston samples. Blanks consisted of G/FC filters run through the same cleaning and processing regimen as sample G/FC filters and then treated with the same lot of BES extractant. Along with seston-samples, 1-ml sub-samples of extractant from these blanks were analyzed for mercury. Mercury levels measured in blanks were then corrected for in net sestonic-HgT calculations.

Mercury Analysis

Atomic fluorescence spectroscopy with the aid of a Gilson model 222 encased automatic sampler was used to determine HgT levels in each sample. The method is based on a 'purge & trap' procedure for isolating and pre-concentrating HgT from the sample and on detection by atomic fluorescence. Using acid-washed polyethylene centrifuge tubes, 1 mL sub-samples of extractant from each sample was injected into 40 mL of reverse-osmosis (R.O.) water. Each centrifuge tube with aqueous sample was placed in the automatic sampler rack where a Teflon tube could draw the sample into c-flex tubing which transported the sample to a purge vessel. In the purge vessel, a solution of sodium borohydride in NaOH was added to both decompose Hg compounds and reduce free Hg (II) to Hg (0). The sample was first purged with Hg free argon gas and then flushed into and trapped by amalgamation onto gold-coated sand. Following pre-concentration, the Hg was thermally absorbed and flushed into a detector. The instrumental detection limit for HgT in aqueous media was 10 pg and sample viability was dependent on background contamination always being less than 50% of HgT measured. OMEE quality assurance protocol was implemented for all sample runs. Correction curves were used to account for sensitivity drift throughout each run of samples analyzed.

Seston Dry-Weight and Algal Productivity Analysis

Seston dry-weights were determined by desiccating the seston samples on their GF/C filters in a food dehydrator for 24 hours and then transferring them to a Nalgene desiccator with Dry-Rite anhydrous calcium sulfate pellets for 1 hour. The seston filters were weighed in an Ohaus enclosed microbalance (0.000g detection) with a Petri dish of anhydrous calcium sulfate pellets set inside the housing chamber. Chlorophyll *a* was extracted with 90% reagent grade acetone for one hour in a freezer. A Milton Roy 301

spectrophotometer was used to determine absorbence readings. Both Total (viable and degrading algae) and Corrected (phaeopigment-corrected for viable algae only) chlorophyll *a* concentrations were calculated. For the determination of viable algal biomass and composition, 5 mL sub-samples of preserved lake water were settled for 24 h in algal settling chambers. Using 200x magnification, algal cells and colonies were counted and taxonomically identified along one full transect. The entire slide was scanned for large cells and colonies to ensure their proportion in the sample was accurately recorded. Algal bio-volumes (biomass) were calculated by approximation to geometric shapes. Average dimensions of the algae were determined with the aid of an eye-piece micrometer at 400x magnification.

RESULTS AND DISCUSSION

Sestonic Mercury Dynamics

In Figure 1.3, mean seasonal distributions with Standard Error bars for sestonic-HgT per 1-L of lake water are displayed for each lake individually. For both lakes it appears there is a gradual decrease of HgT in the metalimnia and a marked increase of HgT in the hypolimnia has occurred. However, One-way ANOVA indicates that there were no significant differences among dates in the metalimnion of each lake, although there was a significant decrease in sestonic-HgT from the beginning to the end of the season in Ranger L (Student's t-test, $p < 0.05$). The hypolimnion of each lake showed significant differences among dates (ANOVA, $p < 0.05$), where there significant increases in sestonic-HgT from the beginning of the season to the end of the season (Student's t-test, $P < 0.05$).

Both limnetic depths exhibit similar HgT levels at the beginning of the season, a time when spring turn-over occurred and stratification was initiated. It would seem that lake mixing had created a homogeneous HgT distribution in the water column initially but stable stratification over the season caused HgT levels in the respective strata to diverge. If samples had been collected during fall mixis, I may have seen similar HgT values again between limnetic depths, although compared to spring values, there may have been a net increase in sestonic-HgT considering the contributions of hypolimnetic HgT concentrations witnessed on the last sampling date.

Another important contrast between limnetic depths are the rates of HgT loss and accumulation. The data show that sestonic-HgT levels do not significantly change over the season in the metalimnia, regardless of the amount of seston present on each date. This

suggests that atmospheric and watershed inputs may be contributing to the metalimnetic HgT pool consistently throughout the season. If this is the case, there is perhaps a constant level of HgT being maintained in the metalimnion, despite losses from sinking seston. Another explanation for the apparently low net loss of HgT from the metalimnia over the season involves the relatively high algal productivity that occurs here. HgT may be incorporated into the seston via adsorption and/or accumulation by algal physical and metabolic attributes. Release of HgT from decomposing algae would also be available for uptake by viable algae in the metalimnion. Perhaps changes in the ratio of living : dead algae in the seston may help to sustain mercury levels over the season, even though the total amount of seston may seasonally vary. If these processes do occur, it would implicate the metalimnion as an important site for HgT retention and cycling in the water column. In the hypolimnia, stable lake stratification would promote the sedimentation of HgT-laden seston from upper waters to hypolimnetic depths. As the density of water is relatively highest in the hypolimnion, settled seston could be trapped here, resulting in a net increase of HgT by season's end.

In Figure 1.4, I have standardized the data to present changes in weight-specific sestonic-HgT over the season. Mouse L. exhibits highest metalimnetic values of HgT per unit seston in July whereas, hypolimnetic concentrations were highest in August (Figure 1.4 a). By comparison in Ranger L., weight-specific HgT in metalimnetic samples continued to decline through the season, although values for the last three dates were not significantly different from one another ($p>0.05$). In the hypolimnion of Ranger L., decreasing HgT levels occurred throughout the season until September, when sestonic-HgT concentrations peaked (Figure 1.4 b). These differences in weight-specific HgT dynamics in seston between lakes demonstrate the difficulty in generalizing about the forces that control HgT loss and incorporation. It is clear that in addition to physically

accumulating a greater quantity of seston in the hypolimnion over the season, there is a disproportionately higher concentration of HgT in a given unit of seston by the end of the summer. Conversely, there appears to be a reciprocal relationship for metalimnetic samples, where there is a net reduction in HgT per unit seston at season's end compared to early summer.

The Role of Algal Productivity

Weight-specific HgT was regressed against various limnological parameters for both lakes to reveal any significant relationships (Table 1.2). The independent variables included: Total chlorophyll *a*; Corrected chlorophyll *a*; Algal biomass; Seston dry-weight; Dissolved oxygen concentration; and water temperature. Of these parameters, only those associated with algal productivity yielded statistically significant regression coefficients ($p<0.05$). The best predictor of sestonic-HgT concentration for Mouse L. was Corrected chlorophyll *a* ($r^2=0.32$) whereas Total chlorophyll *a* ($r^2=0.24$) was the best predictor for Ranger L. The strongest relationships emerged when data were first sorted by lake and stratum prior to the regression analysis. For example, when data were analyzed from the metalimnion of Mouse L., Corrected chlorophyll *a* explained 82% of the variation in HgT concentrations (Figure 1.5 a). In the same way, Algal biomass explained 66% of the variation in data corresponding to metalimnetic samples from Ranger L. (Figure 1.5 b).

Considering the strong linear relationship between Corrected chlorophyll *a* and Sestonic-HgT concentrations in the metalimnion of Mouse L., it is not surprising that chlorophyll *a* is also an important predictive variable in the hypolimnion. However, Total chlorophyll *a* explains more of the variation ($r^2=0.87$) here, suggesting that both living and dead algal cells are driving seston HgT concentrations in the hypolimnion (Figure 1.5 c). Perhaps the physico-biological environment (i.e. anoxia and increased mercury

methylation) in the hypolimnion of Mouse L. promotes the ad/absorption of mercury by both dead and living cells. In Ranger L., Algal biomass is still the most important predictor of sestonic-HgT in the hypolimnion (r^2=0.47, log transformed), albeit the relationship between the two is negative (Figure 1.5 d). It is apparent that the amount of HgT per unit weight is heavily influenced by the standing stock of phytoplankton in the different lake strata. However, in 3 of the 4 situations (Figure 1.5 a-c), there was a direct relationship whereas in the hypolimnion of Ranger L. (Figure 1.5 d), the relationship appears to be indirect.

In order to understand why the relationship between algal biomass and sestonic-mercury concentration in Ranger L was negative, I re-analyzed the data-sets after sorting by limnetic depth. In the hypolimnion of Ranger L., I found that when the proportion of algal cells > 20 μm increased relative to those cells < 20 μm, the concentration of mercury measured decreased. This algal cell size was approximately the median cell size found in the community. Cell-size ratios were determined by dividing large cell (>20 μm) biomass sums by small cell (<20 μm) biomass sums for each sampling date. The only significant relationship occurs in Ranger's hypolimnion, where cell-size ratio explains 58% of the variation in sestonic mercury concentration (Table 1.3). This relationship suggests that as the proportion of large cells increase in the seston, the concentration of HgT per unit seston decreases. Alternatively, sestonic-HgT concentrations increase when small cells are dominant.

This 'dilution' effect by large cells would most likely be due to the decrease of surface : volume ratio compared to small cells. As cell size increases, the volume grows much more rapidly than the surface area. For a round cell, surface area increases as the square of diameter whereas volume increases as the cube (Raven and Johnson, 1988). Therefore,

large cells have much less surface area per unit volume than small ones. Theoretically, the relative large surface area: volume ratios for small cells should have an effect on HgT uptake and accumulation in algae. Small cells should have a proportionately higher number of sites for HgT uptake into the cell in conjunction with a relatively low cell volume for HgT to accumulate in. It is interesting to note that a stronger significant linear relationship exists between algal cell-size ratios and sestonic-HgT (r^2=0.58, p = 0.02) than for Total algal biomass and sestonic-HgT (r^2=0.39, p = 0.1).

If algal cell-size ratios offer an explanation to what is happening in the hypolimnion of Ranger L., why does it not explain mercury concentrations for all limnetic depths? When all of the depth data are pooled to test this relationship between cell-size ratios and sestonic-HgT, there was no significant relationship (p > 0.1). However, one of the most striking differences between the hypolimnion in Ranger L. compared to all other limnetic depths, was the tight relationship (r^2 = 0.97) between algal biomass and seston dry-weight (Table 1.3). This relationship suggests that the viable algal community in the hypolimnion of Ranger L. reflects the hypolimnetic seston. Considering that mercury measurements were for seston and not just viable algae, it seems reasonable that effects from changing cell-size ratios would be more evident in the hypolimnion of Ranger L. than the other limnetic depths studied. As such, this may be one explanation as to why cell-size ratio effects were not accounted for in the other limnetic depths. Perhaps the unknown viable : dead proportion over the season in the other limnetic depths may have had confounding effects on sestonic-HgT concentrations. It is evident, however, that future controlled *insitu* experiments would be required to confirm this cell-size ratio hypothesis.

Community Differences Between Lakes

For each limnetic depth in Mouse L. and Ranger L., algal productivity seems to be playing an important role in controlling sestonic-HgT concentrations (Table 1.2). However, it is also apparent that the productivity variables used do not convey the same meaning where sestonic-HgT is concerned. Chlorophyll *a* was highly correlated with sestonic-HgT in Mouse L. whereas only algal biomass (based on cell counts), correlated well with sestonic-HgT in Ranger L. Although both of these algal productivity estimates represent viable algae, chlorophyll *a* measurements are an indication of photosynthetic activity only, whereas algal biomass reflect the presence of both photoautotrophic and heterotrophic protists. As indicated in Table 1.1, the only significantly different parameters between lakes are DOC levels and pH, where Ranger L. had higher values for both. Data collected in 1995 (Table 1.4) indicated that there were significantly lower Secchi measurements in Ranger L. compared with Mouse L., suggesting that light availability was more limiting in Ranger L.. As such, I would expect mixotrophic growth to be more important in Ranger L.. This may explain why biomass estimates accounted for more of the variation in sestonic-HgT levels than did chlorophyll *a*..

There were notable differences between lakes with respect to algal group composition (Figure 1.6). Both Mouse L. and Ranger L. contain algal groups with species that are known photoautotrophs (Blue-Greens, Greens [namely Desmids] and Diatoms) and mixotrophs (Euglenoids, Chrysophyta, Cryptophyta and Dinoflagellates (Moss, 1988; Smol and Sandgren, 1994). It is important to note, however, that the proportional representation of these groups in each lake are different. Almost 40% of algal biomass for the majority of the season in Mouse L. are Blue-Greens and Greens compared to a maximum of 15% for these groups on one date in Ranger L (Figure 1.6). This suggests

that light availability is less limiting in Mouse L. and may therefore support a larger community of obligate photoautotrophs.

In the metalimnion of Ranger L., Cryptophytes, Chrysophytes and Dinoflagellates were generally abundant through the season, although Diatoms were the most dominant algal group in July (Figure 1.6 b). Although Cryptophytes, Chrysophytes and Dinoflagellates are capable of photosynthetic growth, they have been reported to contain mixotrophic genera (Holen, D.A. and M.E. Boras, 1994 (Chp. 6, Smol and Sandgren). The predominant algal genera found in Ranger L. include *Chrysophaerella*, *Dinobryon*, *Uroglena* and *Cryptomonas*, all of which have confirmed mixotrophic species (Sanders and Porter, 1988; Nygaard and Tobiesen, 1993 and Moestrup, 1994 as summarized in Chp. 6 Smol and Sandgren). Mixotrophy can be beneficial to an organism living in a light limited system, a scenario consistent with the conditions of Ranger L.. If mixotrophy were the predominant means of carbon assimilation in Ranger L., it could explain why a poor correlation exists between chlorophyll *a* and algal biomass estimates here.

