University of Alberta

Zooplankton and alternate states in western boreal wetland lakes

by

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©

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Abstract

To understand how biota influence the development of clear- versus turbid-water states in boreal wetland lakes, a survey of zooplankton communities in twenty fishless and four fish-bearing lakes in northern Alberta was conducted in 2001/2002. The vast majority (>96%) of sites with zooplankton communities dominated by macrophyte associated cladocerans were clear. This suggests that grazing by zooplankton is an important mechanism by which submerged aquatic vegetation (SAV) maintains clear-water conditions. However, the ability of SAV and its associated zooplankton to maintain clear-water states appears to weaken as phosphorus concentrations exceed ~138μg L^{-1}TP. Moderate densities of fish (stickleback) suppress medium/large-cladocerans, but the small-cladocerans that replace them (along with calanoid copepods) also seem capable of suppressing phytoplankton. Thus, practices (e.g. ditching) that spread stickleback may not increase the propensity of turbid water states. However, other disturbances (e.g. pesticides) inhibiting cladoceran zooplankton will likely negatively impact water clarity in Canada's western boreal wetlands.

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Chapter 1. Introduction

Western boreal forest (WBF) wetlands are diverse and productive ecosystems second only to the Prairie Pothole region in importance for North American waterfowl (Ducks Unlimited Canada 2003). However, our ignorance of the processes that dictate biological productivity in these systems makes it unclear how susceptible they are to anthropogenic disturbance (Moser et al. 1998). In general, the boreal region ecosystem is threatened by global warming, acid precipitation, UV depletion, and a range of other processes arising from human activities (Prepas et al. 2001;McEachern et al. 2000;Schindler 1998). Of particular concern for the wetlands of northern Alberta are disturbances associated with the extraction of the abundant fossil fuel and lumber resources characteristic of the region. To manage the environmental impacts of oil and gas and logging activities, we need to understand the relationships between, and mechanisms governing, forest runoff, nutrient status, and productivity of these valuable wetland ecosystems.

Preliminary work in Alberta's WBF region has identified numerous shallow wetland lakes that have relatively clear water and abundant submersed aquatic vegetation (SAV), while others are turbid with dense phytoplankton blooms and relatively little SAV (Bayley and Prather 2003). Studies of shallow water systems in Europe have found that grazing by zooplankton can govern the development of low-turbidity/SAV-dominated systems versus high turbidity/phytoplankton-dominated states (Bronmark and Hansson 1998). In general, clear-water lakes tend to have zooplankton communities composed of larger species (e.g. copepods), while turbid

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lakes have populations dominated by smaller species (e.g. rotifera). Larger zooplankton are thought to maintain the clear-water state by preying on a wider size range of phytoplankton and having lower nutrient excretion per unit mass (Carpenter et al. 1985;Queimalinos et al. 1998).

Differences in zooplankton community composition between sites can be the result of a range of factors including contrasts in macro-invertebrate predator abundance, habitat quality (e.g. salinity, nutrient levels, oxygen), and SAV species and abundance (Wetzel 1983;Scheffer and Jeppensen 1997). However, the majority of studies have found that the most important factor dictating zooplankton structure are planktivorous fish suppressing or eliminating larger crustaceans (Brett and Goldman 1997). The popular conception has been that planktivorous fish lead to increased phytoplankton production and turbid waters; conversely, when planktivorous fish are absent macro-invertebrates selectively predate small zooplankton thereby favouring large sized zooplankton and clear-water states (Carpenter et al. 1985). Recent studies have suggested, however, that some macro-invertebrate predators, especially those found in biologically complex shallow lakes, are also capable of suppressing large zooplankton (Burks et al. 2001;Wissel et al. 2000).

Since the majority of our knowledge regarding the dynamics of alternate states in shallow lakes comes from studies of polluted, fish-bearing systems in Europe (e.g. Scheffer and Jeppensen 1997), it is unknown if their findings apply to the primarily fishless, naturally productive wetland lakes of the WBF. Through a synoptic survey of

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twenty-four wetland lakes representing a range of nutrient and geologic conditions in northern Alberta I hoped to determine:

1) what the common zooplankton community types in WBF wetland lakes are,
2) what combinations of environmental conditions produce these communities,
3) what role zooplankton community type plays in the development of alternate clear- and turbid-water states in these lakes, and
4) what impact the presence of planktivorous fish has on the development of these states.