Implications for Trophic Transfer Modeling

The seasonal and vertical fluctuations in weight-specific HgT in the seston of these lakes implies that using a mean sestonic-HgT value for integrated water samples taken once or twice in the season is not truly representative of potential HgT available for biomagnification. As such, I recommend that seasonal sestonic-HgT concentrations for each limnetic depth be obtained when developing trophic transfer models. Although the MeHg proportion in HgT was not measured in this study, it is most probable that the MeHg fraction was greatest in the hypolimnetic samples based on the optimal conditions for mercury methylation here (Xun, L. et. al. 1987; Watras and Bloom, 1994). It is important to note that HgT concentrations may still be relevant to trophic transfer models as

it is not yet known if the guts of consumers can methylate the inorganic mercury component of ingested algae.

Sebalj (1995) found that the highest zooplankton grazing rates occurred in the metalimnia of these lakes over the season, an important finding with respect to mercury biomagnification potential. As weight-specific sestonic-HgT concentrations tend to be generally higher in the hypolimnia by seasons end, I suggest that optimal zooplankton grazing in the metalimnia favours lower HgT biomagnification potential at this time in the season. However, the edible algal size range tends to be less then 30-μm, suggesting that trophic transfer of mercury is optimized by the high mercury concentrations found in small algal cells relative to larger ones.

Table 1.1: Summary table of physico-chemical parameters showing seasonal means for 5 matched sampling dates from June to October in Mouse and Ranger lakes over 4 years. Standard Errors (S.E.) represent a pooled estimate of error variance and a p-value greater than 0.05 indicates no significant year to year differences. When One-Way ANOVA is performed to compare parameter values between Mouse and Ranger, the only significant differences determined were for DOC and pH, where Ranger had significantly higher values for both.

	Years				
Mouse	**1991 Mean(S.E.)**	**1992 Mean(S.E.)**	**1993 Mean(S.E.)**	**1994 Mean(S.E.)**	**p-value**
DIC	3.32(0.66)	4.38(0.66)	2.90(0.63)	3.85(0.70)	0.42
DOC	5.01(0.33)	5.77(0.33)	5.48(0.31)	5.45(0.35)	0.45
pH	5.55(0.06)	5.62(0.06)	5.66(0.06)	5.71(0.06)	0.37
TP	23.29(4.57)	25.58(4.57)	16.95(4.33)	23.49(4.85)	0.55
TNN	10.00(4.99)	16.33(4.99)	18.90(4.73)	10.25(5.29)	0.50
Fe	1.44(0.55)	2.30(0.55)	1.55(0.52)	2.00(0.58)	0.66
Ranger					
DIC	4.69(0.50)	4.57(0.50)	2.95(0.50)	3.87(0.56)	0.07
DOC	6.61(0.31)	6.00(0.29)	5.97(0.29)	6.23(0.32)	0.41
pH	5.69(0.09)	5.83(0.09)	5.84(0.09)	5.81(0.10)	0.67
TP	24.3(2.26)	22.31(2.26)	15.79(2.26)	21.89(2.53)	0.07
TNN	33.50(16.40)	28.30(16.40)	82.40(16.40)	58.75(18.34)	0.10
Fe	2.55(0.53)	2.23(0.53)	1.60(0.53)	2.20(0.59)	0.64

Table 1.2: Summary statistics pertaining to the least squares linear regression analysis of *weight-specific* sestonic HgT (pg/mg DW) against various lake parameters. Numbers in brackets are the Standard Errors of the slope. P-value is the probability that the slope is significantly different from zero at a = 0.05.

Data Set	**Parameter**	**Intercept**	**Slope**	r^2	**p**
Pooled depth data for **both** lakes over the season	Total Chlorophyll	174.04	0.99(0.44)	0.25	0.04
	Corrected Chlorophyll	170.06	5084(3.16)	0.19	0.08
	Algal Biomass	213.74	-0.01(0.07)	0.00	0.93
	Seston Dry Weight	201.22	3.72(9.93)	0.01	0.71
	Dissolved O_2	223.02	-1.58(5.07)	0.01	0.76
	Temperature	217.67	-0.44(4.29)	0.00	0.92
Data for **Mouse** L. only	Total Chlorophyll	161.13	0.99(0.42)	0.30	0.03
	Corrected Chlorophyll	153.57	7.62(3.09)	0.32	0.03
	Algal Biomass	220.55	-0.01(0.06)	0.00	0.91
	Seston Dry Weight	176.57	10.30(10.85)	0.06	0.36
	Dissolved O_2	227.07	-1.83(6.47)	0.01	0.78
	Temperature	202.90	1.04(5.47)	0.00	0.85
Data for **Ranger** L. only	Total Chlorophyll	116.18	3.29(1.54)	0.24	0.05
	Corrected Chlorophyll	191.4	2.37(5.12)	0.02	0.65
	Algal Biomass	218.14	-0.02(0.12)	0.00	0.87
	Seston Dry Weight	241.90	-13.89(14.48)	0.06	0.35
	Dissolved O_2	213.24	-0.68(5.78)	0.00	0.91
	Temperature	240.34	-2.64(4.64)	0.02	0.58
Data for **Mouse** L. **metalimnetic** samples only	Total Chlorophyll	-36.85	22.17(41.07)	0.07	0.62
	Corrected Chlorophyll	-9.49	78.89(18.14)	0.82	0.01
	Algal Biomass	125.60	0.05(0.04)	0.29	0.27
	Seston Dry Weight	64.98	80.61(58.0)	0.33	0.24

Table 1.2 (cont.)

Data Set	Parameter	Intercept	Slope	r^2	p
	Dissolved O_2	22.08	14.01(7.34)	0.48	0.13
	Temperature	-46.78	11.66(13.26)	0.16	0.43
Data for **Ranger** L. **metalimnetic** samples only	Total Chlorophyll	89.15	3.35(4.13)	0.10	0.45
	Corrected Chlorophyll	204.84	-0.61(8.19)	0.00	0.94
	Algal Biomass	9.29	0.30(0.09)	0.66	0.01
	Seston Dry Weight	155.01	32.20(84.28)	0.02	0.72
	Dissolved O_2	93.82	9.98(9.40)	0.16	0.33
	Temperature	481.99	-16.70(7.04)	0.48	0.05
Data for **Mouse** L. **hypolimnetic** samples only	Total Chlorophyll	64.85	1.67(0.27)	0.87	<0.01
	Corrected Chlorophyll	75.20	11.30(2.57)	0.76	<0.01
	Algal Biomass	241.97	-0.03(0.16)	0.01	0.84
	Seston Dry Weight	57.36	27.63(21.85)	0.21	0.25
	Dissolved O_2	327.13	-46.15(13.58)	0.66	0.01
	Temperature	-271.85	67.45(38.85)	0.33	0.13
Data for **Ranger** L. **hypolimnetic** samples only	Total Chlorophyll	125.02	3.97(2.06)	0.38	0.10
	Corrected Chlorophyll	145.03	21.04(12.84)	0.31	0.15
	Algal Biomass	435.18	-0.68(0.35)	0.39	0.10*
	Seston Dry Weight	328.60	-31.62(22.61)	0.25	0.21
	Dissolved O_2	228.14	-2.67(18.18)	0.00	0.89
	Temperature	-169.46	54.51(34.85)	0.29	0.17

* this p-value becomes significant ($p < 0.05$) and the r^2 is increased ($r^2 = 0.47$) when the data are log transformed.

Table 1.3: Least squares linear regression analysis for cell size-ratios against algal biomass (ug/L) and seston DW against algal biomass (ug/L) for limnetic depths in each lake, where $p \leq 0.05$ indicates significant relationships.

Lake	Limnetic Depth	Cell Size-Ratios r^2	Seston DW (mg/L) r^2	p-value
Mouse	metalimnion	0.14	0.69	Not Sig.
Mouse	hypolimnion	0.43	0.00	Not Sig.
Ranger	metalimnion	0.00	0.00	Not Sig.
Ranger	**hypolimnion**	**0.58**	**0.97**	**Sig.**

Table 1.4: Summary table of the 1995 seasonal means of physico-chemical and biological variables for Mouse and Ranger lakes where Standard Errors (S.E.) represent a pooled estimate of error variance and p-values greater than 0.05 indicates no significant differences between lakes. Samples were collected from discrete depths in the euphotic zone monthly, from June to September.

	Mouse Lake Mean(S.E.)	**Ranger Lake Mean(S.E.)**	**p-value**
Secchi Depth (m)	3.9(0.21)	2.9(0.18)	0.015
D.O. (mg/L)	6.92(1.60)	7.23(1.60)	0.892
Temperature (°C)	13.61(2.00)	12.72(2.00)	0.758
Total Chl a (mg/L)	47.25(15.58)	25.94(15.58)	0.348
Corr. Chl a (mg/L)	7.05(2.36)	6.62(2.36)	0.900
Algal Biomass (mg/L)	584.30(138.57)	471.41(138.57)	0.574
Seston DW (mg/L)	3.62(0.85)	2.29(0.80)	0.273
Sestonic HgT (pg/L)	776.15(220.05)	448.00(220.05)	0.307
Sestonic HgT (pg/mg/DW)	212.17(34.22)	212.01(32.26)	0.997