I hypothesized that:

1) large zooplankton species would dominate in low predator (fish and macro-invertebrate) conditions,
2) communities of large crustacean zooplankton would be the most important factor differentiating clear- from turbid-water sites, consistent with the theory that top-down control by herbivorous zooplankton dictates the existence of alternate states, and
3) the presence of planktivorous fish would correspond with turbid-water conditions due to the suppression of large bodied zooplankton species

I set out to address these questions in two steps. First, in Chapter 2, I characterize the different zooplankton community types that exist in these small wetland lakes and the factors (e.g. predator communities) associated with their formation. Then, in Chapter 3, I identify those environmental factors (e.g. zooplankton community types; nutrient concentrations) most useful for predicting the existence of

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clear- versus turbid-water conditions. Based on the results from these two chapters I am then able to make conclusions regarding: 1) the relative importance of top-down control by zooplankton for regulating alternate states and, 2) what impact an increased presence of planktivorous fish (sticklebacks) may have on water quality in western boreal wetland lakes.

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Chapter 2. The effect of fish and submerged macrophytes on zooplankton community structure in western boreal wetland lakes.

Introduction

Zooplankton plays a functionally important role in lakes by consuming primary producers and heterotrophic bacteria then re-releasing nutrients or serving as prey for higher trophic levels (Hillbricht-Ilkowska 1977). The rate nutrients are recycled (Soltau and Kilham 1984;Lehman 1984; Main et al. 1997) and the availability of zooplankton as food for planktivors (Hampton & Gilbert 2001;Hanazato 1990) depend on the zooplankton species present. Zooplankton community composition may be influenced by predation (vertebrate and invertebrate) (Irvine et al. 1990;Donald et al. 2001;Christoffersen 1990;Hampton and Gilbert 2001), water chemistry (e.g. salinity) (Moss 1994), food source (Hillbricht-Ilkowska 1977;Ghadouani et al. 1998), and submerged aquatic vegetation (SAV) density and composition (Lauridsen et al. 1998;Duggan et al. 2001). Little is known, however, about zooplankton communities or the key environmental factors determining their existence in western boreal forest (WBF) wetland lakes. We need to discern what mechanisms govern zooplankton community structure, and thereby the functional ecology, of these naturally rich shallow water lakes to better predict the environmental impacts that will result from human alteration to the WBF landscape.

In studies of small lakes in other regions, predation has typically been identified as the key factor influencing zooplankton community structure (Brett and Goldman

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1997;Moss et al. 1998;Rodriguez et al. 1993;Zimmer et al. 2000). Due to harsh winter conditions, shallow (<2.0m), isolated WBF wetland lakes tend to contain only planktivorous brook stickleback (*Culea inconstans*), if any fish at all (Conlon 2002). In a study of *Gasterosteus aculeatu* (three-spined sticklback) in France, Komarkova (1998) found larger cladocerans such as *Daphnia sp.* and *Semocephalus sp.* were reduced or eliminated by stickleback predation. It is not known, however, if brook stickleback in WBF wetland lakes have a similar effect. Based on studies of deeper-water lakes one would expect that in the absence of planktivorous fish, large-bodied zooplankton (e.g. *Daphnia*) would tend to dominate (Carpenter et al. 1985;Declerck et al. 1997). However, this may not be the case in fishless, shallow WBF lakes where complex macro-invertebrate predator communities may also be capable of suppressing large cladocerans (Pagano et al. 2003;Arnott and Vanni 1993;Repka et al. 1995;Hanazato 1990).

Since submerged aquatic vegetation (SAV) has previously been identified as a key factor influencing the functional ecology of shallow western boreal lakes (Bayley and Prather 2003), one would expect that zooplankton composition depends, in part, on SAV abundance. Numerous studies have documented the positive effect SAV has on medium/large cladocerans by providing a stable source of epiphytic algae (Burks et al. 2002;Jeppesen et al. 2002) and refuge from predators (Irvine et al. 1990;Jeppesen et al. 1998) . High SAV concentrations also cause a shift from pelagic to littoral rotifer species and an overall decrease in rotifer concentrations in the water column (Duggan

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2001;Duggan et al. 2001), thereby further favouring the existence of zooplankton communities with proportionately high densities of crustaceans.

High salinity levels can also effect zooplankton structure by inhibiting freshwater cladocerans (Hall and Burns 2002). However, in WBF wetland lakes ion concentrations do not typically exceed 0.6ppt (Bayley and Prather 2003) which is well below the 1.0ppt level identified in the majority of literature as being critical for freshwater species (Jeppesen et al. 1994;Hall and Burns 2001;Teschner 1995). In some cases food particle size (Hillbricht-Ilkowska 1977) and toxic blue-green bacteria (Ghadouani et al. 2003) have also been found to impact zooplankton structure. However, most studies conclude that food source is relatively unimportant for determining zooplankton structure compared to other factors (e.g. predation) (Brett and Goldman 1997).