Figure 1.1: Mouse L. morphometry and depth distribution

Figure 1.1

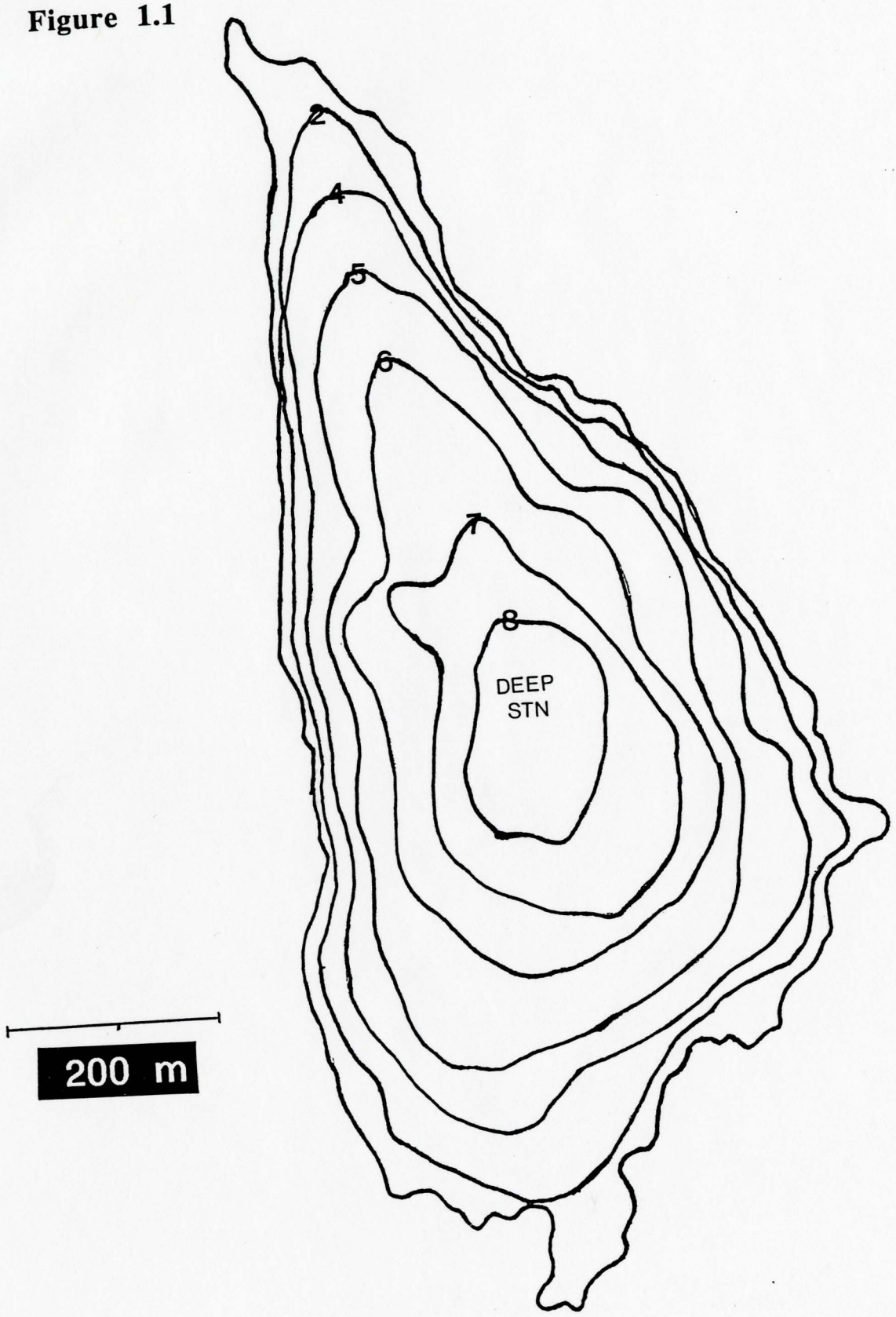


Figure 1.2: Ranger L. morphometry and depth distribution

Figure 1.2

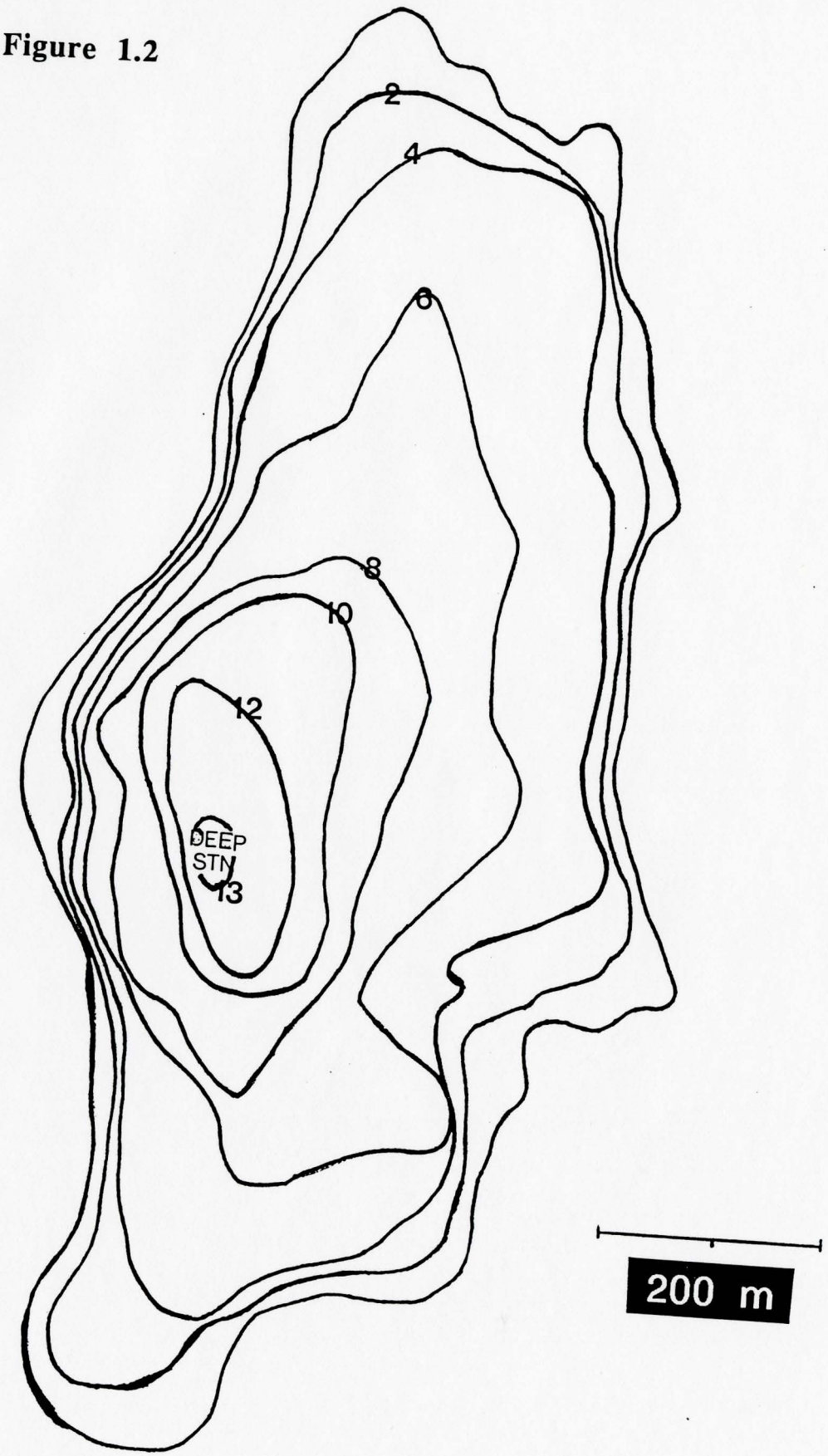
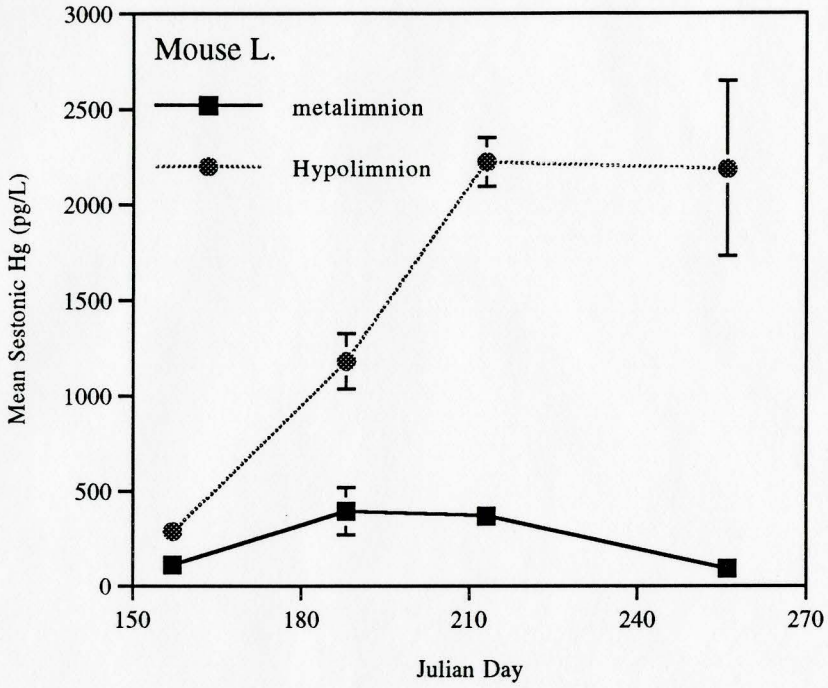


Figure 1.3: Seasonal dynamics of sestonic-HgT (pg/L) for Mouse L. (a) and Ranger L. (b)

Figure 1.3

a)


Mouse L.
metalimnion
Hypolimnion
Mean Sestonic Hg (pg/L)
3000
2500
2000
1500
1000
500
0
150
180
210
240
270
Julian Day

b)

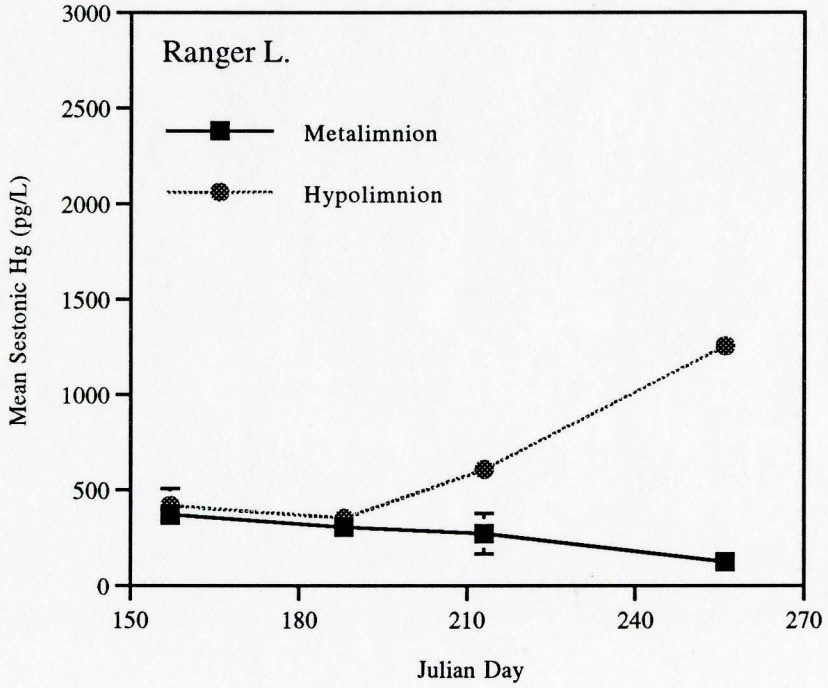
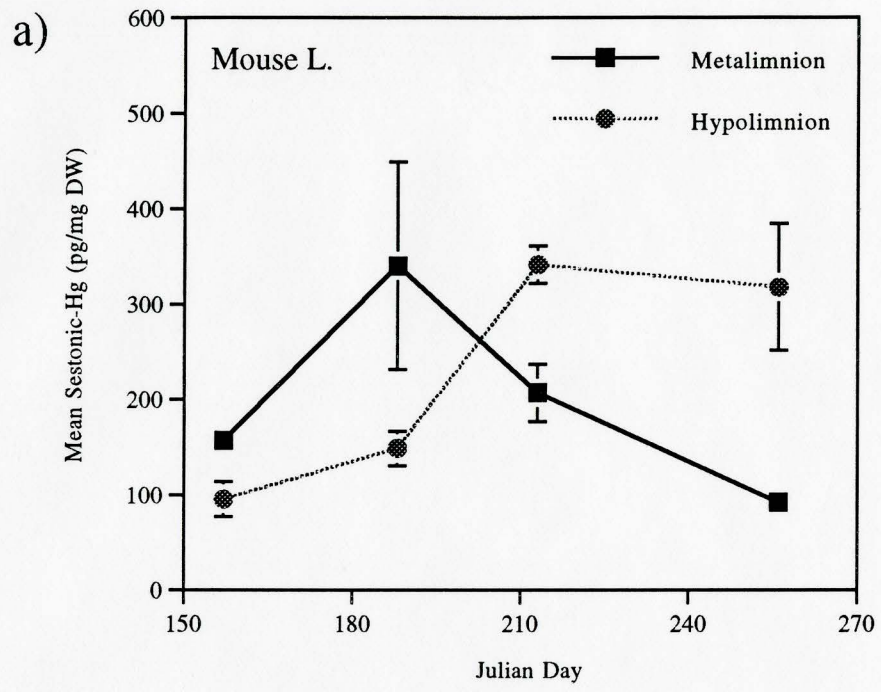

Ranger L.
Metalimnion
Hypolimnion
Mean Sestonic Hg (pg/L)
3000
2500
2000
1500
1000
500
0
150
180
210
240
270
Julian Day

Figure 1.4: Seasonal dynamics of weight-specific Sestonic-HgT (pg/mg DW) for Mouse L. (a) and Ranger L. (b)

Figure 1.4


a)
Mouse L.
Metalimnion
Hypolimnion
Mean Sestonic-Hg (pg/mg DW)
600
500
400
300
200
100
0
150
180
210
240
270
Julian Day

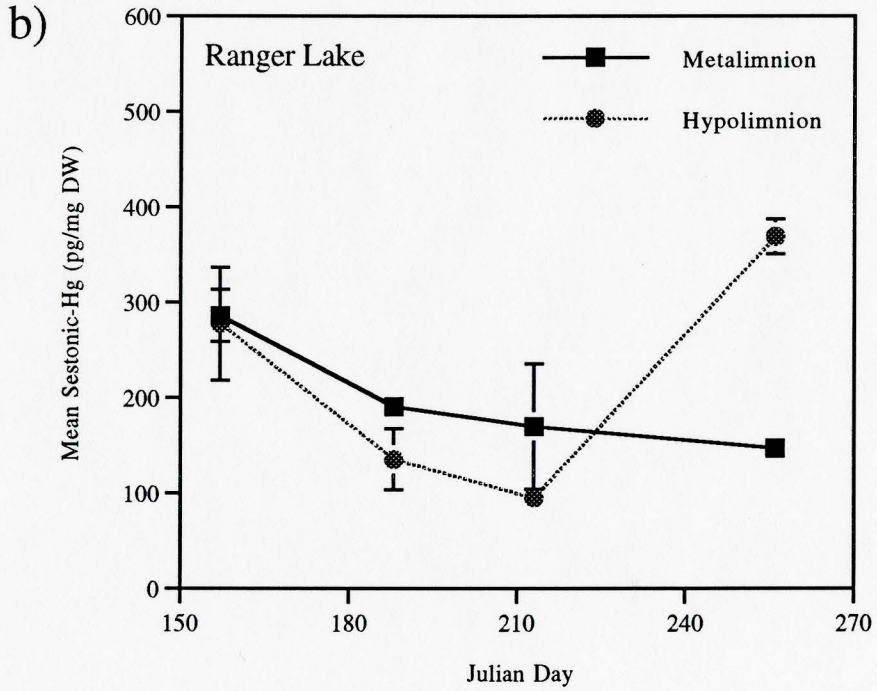

b)
Ranger Lake
Metalimnion
Hypolimnion
Mean Sestonic-Hg (pg/mg DW)
600
500
400
300
200
100
0
150
180
210
240
270
Julian Day

Figure 1.5: Seasonal dynamics of various algal productivity parameters with weight-specific sestonic-HgT (pg/mg DW) for Mouse L. metalimnion (a), Ranger L. metalimnion (b), Mouse L. hypolimnion (c), and Ranger L. hypolimnion (d).

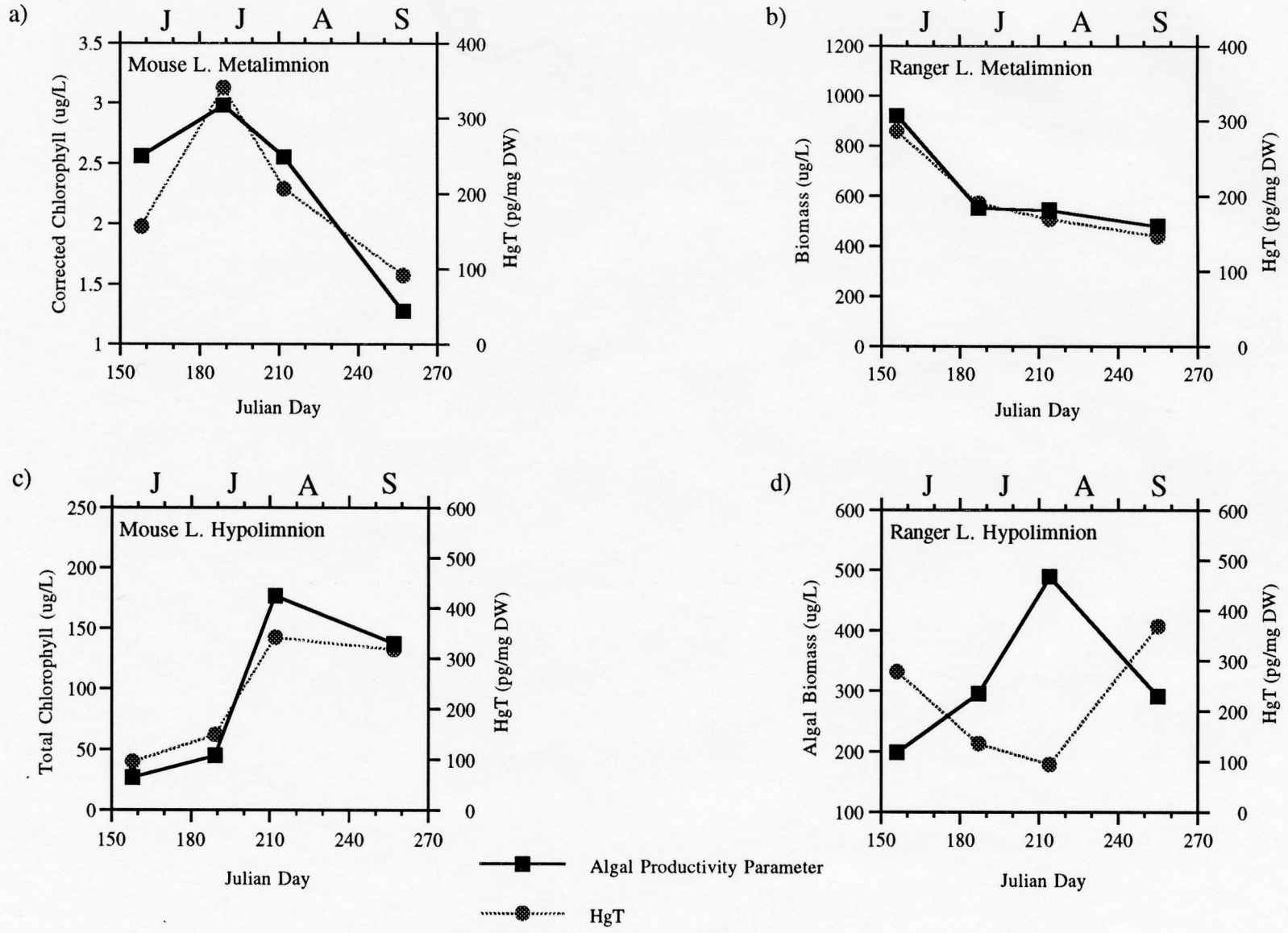
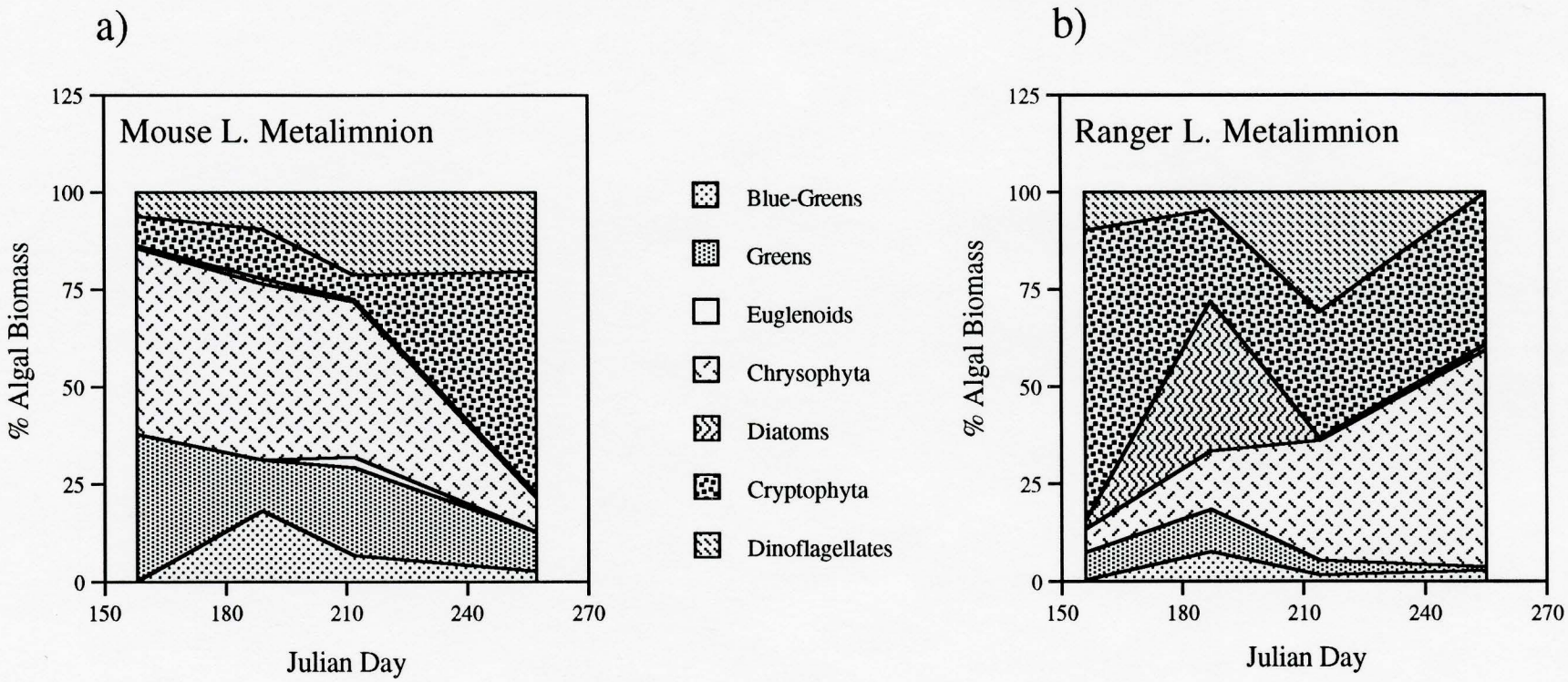

a)
J J A S
Mouse L. Metalimnion
Corrected Chlorophyll (ug/L)
HgT (pg/mg DW)
Julian Day
b)
J J A S
Ranger L. Metalimnion
Biomass (ug/L)
HgT (pg/mg DW)
Julian Day
c)
J J A S
Mouse L. Hypolimnion
Total Chlorophyll (ug/L)
HgT (pg/mg DW)
Julian Day
d)
J J A S
Ranger L. Hypolimnion
Algal Biomass (ug/L)
HgT (pg/mg DW)
Julian Day
Algal Productivity Parameter
HgT

Figure 1.5

Figure 1.6: Relative abundances of algal groups over the season in Mouse L. metalimnion (a) and Ranger L. metalimnion (b)

Figure 1.6


a)
b)
Mouse L. Metalimnion
Ranger L. Metalimnion
% Algal Biomass
Julian Day
125
100
75
50
25
0
150
180
210
240
270
Blue-Greens
Greens
Euglenoids
Chrysophyta
Diatoms
Cryptophyta
Dinoflagellates

CONCLUSIONS

The seasonal distribution of sestonic-HgT (pg/L) in Mouse and Ranger lakes illustrate the effects of both seston sedimentation and external HgT inputs over the season for both limnetic depths. Although the relative amount of HgT in the seston fluctuated seasonally, the variations were not easily explained by particle sedimentation and external inputs alone. Each lake exhibited a strong correlation between algal productivity and sestonic-HgT concentrations. With respect to the metalimnia of both lakes, the viable algae component seemed to be an important controlling variable of sestonic-HgT concentrations. Viable algal biomass was also an important predictor of sestonic-HgT in the hypolimnion of Ranger L. although both viable and decomposing algae (indicated by Total chlorophyll*a*) were important when predicting sestonic-HgT in the hypolimnion of Mouse L.. These data, therefore, support past *in vivo* studies which demonstrated the ability of algae to accumulate heavy metals (Vymazal, 1984; Gadd, 1990; Harris and Ramelow, 1990; Majidi et. al., 1990).

Although algal productivity appears to regulate sestonic-HgT concentrations, it is also apparent that algal size distribution in the community may have important mitigating effects. As seen in the hypolimnion of Ranger L., changes in community cell-size ratios may influence the magnitude of HgT concentrated on and in algal cells. If this relationship exists, higher mercury bioconcentration in small cells may increase the mercury biomagnification potential for consumers (eg. *Diaptomus spp.*) of small algae. Considering that the metalimnetic communities of both lakes are dominated by small cell assemblages and that highest zooplankton grazing rates also occur here, there is justification for this concern. However, the life-cycle morphologies of these cells (uni-

cells, small colonies or large colonies) are important in determining whether or not they can be ingested (Chow-Fraser, 1986 and Campbell, 1994).

The findings of this study not only shed light on seasonal dynamics of sestonic-HgT but emphasize the differences in HgT concentrations between the metalimnion and hypolimnion over the season. Inter-lake differences between the type of algal-productivity variable used to predict sestonic-HgT suggests that future studies include the measurement of more than one type of productivity parameter. As such, these factors should be taken into consideration when modeling the trophic transfer of mercury between algae and consumers. In general, analysis of *in situ* sestonic-HgT has demonstrated the high affinity for algae to accumulate this environmentally significant heavy metal.

Chapter 2:

EFFECT OF WHOLE-LAKE BIOMANIPULATION ON PHYTOPLANKTON BIOMASS AND COMMUNITY STRUCTURE IN TWO PRECAMBRIAN SHIELD LAKES

ABSTRACT

As part of a collaborative research effort to determine the effects of fish biomanipulation on the food-webs of two Precambrian shield lakes with differing trophic structures (i.e. Top-piscivore vs. Top-planktivore dominated), I focused on phytoplankton biomass and community structure of these systems over a four year period (1992-1995. In the fall of 1993, Top-piscivores were removed from Ranger L. and added to Mouse L. which had no previous piscivore community for at least 30 years. Trophic cascade and Top-Down:Bottom-Up theories predict that algal biomass would significantly increase with piscivore removal (Ranger L.) and decrease with piscivore addition (Mouse L.). As there were no significant differences between 1992-1993 (pre-manipulation years) and 1994-1995 (post-manipulation years), these years were combined to form pre- and post-manipulation data-sets.

In both lakes, algal biomass significantly increased (Student's t-test, $p \leq 0.05$) in years following the biomanipulation. This suggests that "Bottom-Up" (BU) forces were controlling algal biomass from year to year, regardless of changes in the fish communities. When algal size-classes were tested, "edible" cells (10 - 30 μm) increased in Mouse L. whereas only large "inedible" cells and colonies (> 30 μm) increased in Ranger L.. Both of these results were contrary to what was predicted. With respect to algal group composition, Greens and Cryptomonads significantly increased in Mouse L. whereas only Greens significantly increased in Ranger L.. Both of these groups were considered to be edible and thus these results were not consistent with the model predictions. As such, I suggested that "bottom-up" influences were important in controlling both size-class and taxonomic abundances.

However, when individual size-classes of representative algal genera were compared between pre- and post-manipulation years, there were some effects which may be attributed to the biomanipulation. In particular, large Green colonies became prevalent in Mouse L. during post-manipulation years as a probable response to increased grazing pressure. Conversely, "edible" Greens became prevalent in Ranger L. after the biomanipulation, supporting the prediction of reduced zooplankton grazing pressure. These results have revealed the necessity to test specific algal genera of varying size-classes in order to improve analytical sensitivity to biomanipulation effects. They also showed that the majority of algal genera, regardless of size, were not affected by the biomanipulation. Limitations to my interpretation of the data are discussed and vary from time-scale issues to consumer and resource availability unknowns. In conclusion, the results of this study do not provide irrefutable support of TD control but rather illustrate the resilience to herbivory by the phytoplankton community as a whole.