The overall objectives of this study were to identify the major patterns in zooplankton distribution and the environmental variables associated with these patterns in WBF wetland lakes. In particular, I hypothesized that:

1. stickleback (*Culea inconstans*) predation inhibiting large cladoceran species would be a primary mechanism influencing zooplankton community structure,
2. in fishless lakes, large cladocerans would dominate only if macro-invertebrate predator numbers were low,
3. lakes with high SAV abundance would have a high biomass of medium and large sized cladoceran species and low numbers of planktonic rotifers,

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4. salinity would not be an important factor impacting zooplankton structure since concentrations would not exceed previously identified critical levels, and
5. patterns in zooplankton composition would not correspond with patterns in phytoplankton composition, indicating that food source is not a key factor influencing zooplankton community structure.

Methods

Site Description

The study area was part of the Hydrology, Ecology, and Disturbance (HEAD) research project located in north-central Alberta, Canada, near Utikuma Lake, approximately 300km north of Edmonton (Fig. 2.1). Deep glacial till covers the area with gray Luvisols and Brunisols in the uplands and organic deposits (peatlands) in the depressions being the predominant soil types. The twenty-four study lakes were distributed along a 45km transect running northwest to southeast (from $115^{0}42'$W $56^{0}07'$N to $115^{0}09'$W $55^{0}57'$N) spanning outwash plain (dominated by sands), moraine (with more depressions) and lacustrine plain (extensive peat-lands often underlain with clay) landforms. A minimum of six lakes were located in each landform type with a change in elevation from 645m to 630m above sea level from the top to the bottom of the transect.

Located in the central mixedwood subregion of the boreal forest natural region, the area receives an average annual precipitation of 503mm (Environment Canada 2002a), although during this study precipitation was much lower at around 288mm in

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2001 and 376mm in 2002 (Environment Canada 2002b). The lakes are exposed to long, cold winters with average daily mean temperatures in January of –14.5^{0}C (Environment Canada 2002a). Ice typically does not leave even the smallest lakes until late April or mid May. Despite a mean annual temperature of only 1.7^{0}C, the lakes experience mean daily air temperatures of 15.6^{0}C during July (Environment Canada 2002a), allowing for short periods of high biologic productivity.

The study lakes were small, with an average area of approximately 7.0ha (median 3.4ha), and shallow, with an average mean depth of 59cm (min. 7.7cm, max. 101cm), especially during drought conditions in 2002. WBF wetland lakes are typically eutrophic (Bayley and Prather 2003) and during this study the total phosphorus (TP) levels ranged from mesotrophic to hyper-eutrophic with an average of 102μg/L TP (min. 28μg/L, max. 413μg/L, and median 68μg/L). Despite the eutrophic conditions, the lakes appeared not to be nitrogen limited with an average total nitrogen to total phosphorus (TN:TP) ratio of 37:1 and a minimum value for all sites of 17:1.

Sampling

Each of the twenty-four study lakes were sampled twice in 2001 and 2002, once in July and once in August, with the exception of several lakes that were too shallow in 2002 to obtain a reliable sample of the water column. Daytime samples were used since diurnal sampling of fish and fishless lakes indicated no significant difference in composition or abundance between zooplankton samples collected during daylight hours and those collected at peak darkness (data not shown). In each lake, size permitting, five sample sites were selected at random and data collected from each site subsequently

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averaged. The resulting unit of measure for the survey was lake-month, which reflects the conditions in each lake during July and then in August over a two year period. The total number of samples available for analyses represented 83 lake-months; however, algal community data was not available for August 2002, leaving only 63 lake-months for phytoplankton analyses.

Abiotic variables

Physical and nutrient conditions for each lake-month were described using eleven abiotic variables (Appendix 1). Turbidity was determined in the field using a Turner Designs Aquafluor Turbidimeter. Conductivity, pH, and temperature were measured in-situ using a Hyrolab Quanta field probe. Salinity was calculated by summing the eight major ions (Ca^{++}, Mg^{++}, Na^{+}, K^{+}, HCO_3^{-}, CO_3^{2-}, SO_4^{2-}, Cl^{-})(Wetzel 1983); ion concentrations were determined following the methods outlined in Bayley and Prather (2003). Total phosphorus, total dissolved phosphorus, inorganic nitrogen, total nitrogen, soluble reactive phosphorus, and dissolved organic carbon values for all the lakes were also determined using the methods outlined in Bayley and Prather (2003).