INTRODUCTION

Over the last few decades, lake managers have implemented a variety of aquatic ecosystem alterations to either improve water quality in lakes and ponds or enhance ecosystem productivity. One such alteration, "biomanipulation", involves changing the food-web hierarchy of these systems. Biomanipulation theory (Shapiro et al., 1975) and the "Trophic Cascade" hypothesis (Carpenter et al., 1985) are based on the rationale that increased piscivore abundance will decrease planktivore abundance which would in turn increase zooplankton abundance. With an increase in zooplankton abundance, phytoplankton abundance should diminish, resulting in improved water clarity.

Aspects of these hypotheses have been supported (Hrbacek et al., 1961; Losos and Hetesa, 1973; Leah et al., 1980; Lynch, 1979; Gophen, 1984; Olrik et al., 1984; Shapiro and Wright, 1984; Carpenter et al., 1987; Mills et al., 1987; Ranta et al., 1987) and refuted (Grygierek et al., 1966; Hall et al., 1970; Spodniewska and Hillbricht-Ilkowska, 1978; Hillbricht-Ilkowska and Weglenska, 1978; Edmondson and Litt, 1982; Vijverberg and Van Densen, 1984; Scavia et al., 1986; Carpenter et al., 1987; Lehman, 1988; Benndorf et al., 1988; McQueen et al., 1989) in a number of whole-system studies. In any event, it has become apparent in recent years that both "top-down" (top-fish community) and "bottom-up" (physico-nutrient parameters) controls are important in maintaining trophic-level abundances in fresh-water systems (McQueen and Post 1986; Carpenter (ed.), 1987; Ramcharan, 1995).

A third hypothesis has been suggested by McQueen and Post (1986) called the "Top-Down:Bottom-Up" (TD:BU) theory. This theory combines the controlling influences of both consumers (TD) and resource availability (BU) on food-web structure. The model

predicts that maximum attainable biomass is determined by nutrient availability but that actual biomass is determined by the combined effects of TD:BU forces. This model also predicts that cascading effects starting at the top of the food-web would progressively weaken towards the bottom of the food-web, particularly in eutrophic (high-nutrient) systems. Conversely, the greatest TD effects should be seen in oligotrophic systems, where changes in grazing pressure on phytoplankton are measurable due to available nutrient restrictions. Regardless of the predictive model used, there have been concerns about the spatial and temporal scale effects not considered in past studies, particularly those using enclosures (Carpenter (ed.), 1987; Faafeng et. al., 1990; McQueen, 1992).

In 1991, the Dorset Research project was initiated (D. McQueen, P.I.), in part, to address the concerns of spatial and temporal scales by performing biomanipulations on whole-lake systems. Two lakes with similar morphological and physico-chemical characteristics but differing food-web hierarchies were selected near Dorset, Ontario to perform biomanipulation experiments. Ranger L. had a top-piscivore community whereas the other Mouse L. was dominated by a planktivorous fish community (Ramcharan et al., 1995). In the fall of 1993, an attempt was made to remove all piscivorous fish from Ranger L.. These fish (plus additional piscivores from nearby lakes to make the piscivore density equal to Ranger L.) were added to Mouse L. at the same time.

As part of the collaborative research effort to study biomanipulation effects on the entire food-web, I focused on the first trophic level, namely the phytoplankton community of each lake. Four years of seasonal data were collected, including two pre-manipulation years (1992 and 1993) and two post-manipulation years (1994-1995). To determine if there were any effects from the biomanipulation (i.e. top-down) in each lake, I compared pre-manipulation and post manipulation data ranging from general (eg. mean seasonal

algal-biomass) to specific (genera/size-class biomass) aspects of the data-set. BU influences were tested by comparing Total Phosphorus (limiting nutrient for algae) and Secchi depths (estimation of light availability and algal productivity) over the four years. I attempted to distinguish between TD and BU effects on the phytoplankton community in addition to acknowledging the numerous limitations in this study.

METHODS

Study Sites and Food-Web Structure

Please refer to Chapter 1 for descriptions on the physical characteristics of Mouse L. and Ranger L. and the sampling locations. In pre-manipulation years (1992 and 1993), Mouse L. was dominated by a planktivorous-fish community (eg. Pumpkinseed, Yellow-Perch) whereas Ranger L. was dominated by a top-piscivore community (large and small-mouth bass). Herbivorous zooplankton communities in both lakes consisted of large (*Holopedium gibberum* and *Daphnia catawba*) cladocerans and small (*Diaptomus minutus*) copepods. It should be noted that during pre-manipulation years, *Daphnia* was rare in Mouse L. and very common in Ranger L.. Predatory invertebrates such as *Chaborus spp.* and *Leptodora spp.* were present in both lakes (Ramcharan et. al., 1995).

In the fall of 1993, piscivorous fish were removed from Ranger L. and added to Mouse. L., which shifted the food-web hierarchies of each lake. In post-manipulation years (1994-1995), over 90% of piscivorous fish was removed from Ranger L. (C. Ramcharan, pers. comm.). By 1995, *Daphnia* had dramatically increased in abundance in Mouse L. and *Holopedium* declined in Ranger L (P. Chow-Fraser, unpublished data). Algal morphology in each lake was generally dominated by large (flagellated) and small (flagellated and non-flagellated) colonies (< 30 μm). (Appendices 2 and 3). Phytoplankton communities were dominated by Chrysophytes and Cryptophytes in each lake (Appendix 2a and b). These algal groups are common to coloured, oligotrophic lakes (Moss, 1988).

Sampling and Analysis

From early June to the middle of September, matched monthly phytoplankton samples were collected from the deep station of Mouse L. and Ranger L. over four seasons (1992-1995). In conjunction with the collection of lake-water samples, Secchi depths were measured using a 30 cm diameter weighted disk. I collected lake-water for Total Phosphorus (TP) analysis in 1995 and obtained TP data for previous years from the Dorset Research database (D. McQueen, P.I.). TP samples were processed according to standard protocols established by the Ministry of the Environment and Energy (OMEE) (i.e. modified molybdenum blue method of Murphy and Riley, 1962).

Integrated water samples were collected by immersing weighted Tygon-tubing (5/8" diameter) to 6 m depths in the water column. This depth encompassed the euphotic zone (area where light is available for photoautotrophic growth) for both lakes. Water collected in the tubing was released into a bucket where it was swirled to ensure homogeneous distribution. 125-ml sub-samples were collected in glass bottles and preserved immediately with Lugol's acid-iodine.

For the determination of viable algal biomass and composition, 5-mL sub-samples of preserved lake-water were settled for 24-h in algal settling chambers. Using 200x magnification, algal cells and colonies were counted and taxonomically identified along one full transect of each settled slide. The entire slide was scanned for large cells and colonies to ensure their proportion in the sample was accurately recorded. Algal bio-volumes (biomass) were calculated by approximation to geometric shapes. Average dimensions of the algae were determined with the aid of an eye-piece micrometer at 400x magnification. All samples from all years were counted by myself to ensure confidence when comparing

the data for each date and year (i.e. consistencies in taxonomic identification and size classification).

Data Analysis

All viable algal cells and colonies were identified to algal group:

Algal Group	Abbreviation
Blue-Greens	BG
Greens	GR
Chrysophytes	CH
Diatoms	DM
Cryptophytes	CR
Dinoflagellates	DF

Most of these cells and colonies were identified to genus. The exceptions included some Green colonies and Dinoflagellates, which were difficult to identify to genus without living specimens. In conjunction with taxonomic classification, algal cells and colonies were categorized into "edible" and "non-edible" size classes:

Class	Morphology	Longest Linear Dimension	Type
1	cell	< 10 µm	edible
2	cell	10 - 30 µm	edible
3	cell	> 30 µm	non-edible
4	colony	< 30 µm	edible
5	colony	> 30 µm	non-edible
6	filament	> 30 µm	non-edible

These size classes were developed from a number of literature sources regarding "ingestibility" or "edibility" of algae (Gliwicz, 1977; Chow-Fraser and Knoechel, 1985; Lehman and Sandgren, 1985; Chow-Fraser, 1986; Chow-Fraser and Maly, 1992). A thesis which included gut-content analyses of zooplankton from Mouse L. and Ranger L was also an important reference source (Campbell, 1994). According to these sources, groups 1, 2 and 4 were generally considered to be edible whereas only certain larger cells and colonies were edible to particular zooplankton genera.

RESULTS AND INTERPRETATIONS

A) *Top-Down Effects*

Comparison of Algal Biomass Abundances

In Table 2.1, I used One-way ANOVA and found no significant differences among years for either lake and that in particular, Tukey-Kramer HSD analysis did not find significant differences within pre- and post-manipulation years. Therefore, I amalgamated data from pre-manipulation years and post-manipulation years to determine if significant changes in algal biomass occurred after the biomanipulation in each lake (Table 2.2).

According to the Trophic Cascade and TD:BU (considering these lakes are both oligotrophic) hypotheses, there should be a significant increase in algal biomass once top-piscivores were removed from Ranger L. and, alternatively, a significant decrease in algal biomass once top-piscivores were added to Mouse L.. Based on this expectation, the significant algal biomass increase in post-manipulation years in Ranger L. (Table 2.2) support the prediction of each hypothesis. However, the significant increase in algal biomass in post-manipulation years in Mouse L (Table 2.2) do not support these hypotheses.

Comparison of Algal Size-Class Abundances

Some studies have shown that algal size assemblages can be impacted by changes in zooplankton grazing pressure (Lehman and Sandgren, 1985; Mazumder et al., 1990; Dawidowicz, 1990) and as such, I tested for significant changes in size-class abundances. In Mouse L., the only size-class that changed significantly were edible cells (10 - 30 μm) (Table 2.3). Assuming that there was greater grazing pressure in Mouse L. following the

biomanipulation, I did not expect to find increases in the edible size-classes. Also, I did not expect to see significant increases in large cell and colony (> 30 μm) biomass in Ranger L. where grazing pressure was expected to have been reduced in post-manipulation years (Table 2.3). Mean biomass values with Standard Errors and p-values for each size class in each lake are provided in Appendices 4 and 5 respectively.

Comparison of Algal Group Abundances

In conjunction with cell size, certain algal groups tend to be selectively grazed by zooplankton more so than other groups (Thatcher, et al., 1993). In these lakes, L. Campbell (1994) found that in general, Diatoms were not ingested by large cladocerans nor the small copepod, *Diaptomus*. As such, I tested for significant changes in algal group abundances. The mean biomass values with Standard Errors and p-values for each algal group in each lake are provided in Appendices 6 and 7 respectively.

Both Greens and Cryptophytes significantly increased in Mouse L. (Table 2.4) whereas only Greens significantly increased in Ranger L. (Table 2.4) in post-manipulation years. Greens, in general, are a preferred food item for a number of zooplankton taxa (Sze, 1986; Moss, 1988) and thus I expected changes in consumer impacts to be reflected by this algal group. However, with increased grazing pressure in Mouse L., I would not expect to see an increase in Green abundances. This conflicting result will be explained in the next section of this chapter when cell morphology of Greens are taken into account. Although increases in Greens in Ranger L. support the model predictions, it is the relative increase in Green size-classes which clarify the TD effect. With respect to Cryptophytes in Mouse L., I am not clear as to why they would increase when they are a prey item for zooplankton at certain times in the year. Again, the size structure of Cryptophytes may help to clarify this result.

Comparison of Size-Class Abundances for Representative Algal Genera

Thus far, I have organized my results according to size or taxonomic affiliation. In order to screen for more specific impacts of the biomanipulation, I decided to test certain size-class ranges within representative genera/sub-groups. The genera/sub-groups selected were based on either their high relative abundance in these lakes or their identification as important genera in the literature (Carpenter et al., 1987; Vanni, 1987). Some were selected based on their dramatic changes in representation between pre- and post-manipulation years (eg. *Asterionella*). Those genera/sub-groups not included in the analysis were considered to be rare in the phytoplankton community.

Not all genera/sub-groups of each size-class were found on all 4 sampling dates each year. This meant that "0" was recorded as a biomass value every time a genus/sub-group was not present for a particular sample date. This procedure balanced the data-set for statistical testing but made it difficult to use ANOVA (based on the problems with variance created by "0" values). As a result, non-parametric Wilcoxon tests were performed to determine whether or not significant changes in biomass occurred after the biomanipulation for all representative genera and size-classes. The actual p-values derived from these tests are provided in Appendices 8 and 9 for each lake respectively.

Significant results supporting the model predictions in Mouse L. include the increases in large Green colonies, large *Cryptomonas* and large Dinoflagellates and conversely, decreases in small *Chrysophaerella* colonies (Table 2.5). The remaining genera with edible and non-edible size-classes did not significantly change, suggesting that biomass abundances of these groups were ultimately controlled by BU forces. Increases in edible *Cryptomonas* (10 - 30 μm) do not support TD effects and as such, are not clearly

understood. Since both *Cryptomonas* size-classes increased in biomass, they were most likely the result of BU forces that encouraged *Cryptomonas* growth during post-manipulation years. The significant decreases in *Asterionella*, also support TD effects, albeit indirect. The virtual elimination of this diatom genus cannot be explained by increases in zooplankton grazing pressure since they are not eaten by the zooplankton of these lakes (Campbell, 1994). However, expected increases in the invertebrate *Chaoborus*. may explain why *Asterionella* disappeared during post-manipulation years in Mouse L. *Chaoborus*, as well as other large opportunistic invertebrates, can eat a variety of Diatoms (Horne and Goldman, 1994). Since *Asterionella* was never a dominant algal genus in Mouse L., it would not be surprising for modest increases in consumption by *Chaborus* to have severely decreased *Asterionella* abundance in the algal community.

In Ranger L., TD predictions are supported by the significant increases of edible Green cells and, indirectly, by increases in *Asterionella* colonies (Table 2.5). With theoretical declines in *Chaoborus*, Asterionella may have been able to emerge in post-manipulation years, particularly in 1995. In contrast to Mouse L., Green colonies did not significantly change, suggesting that the biomanipulation neither hindered nor promoted their abundance. Significant increases in large *Cryptomonas* is puzzling considering that grazing pressure should be reduced. *Cryptomonas* is a unique genus compared to other algae in that they do not have a true cell wall. Instead, their outer covering consists of a cell membrane underlined with a periplast. As a result, this genus may have the ability to grow larger prior to cell division with decreased grazing pressure. However, a BU explanation is more probable considering that large cells of *Cryptomonas* increased in both lakes after the biomanipulation. As in Mouse L., the majority of algal genera were not significantly altered by the biomanipulation, a trend which suggests that the algal community is generally resilient to TD effects.

B) *Bottom-up Effects*

Comparison between Algal Biomass and Secchi Depth

Secchi depth (an estimate of light availability and water clarity) can also be an indirect estimate of algal productivity, particularly in non-coloured lakes. Generally, algal abundance is negatively correlated with Secchi depth (Shapiro and Wright, 1984; Carpenter et al., 1987). McQueen et al. (1990) found that planktivore abundance was significantly correlated ($r = -0.36$) with Secchi depth in 28 lakes studied over a trophic gradient. In this study, I did not find a significant relationship between chlorophyll *a* (an estimate of algal biomass) and Secchi depth nor between algal biomass and Secchi depth in either lake (Mouse L.: $p > 0.10$, $n = 16$; Ranger L.: $p > 0.10$, $n = 16$). Ranger L. also did not have a significant relationship between algal biomass and Secchi depth ($r = -0.26$, $n = 16$). I presumed that this was due to the high colour (high DOC) in these waters which can contribute to shallower Secchi depths, regardless of suspended particulate content (i.e phytoplankton).

Secchi depth did not change significantly from year to year in Mouse L. until 1995, when it significantly decreased (Table 2.6). Ranger L. had much greater annual variation in Secchi depth (Table 2.6) where Secchi depth in Ranger L. only significantly differed between pre-manipulation year 1992 and post-manipulation year 1994. The high Secchi depth in 1992 coincided with low algal biomass measured for this year (Table 2.1) and the low Secchi depth in 1994 coincided with high algal biomass measured for 1994 (Table 2.1). Nevertheless, Secchi depth was not a good predictor of over-all algal productivity in either lake. Even though McQueen et al. (1990) found a significant relationship between planktivore abundance and Secchi depth (inferring a trophic effect on water clarity) they found no significant relationship between planktivore abundance and chlorophyll *a*.. This

scenario holds true for Mouse L., where assumed decreases in planktivores occured with significantly lower Secchi depth. Explanations for planktivore abundance correlating with Secchi depth and not algal biomass are unclear and thus make it difficult to interpret these data.

Comparison between Algal Biomass and Total Phosphorus (TP)

With respect to BU forces, Phosphorus is normally the key limiting nutrient in most oligotrophic lakes and thus levels of this macro-nutrient are indicative of algal productivity (Harris, 1980; Sze, 1986; Moss, 1988; Carpenter (ed), 1987). When the relationship between algal biomass and TP is tested, there is no significant relationship in Mouse L. ($r = -0.25$, $n = 12$) or Ranger L. ($r = -0.15$, $n = 8$). The relationship lacking between TP and algal biomass suggests that the carbon:phosphorus ratios in these lakes are highly variable each season. This is based on the premise that algal biomass is a reflection of fixed carbon and phosphorus stores. As phosphorus becomes limiting in the environment, stores of it in algae become diminished, even though carbon content may not change (Turpin, 1988). This implies that the phosphorus content in phytoplankton can fluctuate as algal biomass remains constant. It is interesting to note that TP does not significantly change in Mouse L. until 1995 when it significantly decreases (Table 2.10). In Ranger, TP was not significantly different from year to year (Table 2.10). As found with Secchi depth, these data suggest that TP levels in these lakes do not reflect algal abundances and thus was not a major controlling variable of algal biomass.

A)

Table 2.1: ANOVA for seasonal algal-biomass (mg/L) in both lakes for years 1992 - 1995, where $p \leq 0.05$ represents significant differences among years. Matching superscript letters signify means that are **not** significantly different based on Tukey-Kramer HSD analysis.

Lake	**n**	**1992 mean(S.E.)**	**1993 Mean(S.E.)**	**1994 Mean(S.E.)**	**1995 Mean(S.E.)**	**p-value**
Mouse	4	171.40(45.41)^{a}	386.22(119.01)^{a,b}	709.77(145.58)^{b}	470.60(166.07)^{a,b}	0.070
Ranger	4	473.47(318.59)^{c,d}	252.31(54.89)^{c}	543.07(99.20)^{d}	1024.52(148.47)^{d}	0.067

Table 2.2: Student's t-test of matched seasonal algal-biomass (ug/L) for pre-manipulation (1992-1993) and post-manipulation (1994-1995) years in each lake, where $p \leq 0.05$ represents a significant difference between years.

Lake	n	Pre-manipulation Years Mean(S.E.)	Post-Manipulation Years Mean(S.E.)	p-value
Mouse	8	278.81(71.59)	590.111.78)	**0.03**
Ranger	8	362.89(155.38)	783.79(122.92)	**0.05**

Table 2.3 Student's t-test of algal size-class biomass (mg/L) for pre-manipulation (1992-1993) and post-manipulation (1994-1995) years where $p \leq 0.05$ represents a significant difference between years.

Size-Class	Type	Mouse L. Biomass	Ranger L. Biomass
cells < 10 um	edible	Not Sig.	Not Sig.
cells 10 - 30 um	edible	**Increased**	Not Sig.
cells > 30 um	inedible	Not Sig.	**Increased**
colonies < 30 um	edible	Not Sig.	Not Sig.
colonies > 30 um	inedible	Not Sig.	**Increased**
filaments	inedible	Not Sig.	Not Sig.

Table 2.4: Student's t-test of algal group biomass (mg/L) for pre-manipulation (1992-1993) and post-manipulation (1994-1995) years, where $p \leq 0.05$ represents a significant difference between years.

Algal-Group	**Type***	**Mouse L. Biomass**	**Ranger L. Biomass**
Blue-Greens	edible	Not Sig.	Not Sig.
Greens	edible	**Increased**	**Increased**
Chrysophytes	edible	Not Sig.	Not Sig.
Diatoms	inedible	Not Sig.	Not Sig.
Cryptophytes	edible	**Increased**	Not Sig.
Dinoflagellates	edible	Not Sig.	Not Sig.

* based on findings of L. Campbell (1994)

Table 2.5: Summary table of Non-parametric Wilcoxon test results for representative algal genera and size-classes between pre-manipulation (1992-1993) and post-manipulation (1994-1995) years, where $p \leq 0.05$ represents a significant difference between years.

Algal Group	Genus/ Sub-Group	Size Class	Mouse L. Biomass	Ranger L. Biomass
BG	*Merismopedia*	colonies < 30 um	Not Sig.	Not Sig.
		colonies > 30 um	Not Sig.	Not Sig.
GR	*Chlorella*	cells < 10 um	Not Sig.	**Increased**
		cells 10 - 30 um	Not Sig.	**Increased**
	Green Cells	cells < 10 um	Not Sig.	**Increased**
		cells 10 - 30 um	Not Sig.	**Increased**
	Scenedesmus	colonies < 30 um	Not Sig.	not present
	Green Colonies	colonies < 30 um	Not Sig.	Not Sig.
		colonies > 30 um	**Increased**	Not sig.
CH	Monads	cells < 10 um	Not Sig.	Not Sig.
		cells 10 - 30 um	Not Sig.	Not Sig.
	Dinobryon	cells 10 - 30 um	Not Sig.	Not Sig.
		cells > 30 um	Not Sig.	Not Sig.
		colonies > 30 um	Not Sig.	Not Sig.
	Chrysophaerella	colonies < 30 um	**Decreased**	Not Sig.
		colonies > 30 um	Not Sig.	**Increased**
DM	*Asterionella*	cells > 30 um	**Decreased**	Not Sig.
		colonies > 30 um	**Decreased**	**Increased**
CR	*Cryptomonas*	cells < 10 um	Not Sig.	Not Sig.
		cells 10 - 30 um	**Increased**	Not Sig.
		cells > 30 um	**Increased**	**Increased**
DF	Dinoflagellates	cells 10 - 30 um	Not Sig.	Not Sig.
		cells > 30 um	**Increased**	Not Sig.

B)

Table 2.6: ANOVA for seasonal Secchi depths (m), where $p \leq 0.05$ indicates significant differences among years. Matching superscripts represent years that are **not** significantly different.

Lake	n	1992 Mean(S.E)	1993 Mean(S.E.)	1994 Mean(S.E.)	1995 Mean(S.E.)	p-value
Mouse	4	3.55(0.20)^{a,b,c}	3.00(0.20)^{b,c}	3.08(0.20)^{b,c}	3.90(0.09)^{a}	**0.02**
Ranger	4	3.83(0.25)^{a}	2.91(0.17)^{a,b}	2.33(0.14)^{b}	3.03(0.30)^{a,b}	**0.004**

Table 2.7: ANOVA for seasonal Total Phosphorus (ug/L), where $p \leq 0.05$ indicates significant differences among years. Matching superscripts represent years that are **not** significantly different.

Parameter	**n**	**1992 Mean(S.E)**	**1993 Mean(S.E.)**	**1994 Mean(S.E.)**	**1995 Mean(S.E.)**	**p-value**
Mouse	3	10.43(0.35)^{d,e}	9.00(1.14)^{d,e}	11.50(3.08)^{d}	3.01(0.65)^{e}	**0.03**
Ranger	2	12.53(0.93)	6.55(1.30)	14.20(3.30)	7.66(4.41)	0.31

DISCUSSION

By comparing the whole phytoplankton community in each lake before and after the biomanipulation, it is apparent that one lake supports the model predictions (Ranger L.) while the other one does not (Mouse. L.) In fact, both lakes significantly increased in algal biomass in post-manipulation years. This suggests that regardless of food-web changes in these lakes, unknown controlling variables (eg. bottom-up) may be contributing to the increases in biomass measured. This is a reasonable assumption considering the close proximities of these lakes (i.e. similar climatic effects) and their similarities in physico-chemical characteristics (see Table 1.1).

With respect to general algal size effects, there were none which clearly supported the model predictions. This type of analysis, however, confirms that biomanipulation does not have an impact on size-composition in the algal community as a whole. Similarly, analysis of algal groups does not provide clear effects of the biomanipulation and thus suggests that TD impacts are not important to algal group composition in these lakes. This is not to say that algae of different size-classes or algal groups were immune to TD impacts but rather that these broad forms of analysis were not sensitive enough to specific biomanipulation effects. In fact, during years before the biomanipulation when each lake had different fish communities, general algal morphology and taxonomic structure (along with total biomass) did not differ between lakes. Therefore, the attempt to reverse the food-web hierarchies in these lakes should not have been expected to change these aspects of the algal community.

However, there were subtle differences initially between lakes with respect to abundances of specific algal genera including Green cells and colonies and *Asterionella*

abundances. With the analysis of specific algal genera and size-classes it was found that Green colonies significantly increased in Mouse L. during post-manipulation years. Porter (1976) found that gelatinous colonial-Greens were actually promoted by zooplankton grazing. This was due to their opportunistic uptakes of nutrients while passing undigested through the zooplankton gut. Green colonies represented the majority of Green biomass in Mouse L. and were mainly gelatinous forms. This suggests that theoretical increases in grazing pressure actually occurred. Although the total algal community increased in biomass during post-manipulation years, small *Chrysophaerella* colonies declined. This genus was implicated as being selectively edible in both lakes (Campbell, 1994) and thus the demise of this edible size group supports the TD predictions. In Ranger L., all edible Green cells emerged in post-manipulation years, another result consistent with the model predictions. However, edible Green cells in Mouse L. and large Green colonies in Ranger L., did not significantly change after the biomanipulation. In effect, these results seem to indicate that changes in grazing pressure may be as specific (i.e. species-specific) as the responses by the phytoplankton community.