Depth of water was determined by lowering a Secchi disk onto the flocculent sediments and measuring the distance from the top of the disk to the surface of the water. The location of each measurement was recorded using a GPS then referenced to a staff gauge near shore. All measurements were standardized and the maximum and mean depth for any date calculated based on the depth at the staff gauge.

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Biotic variables

Twenty-six different variables describing fish, macro-invertebrates, and submerged vegetation were used to characterize the predator and SAV conditions for each lake-month (Appendix 1). Fish abundance in each lake was determined in June and again in August during 2001 using a minimum of 10 Cuba Minnow Traps placed at approximately 5-10m intervals along a stretch of shoreline (W.M. Tonn personal communication). The traps were left overnight, then the number, species, and length of each fish was recorded before they were released. Severe drought conditions in 2002 made trapping of seven lakes impractical, but the remaining seventeen lakes were trapped at least once during July/August. Results were recorded as fish per trap per night or Catch Per Unit Effort (CPUE).

Samples of planktonic *Chaoborus* and water-mites were collected by standardized sweeps of the water column using a long-handled, D-frame 1000μm-mesh net at each sampling site and fixed in 4% formalin. *Chaoborus* were identified to species using a Wild M38 dissecting scope and the key provided in Uutala (1990). Biomass per litre of mites and *Chaoborus* was estimated based on size/mass categories provided by Ross and Elliott (2003). All other macro-invertebrate biomass data was determined according to the methods outlined in Ross and Elliott (2003).

Submerged Aquatic Vegetation (SAV) abundance was recorded as percent cover (Jeppesen et al. 2002;Muylaert et al. 2003) in one of five classes: 1) 0% coverage, 2) 0-5% coverage, 3) 5-25% coverage, 4) 25-75% coverage, or 5) >75% coverage (Bayley

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and Prather 2003). In cases where SAV coverage was thought to be low or zero and visibility was poor, visual estimates were confirmed by raking the bottom. For computational purposes each class was designated by a whole number 1-5; classes 4 and 5 (>25% coverage) were generally consider high density of SAV (Bayley and Prather 2003). Proportion of total biomass composed by each species was determined from samples collected at twenty random sites in each lake during August in 2001 and 2002 using standardized 1.0m x 0.38m rakes of the bottom. SAV were separated and identified to species using the keys of Burland (1989) and Moss (1983). Separated samples were then dried at 64^0C for a minimum of 48hrs and total dried biomass calculated as g/m^2.

Mean chlorophyll *a* concentrations in each site were determined from replicate surface samples using a Turner Designs Aquafluor Fluorometer correlated to a surface sample collected at the approximate center of the lake. The reference chlorophyll samples were filtered onto Gelman A/E filters within 24 hours of collection and submitted to the University of Alberta Limnology Lab for analyses. Chlorophyll was extracted in 95% ethanol and analyzed with a spectrophotometer at 750, 665, and 649nm following the methods of Bergmann and Peters (1980).

Phytoplankton samples were collected from the same water used for zooplankton samples. Algae were identified and enumerated following the Utermöhl method (Lund et al. 1958). Phytoplankton community structure was defined based on the concentration (number of cells per milliliter) of 14 different taxonomic groups (Appendix 1).

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Zooplankton samples were collected using a 135cm x 6.5cm acrylic tube (Swanson 1978) and pooled in a 20L pail. After mixing thoroughly, a 5L subsample was passed through a 64μm-mesh netting which optimized passage rates (i.e. prevented clogging) while minimizing loss of rotifer species (Bottrel et al. 1976). The resulting concentrate was fixed with a 4% formalin-sugar solution (Prepas 1978). Sub-samples were collected using a wide-bore trigger pipette (Carvalho 1994) and zooplankton identified to the lowest possible taxonomic group using a Sedgewick-Rafter counting cell with a Motic compound light microscope (100x mag.), a Wild M38 dissecting scope (16x mag.), and the zooplankton keys of B.C. Resources Inventory Committee (1997; 1996), Grothe and Grothe (1977), Smith and Fernando (1978), Ruttner-Kolisko (1974), Pennak (1989), and Clifford (1991). Post-nauplier copepods and cladocerans (macro-zooplankton) were assessed separately from nauplii and rotifers (micro-zooplankton) ([EPA] Environmental Protection Agency 1994;Pace 1984;Christoffersen et al. 1993). Two to three sub-samples, with a maximum coefficient of variation of ± 20% between sub-samples, were assessed such that 100 of the most prominent zooplankton species were counted (Timms and Moss 1984;Christoffersen et al.1993;Jeppesen et al. 1994). In cases where micro-zooplankton abundance was insufficient for sub-sampling, a minimum of 15% of the entire sample was assessed (Patalas and Salki 1993;Hairston et al. 2000). The entire sample was assessed in cases where there were less than 100 of the most prominent macro-zooplankton species (Christoffersen et al. 1993). The first ten individuals of each species were measured using an eyepiece micrometer and from these measurements an average length was determined for each zooplankton species. Biomass