Significant changes not expected after the biomanipulation were the evident inter-changes of *Asterionella* abundances and the increase of *Cryptomonas* biomass, in each lake. As mentioned earlier, the disappearance of *Asterionella* in Mouse L. and the emergence of *Asterionella* in Ranger L., may be the result of TD effects via changing *Chaoborus* abundances. With respect to potential BU effects, Diatoms are known to be limited by silica availability (Soltau-Kilham and Kilham, 1978). If silica were limiting in these lakes, I would expect it to occur at the same time based on their similar sources of silica (granite/sand basins). Since both lakes had similar silica levels during pre-manipulation years (Dorset Project Database), why was *Asterionella* present in Mouse L. and not Ranger L.? In fact, total Diatom biomass did not significantly change in either

lake, a result that supports the belief that silica was not limiting to Diatom abundance. Therefore, some aspect of the environment was discouraging *Asterionella* growth in Mouse L. and promoting *Asterionella* growth in Ranger L. after the biomanipulation. This is why alterations to *Chaoborus* abundance after the biomanipulation may partially explain these drastic effects to *Asterionella.*

Increases in *Cryptomonas* biomass in both lakes suggest that controlling BU effects occurred coincidentally with the biomanipulation. Even if this genus was not impacted directly by grazing, according to TD theory, I could have seen the indirect selective effects of nutrient competition. Because total algal community biomass increased in both lakes after the biomanipulation, I can rule out the selective advantages of nutrient limitation to *Cryptomonas* alone. The ecology of *Cryptomonas* distinguishes it as a generalist genus found in both oligotrophic and eutrophic waters. It tends to do well in light limited systems because of its ability to migrate (Sommer, 1985; Smolander and Arvola, 1988) and use phagotrophy as an alternative source of carbon (Smol, 1994). Perhaps these traits in conjunction with one another allowed *Cryptomonas* to prosper in each lake during post-manipulation years. However, further evidence on BU and TD variables in these lakes are required before the these significant changes can be explained. As the majority of genera did not significantly change, I suggest that whatever the controlling variable(s) of total algal biomass is, has remained relatively consistent after the biomanipulation.

However, all of my interpretations up to this point are subject to a number of limitations which affect both TD and BU assumptions. The most obvious limitations are the presently unknown changes to the higher trophic levels in each lake. Without knowing actual abundances of potential consumers, it is difficult to confirm consumption effects on phytoplankton. Also, the conventional assumption that only herbivorous zooplankton have

an impact on algal biomass may not be true, as in the case of *Chaoborus*'s possible effect on *Asterionella.*

If the persistence of algal biomass in post-manipulation years occurs with a persisting zooplankton community, it would be difficult to say that TD effects were not important. Zooplankton my execute diel vertical migration as a defense against increased predation pressure (Dodson, 1990; Leibold, 1990; Dini and Carpenter, 1992). As such, zooplankton size and biomass may prevail as a result of this behavioural response. Both Mouse and Ranger achieve anoxia by mid-summer in the hypolimnion. This may serve as a refugia against planktivores that cannot tolerate low oxygen levels. The year-class proportions in the fish community may be also be important because a fish community dominated by young fish may be planktivore-dominated, even though these fish are piscivorous as adults. As a result, time-scale can also be considered a limitation if the study is not long enough to account for populations requiring years to balance out. In general, there are a number of possible scenarios which haven't been explored and thus make it difficult to assess the TD impacts from the biomanipulation.

Although individual nutrient data have been collected from the outset and there have been no significant changes (Table 1.1), these data are not useful when determining their limitations to algal growth. The most useful way to determine nutrient limitation effects is by calculating a ratio with other limiting nutrients, such as N:P and Si:P (Soltau-Kilham and Kilham, 1978; Hecky and Kilham, 1988). Perhaps if enclosure experiments were set up in these lakes to assess the impact of variable nutrient proportions (through nutrient addition), I could have ascertained these BU affects to the algal community.

In recent studies, C:P (Giani, 1991; Brett, 1993) and fatty acid content (Ahlgren et al., 1990 and 1992) in phytoplankton have been shown to affect zooplankton abundance. *Daphnia* in particular are dependent on low C:P in their food. If high C:P persist in algal food, *Daphnia* populations can crash (Sterner, 1993). Elser et al. (1995) found that these ratios can cause stoichiometric constraints on food-web dynamics in there entirety, without effecting algal biomass. Low C:P ratios are enhanced when P is not limiting to algal growth (Olsen et al., 1986). Therefore, without measuring these ratios in the phytoplankton, it is difficult to distinguish the impacts of planktivores and food quality on zooplankton populations.

Although this study was inconclusive with respect to determining clear TD and BU effects on algal biomass, it has demonstrated the resilience of the phytoplankton community from year to year (Table 2.1). Complex interactions between algal species can include resource competition, predation (via phagotrophy) and DOC production and utilization, all of which have confounding effects on one another. Modeling of these antagonistic and synergistic factors in conjunction with trophic interactions may prove to be very difficult. Even so, future management of fresh-waters will ultimately depend on our advanced understanding of phytoplankton dynamics if healthy aquatic ecosystems are to be sustained.

FUTURE CONSIDERATIONS

Although I have attempted to offer new insights on sestonic-HgT levels and the effects of biomanipulation on phytoplankton communities in whole-lake systems, I believe that much work has yet to be done to advance our knowledge in these areas. Having used two whole-lakes in both of these studies is in itself an improvement on what information is available in the literature. The establishment of a data-set based on a larger sample of lakes (i.e. $n > 2$), would provide greater confidence when generalizing not only about sestonic-mercury dynamics but mercury movement within the entire food-web. Perhaps the lakes sampled could be representative of a trophic gradient or pristine to polluted gradient. This approach would enable researchers to distinguish inter-lake differences of mercury transfer and fate in aquatic food-webs. To focus on the specific research question as to why some pristine lakes on the Precambrian Shield have high mercury contamination in top-predator fish, future studies should only concentrate on a number of Precambrian Shield lakes.

Determination of seasonal sestonic-mercury justifies the need to use more than one sestonic-Hg concentration as a representative amount in trophic transfer models. Model utilization of seasonal mercury concentrations in seston for each limnetic depth allows for greater estimation of mercury transfer to grazers. Knowing how much mercury is in the seston is not enough to estimate how much actually is ingested by zooplankton . The data required here include an estimation of the edible-seston fraction and the zooplankton ingestion rates in these lakes. In addition, the MeHg proportion in sestonic-HgT would be required if the biomagnification potential of mercury in zooplankton is to be determined.

With respect to the biomanipulation experiment, an increase in the number of study lakes would be useful in addition to an expanded yearly data-set to confirm or refute top-down influences on the algal community. Even so, the entire food-web data-set must be completed before confident interpretations about post-manipulation algal-community structure can be made. I also think it would be important for the Dorset Project to include stoichiometric studies of sestonic C:P:N ratios to address previously described concerns about zooplankton food quality. In order to achieve these objectives, collaboration among researchers in the Dorset Project is essential.

If further studies demonstrate that smaller algal genera have higher affinities to bioconcentrate mercury while experiencing the greatest impacts from Top-Down forces, there would be important mercury transfer implications for the lower trophic levels. It would verify that edible algae (with higher amounts of mercury per unit weight) could be fairly efficient in transporting mercury from the water column into zooplankton. However, if further studies confirm that the phytoplankton community as a whole remains resilient to herbivory, perhaps the majority of mercury measured in the seston would not be available for trophic transfer to zooplankton consumers.

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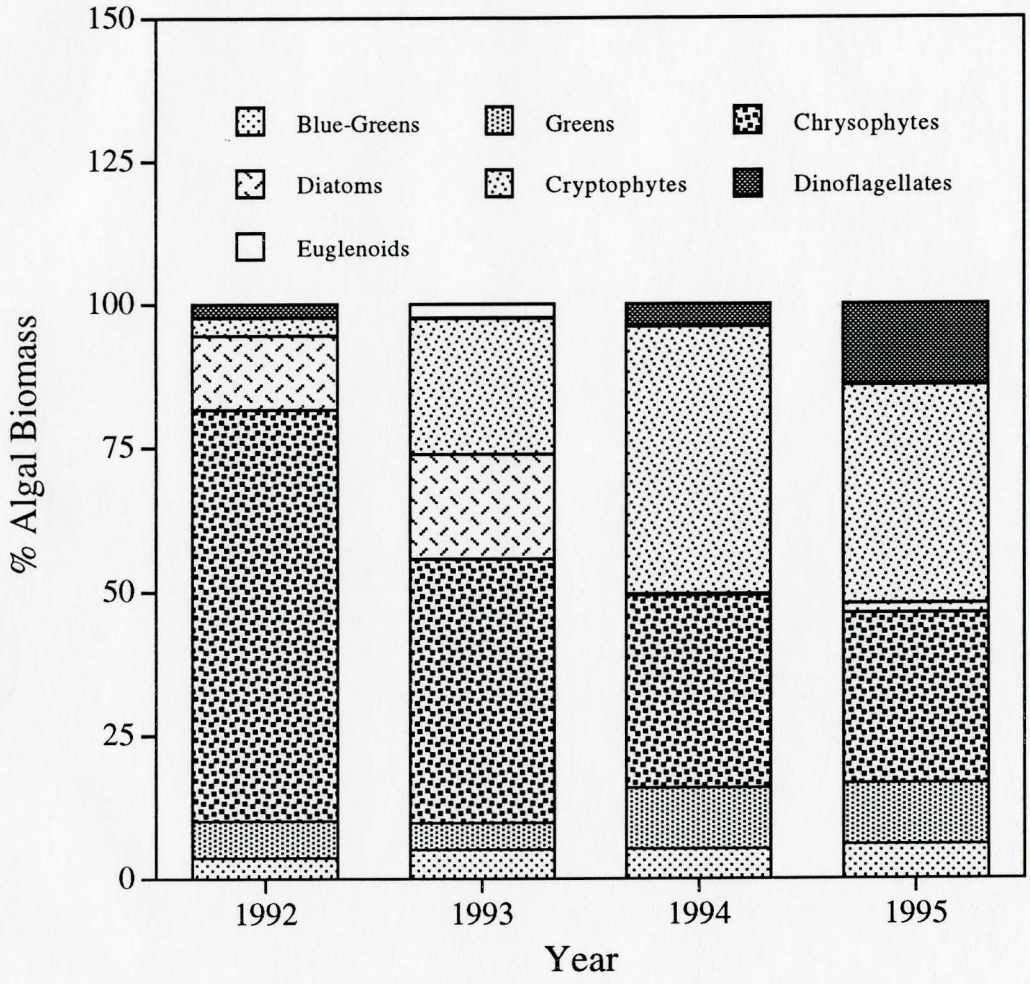
Appendix 1:

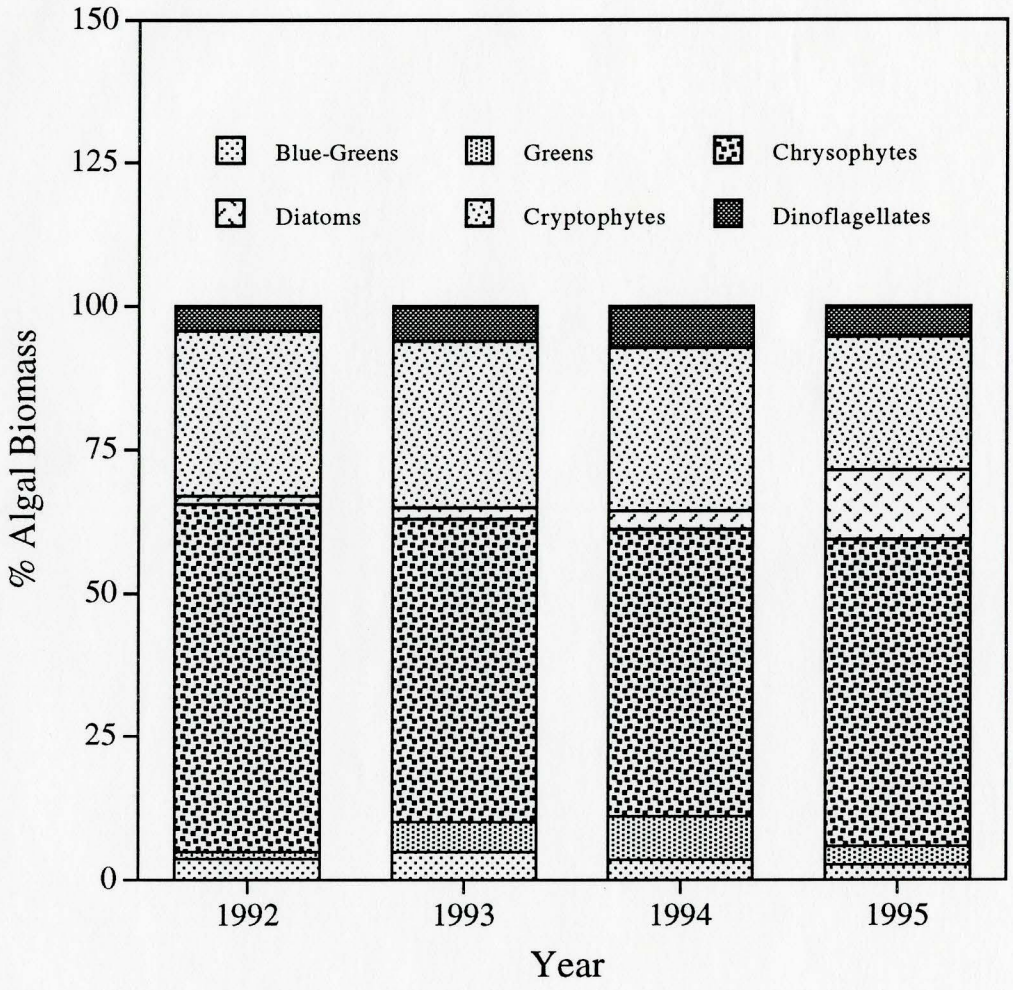
ANOVA comparison of whole water and 63 mm filtered water samples for chlorophyll and algal biomass data using pooled lake data

Parameter	Whole Water Mean(S.E.)	63 mm Filtered Water Mean(S.E.)	p-value
Total Chlorophyll	48.16(11.43)	40.55(10.96)	0.63
Corrected Chlorophyll	8.78(1.55)	7.60(1.49)	0.58
Algal Biomass	298.36(122.30)	88.48(122.30)	0.23

Appendix 2: Relative Algal Group Abundances in Mouse L.