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for the taxa in each sample was then estimated using the length-biomass regression models of Culver et al. (1985), McCauley (1984), and Pauli (1989).

Analyses

Approach

To characterize zooplankton composition in the study lakes, an analysis of zooplankton community structure was done using a combination of clustering, indicator species, and ordination procedures. Little was known about the processes controlling zooplankton community structure in these systems; therefore, I was unable to make assumptions regarding which environmental variables must be accounted for and which could be assumed unimportant. As a result, the number of possible conditions (e.g. combinations of high and low nutrient, physical parameter, and predator states) that needed to be accounted for was incredibly large. Further confounding the issue, many of the factors identified in classical literature as capable of influencing zooplankton community structure tend to change drastically between months of the same year in shallow, small lakes (Bennion and Smith 2000). Given the large number of conditions I wished to account for in my analyses and the variability in environmental conditions between July and August, I chose to treat the samples collected in each month as individual cases (see Appendix 2 for a thorough discussion of the use of lake-month as a sample unit). Although the number of combinations of factors I could include in the analyses was increased using lake-month as a sampling unit, the variance for some factors was artificially lowered relative to what was observed at a lake-year temporal scale. This meant that I could not utilize analyses requiring the strict assumption of sample independence (e.g. in the generation of a p-value). Therefore, I chose to

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compare lakes-months with different zooplankton community types through an exploratory approach utilizing a combination of ordination joint-plots and a classification and regression tree (CART) algorithm. To determine if phytoplankton community structure corresponded with patterns in zooplankton structure, the groupings identified in the previous analyses were overlain with an ordination of lake-months based on phytoplankton species composition.

Zooplankton community structure analyses

To identify what communities existed in the study lakes, cluster analyses were performed using Sorrenson distance measure and the group-linkage method of flexible-beta (beta = -0.25) (Zimmer et al. 2000;McCune and Grace 2002). To characterize the groups identified, indicator taxa were distinguished for each community based on presence and abundance using the Indicator Species Analyses method of Dufrene and Legendre (1997). The significance of each zooplankton taxa/group as an indicator was assessed using a Monte Carlo test (1000 permutations) (Dufrene and Legendre 1997). This analysis implicitly served to further validate group types since the inability to find characteristic species suggests groups are in fact not distinct (McCune and Grace 2002). Prior to analyses, all zooplankton community data was transformed using ln(x+1) to prevent high values from excessively influencing the results (Zimmer et al. 2000).

The data used in the clustering and Indicator Species analyses was then submitted to Non-metric Multi-dimensional Scaling (NMS) (Mather 1976; Kruskal 1964) and overlain with community type to corroborate that communities were distinct and see how groups related to each other. Associations between species and each NMS

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axis were assessed using joint-plots (McCune and Grace 2002). Coefficients of determination greater than 0.2 (the default in PC-ORD) were given the greatest weight with only coefficients greater than 0.1 considered potentially meaningful. This 0.1 cut-off was based on significance at 99% confidence for 82 degrees freedom; however, this cannot be considered as a measure of statistical significance given that the strict assumptions of regression analyses are not met in a joint-plot analyses (McCune and Grace 2002). NMS was run with a Sorensen distance measure, a random starting configuration, 40 runs with real data, and 50 runs of randomized data with a probability of finding the same solution by chance of 0.02. Dimensionality was determined based on the point of diminishing returns on the Scree-plot and the relative increase in the original space represented by each axis. Final stability was defined as $1x10^{-5}$ standard deviations over the last 15 iterations.