Appendix 3: Relative Algal Group Abundances in Ranger L.



Appendix 4:		Summary of Mouse L. Algal Group Biomass for Individual Dates						
		Algal Group Biomass (ug/L)						
Julian day	**Year**	**BG**	**GR**	**CH**	**DM**	**CR**	**DF**	**Total Biomass**
154	1992	0.05	15.25	38.67	1.55	16.88	0.00	72.40
154	1993	0.18	17.45	280.44	42.42	96.30	0.00	436.78
154	1994	0.93	137.55	266.44	2.23	225.35	30.69	663.18
154	1995	2.70	78.64	121.74	5.80	92.89	0.00	301.77
181	1992	1.73	8.90	119.26	2.38	2.32	0.00	134.60
181	1993	5.57	39.59	340.25	180.83	126.70	1.00	693.94
181	1994	11.99	9.80	50.07	0.00	244.89	19.47	336.23
181	1995	37.72	29.52	100.70	4.32	44.06	27.25	243.58
214	1992	12.49	3.59	217.93	26.77	0.69	24.92	286.40
214	1993	69.54	10.93	32.87	1.61	26.79	0.00	141.74
214	1994	36.10	119.23	460.63	0.00	353.17	61.06	1030.20
214	1995	57.90	62.62	249.06	5.28	369.92	217.46	962.24
240	1992	9.08	14.25	102.60	53.03	0.22	12.46	191.64
240	1993	6.00	5.54	74.34	61.27	125.29	0.00	272.44
240	1994	98.12	34.59	177.56	2.23	496.97	0.00	809.47
240	1995	14.40	28.80	88.24	13.83	207.10	22.43	374.79

Appendix 5:		Summary of Ranger L. Algal Group Biomass for Individual Dates						
		Algal Group Biomass (ug/L)						
Julian day	**Year**	**BG**	**GR**	**CH**	**DM**	**CR**	**DF**	**Total Biomass**
154	1992	0.00	0.26	20.89	4.84	15.72	0.00	41.72
154	1993	0.57	25.39	37.17	8.02	31.50	23.37	126.02
154	1994	0.50	60.74	184.62	3.43	222.59	0.00	471.88
154	1995	1.83	39.92	345.89	74.01	362.36	63.55	887.57
181	1992	4.50	7.65	175.45	2.71	129.64	13.46	333.41
181	1993	28.86	21.26	78.98	6.55	109.86	38.88	284.39
181	1994	27.42	75.14	411.49	17.87	214.81	46.73	793.47
181	1995	17.87	18.78	768.78	312.84	119.52	0.00	1237.79
214	1992	31.47	10.56	887.18	14.46	396.96	70.10	1410.73
214	1993	12.72	1.31	176.05	3.57	19.92	0.00	213.56
214	1994	8.22	13.75	265.99	32.13	2.49	0.00	322.59
214	1995	12.97	44.47	824.02	65.25	195.67	158.11	1300.48
240	1992	31.61	5.72	62.38	4.50	3.82	0.00	108.03
240	1993	6.27	5.55	239.85	1.78	131.80	0.00	385.26
240	1994	38.92	15.13	224.34	16.66	176.32	112.96	584.34
240	1995	73.65	28.57	255.12	44.66	270.22	0.00	672.22

Appendix 6:		Summary of Mouse L. Algal Size-Class Biomass for Individual Dates						
		Algal Size-Class Biomass (ug/L)						
Julian day	**Year**	**cell<10 um**	**cell 10-30 um**	**cell>30 um**	**Col.<30 um**	**Col.>30 um**	**Filaments**	**Tot. Biomass**
154	1992	21.72	42.88	1.55	1.15	5.10	0.00	72.40
154	1993	46.25	133.08	20.06	14.72	222.67	0.00	436.78
154	1994	7.93	163.07	368.52	0.93	122.74	0.00	663.18
154	1995	40.88	74.68	56.08	59.82	70.32	0.00	301.77
181	1992	13.52	36.23	2.38	12.09	70.94	0.00	135.17
181	1993	20.84	164.32	189.47	21.02	297.50	0.78	693.16
181	1994	34.37	213.34	65.90	12.66	9.78	0.18	336.04
181	1995	23.91	101.66	3.37	37.33	77.31	0.00	243.58
214	1992	23.77	44.09	17.85	29.25	171.44	0.00	286.40
214	1993	3.90	42.85	1.92	71.80	21.27	0.00	141.74
214	1994	37.53	156.34	405.31	37.70	390.84	2.47	1027.73
214	1995	89.82	387.65	283.65	50.58	150.55	0.00	962.24
240	1992	63.73	20.80	44.41	34.29	28.41	0.00	191.64
240	1993	24.16	94.80	99.86	5.61	46.31	1.70	270.74
240	1994	33.13	304.41	209.36	105.15	152.71	4.73	804.75
240	1995	22.20	257.38	19.65	14.23	61.33	0.00	374.79

Appendix 7:		Summary of Ranger L. Algal Size-Class Biomass for Individual Dates						
		Algal Size-Class Biomass (ug/L)						
Julian day	**Year**	**cell<10 um**	**cell 10-30 um**	**cell>30 um**	**Col.<30 um**	**Col.>30 um**	**Filaments**	**Tot. Biomass**
154	1992	8.84	19.48	4.84	1.08	7.48	0.00	41.72
154	1993	12.83	33.08	50.86	17.40	11.85	0.00	126.02
154	1994	20.65	267.94	83.18	2.79	97.31	0.00	471.88
154	1995	39.34	396.31	76.56	30.41	344.94	0.00	887.57
181	1992	15.48	180.18	19.53	9.43	105.80	2.99	333.41
181	1993	24.77	180.00	22.92	15.06	41.62	0.00	284.39
181	1994	51.14	190.32	290.87	5.05	255.31	0.78	793.47
181	1995	36.88	110.93	58.80	22.64	1008.36	0.19	1237.79
214	1992	46.27	780.66	14.46	54.77	492.39	22.18	1410.73
214	1993	14.26	70.29	14.37	5.73	108.91	0.00	213.56
214	1994	16.33	47.72	0.00	4.11	254.31	0.12	322.59
214	1995	31.40	280.05	202.47	18.37	765.53	2.67	1300.48
240	1992	14.21	34.97	4.50	8.82	15.30	30.23	108.03
240	1993	23.92	78.17	116.78	2.81	163.07	0.51	385.26
240	1994	41.55	143.55	217.64	10.68	166.60	4.32	584.34
240	1995	20.65	218.46	132.24	38.89	204.05	57.93	672.22

Appendix 8:

Student's t-test of size-class algal biomass (ug/L) for pre-manipulation (1992-1993) and post-manipulation (1994-1995) years in **Mouse L.**, where $p \leq 0.05$ represents a significant difference between years.

Size Class	n	Pre-manipulation Years Mean(S.E.)	Post-manipulation Years Mean(S.E.)	p-value
1	8	27.24(6.71)	36.22(8.51)	0.42
2	8	72.38(18.49)	207.31(37.27)	**0.006**
3	8	47.19(23.44)	176.48(57.18)	0.06
4	8	23.74(7.92)	39.80(11.72)	0.28
5	8	107.96(38.43)	129.45(41.09)	0.71
6	6	0.82(0.49)	2.46(1.31)	0.31

Appendix 9:

Student's t-test of size-class algal biomass (ug/L) for pre-manipulation (1992-1993) and post-manipulation (1994-1995) years in **Ranger** L., where $p \leq 0.05$ represents a significant difference between years.

Size Class	n	Pre-manipulation Years Mean(S.E.)	Post-manipulation Years Mean(S.E.)	p-value
1	8	20.07(4.21)	32.24(4.31)	0.06
2	8	172.10(89.75)	206.91(38.71	0.73
3	8	31.03(13.29)	132.72(34.27)	**0.02**
4	8	14.39(6.10)	16.62(4.71)	0.78
5	8	118.30(57.05)	387.05(114.34)	**0.05**
6	6	9.32(5.46)	11.0(9.41)	0.88

Appendix 10:

Student's t-test of algal-group biomass (ug/L) for pre-manipulation (1992-1993) and post-manipulation (1994-1995) years in **Mouse L.**, where $p \leq 0.05$ represents a significant difference between years.

Algal Group	n	Pre-manipulation Years Mean(S.E.)	Post-manipulation Years Mean(S.E.)	p-value
BG	8	13.08(8.21)	32.48(11.67)	0.20
GR	8	14.44(3.97)	62.59(16.31)	**0.01**
CH	8	150.79(40.72)	189.30(47.30)	0.55
DM	8	46.23(21.0)	4.21(1.58)	0.07
CR	8	49.40(20.05)	254.30(52.69)	**0.003**
DF	6	6.40(4.21)	63.06(31.48)	0.10

Appendix 11:

Student's t-test of algal-group biomass (ug/L) for pre-manipulation (1992-1993) and post-manipulation (1994-1995) years in **Ranger L.**, where $p \leq 0.05$ represents a significant difference between years.

Algal Group	n	Pre-manipulation Years Mean(S.E.)	Post-manipulation Years Mean(S.E.)	p-value
BG	8	14.50(4.93)	22.67(8.59)	0.42
GR	8	9.71(3.20)	37.06(7.91)	**0.006**
CH	8	209.74(100.57)	410.03(88.06)	0.16
DM	8	5.81(1.42)	70.86(35.63)	0.09
CR	8	104.90(45.79)	195.50(37.30)	0.15
DF	4	36.45(12.38)	95.34(25.02)	0.08

Appendix 12:

Summary table of Non-parametric Wilcoxan tests of representative algal genera and size-classes betweem pre-manipulation (1992-1993) and post-manipulation (1994-1995) years in **Mouse L.**, where $p \leq 0.05$ represents a significant difference between years.

Algal Group	Genus/ Sub-Group	Size Class	p-value	Post-manipulation Biomass
BG	*Merismopedia*	4	0.69	Not Sig.
		5	0.25	Not Sig.
GR	*Chlorella*	1	0.49	Not Sig.
		2	0.38	Not Sig.
	Green Cells	1	0.83	Not Sig.
		2	0.08	Not Sig.
	Scenedesmus	4	0.17	Not Sig.
	Green Colonies	4	0.09	Not Sig.
		5	**0.01**	**Increased**
CH	Monads	1	0.75	Not Sig.
		2	0.48	Not Sig.
	Dinobryon	2	0.56	Not Sig.
		3	0.56	Not Sig.
		5	0.75	Not Sig.
	Chrysophaerella	4	**0.01**	**Decreased**
		5	0.57	Not Sig.
DM	*Asterionella*	3	**<0.001**	**Decreased**
		5	**0.008**	**Decreased**
CR	*Cryptomonas*	1	0.06	Not Sig.
		2	**0.03**	**Increased**
		3	**0.01**	**Increased**
DF	Dinoflagellates	2	0.28	Not Sig.
		3	**0.04**	**Increased**

Appendix 13:

Summary table of Non-parametric Wilcoxan tests of representative algal genera and size-classes betweem pre-manipulation (1992-1993) and post-manipulation (1994-1995) years in **Ranger L.**, where $p \leq 0.05$ represents a significant difference between years.

Algal Group	Genus/ Sub-Group	Size Class	p-value	Post-Manipulation Biomass
BG	*Merismopedia*	4	0.56	Not Sig.
		5	0.85	Not Sig.
GR	*Chlorella*	1	**0.01**	**Increased**
		2	**0.01**	**Increased**
	Green Cells	1	**0.002**	**Increased**
		2	**0.002**	**Increased**
	Green Colonies	4	0.34	Not Sig.
		5	0.34	Not Sig.
CH	Monads	1	0.67	Not Sig.
		2	0.12	Not Sig.
	Dinobryon	2	0.27	Not Sig.
		3	0.44	Not Sig.
		5	0.75	Not Sig.
	Chrysophaerella	4	0.12	Not Sig.
		5	**0.002**	**Increased**
DM	*Asterionella*	3	0.10	Not Sig.
		5	**0.001**	**increased**
CR	*Cryptomonas*	1	0.56	Not Sig.
		2	0.21	Not Sig.
		3	**0.01**	**Increased**
DF	Dinoflagellates	2	0.83	Not Sig.
		3	0.12	Not Sig.