Environmental factors affecting zooplankton community structure

The correlation between environmental variables and the patterns identified in the NMS analyses of zooplankton structure was assessed using joint-plots. Only those variables with a coefficient of determination of greater than 0.1 were considered meaningful with those greater than 0.2 given the greatest weight (see previous discussion on the selection of 0.1 cut-off). Where necessary, environmental data were transformed to approximate normality with all macro-invertebrate and SAV composition data transformed using ln(x+1) (Zimmer et al. 2000) (Appendix 1). Values were then relativized before analysis based on N_i/N_{max}, where N_i represents the value for a given lake-month and N_{max} the largest value for all lake-months (McCune and Grace 2002).

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Non-parametric CART structural modeling was also used to identify the environmental conditions associated with each of the groups to avoid the problems associated with the use of conventional linear model statistics in the analyses of ecologic data (De'ath 2002;Urban 2002). The CART procedure recursively partitioned the data into subsets that were increasingly homogenous with respect to the defined groups (De'ath 2002). Minimum group size to be split was set at ten. Optimal CART model size was determined using cost-complexity pruning based on ten step boot-strapping; optimal tree size was the smallest tree within one standard deviation of the lowest overall misclassification rate (Urban 2002). CART model validity was assessed using the total misclassification rate based on jack-knifing (Urban 2002).

Phytoplankton composition and zooplankton community structure

To address the possibility that phytoplankton composition was responsible for patterns in zooplankton community structure, lake-months were ordinated based on phytoplankton concentrations. Zooplankton community type and the node to which each lake-month was assigned in the CART model was then overlain to assess if these patterns were related to phytoplankton community structure. Multiple Response Permutation Procedure (MRPP) and Indicator Species analyses were then used to confirm and characterize the differences in phytoplankton community structure between zooplankton community types or nodes.

Clustering, NMS, Indicator Species analysis, MRPP, and joint-plots were all performed using PC-ORD for Windows version 4.14. The CART model was created in S-Plus 6 for windows with the TREE analyses pack provided by Ripley (1997). Tests

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comparing independent sample means and descriptive statistics were calculated in SPSS 10.0 for windows.

Results

Zooplankton community structure analyses

Sixty-four different species of crustacean and rotiferan zooplankton were identified and subsequently compiled into thirty different taxonomic groups for analyses (Table 2.1). The six communities identified in the cluster analysis (Fig. 2.2) were characterized as:

Group 1: Small cladoceran community

The presence and abundance of the small cladoceran *Bosmina longirostris* and large (>140μm) herbivorous rotifer species characterized community Group 1 (Table 2.2). Compared to the average across all lake-months, sites with this community type had significantly lower numbers of the large and medium sized cladocerans *Daphnia spp* ($U = 197.5$, $\propto = 0.02$), *Polyphemus pediculus* ($U = 261$, $\alpha = 0.06$), *Ceriodaphnia quadrangula* ($U = 149.5$, $\alpha = 0.01$), and Chydoridae ($U = 261$, $\alpha = 0.06$).

Group 2: Littoral cladoceran community

Chydoridae and *Ceriodaphnia quadrangula* and littoral rotifers such as *Mytillina sp.* distinguished community Group 2. The lake-months with this community type exhibited a significantly lower biomass of rotifers compared to the mean of all lake-months ($U = 1029$, $\alpha = 0.04$).

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Group 3: Daphnia community

The presence and abundance of the large cladoceran grazer *Daphnia,* along with the predatory cladoceran *Polyphemus pediculus,* distinguished Group 3 from other zooplankton communities. Sites with this community type had a significantly greater than average *Daphnia spp.* biomass ($U = 204.5$, $\alpha < 0.01$) and a significantly lower than average rotifer ($U = 193.5$, $\alpha < 0.01$) and copepod ($U = 193.5$, $\alpha < 0.01$) biomass.

Group 4: Highly variable, low-cladoceran community

Group 4 was the only community identified in the cluster analyses that lacked a significant indicator species. In fact, only one species had its highest Indicator Species number associated with this group. The only distinguishing characteristic of the zooplankton communities in lake-months exhibiting this type was a significantly lower than average biomass of cladocerans ($U = 156.5$, $\alpha < 0.01$).

Group 5: Rotifer community

The presence and abundance of large-predatory and small-herbivorous rotifers distinguished Group 5. The sites belonging to this group also had significantly lower than average biomass of calanoid copepods ($U = 132.0$, $\alpha < 0.01$) and the littoral cladocerans Chydoridae ($U = 180.0$, $\alpha = 0.03$) and *Ceriodaphnia quadrangula* ($U = 186.0$, $\alpha = 0.04$).

Group 6: Copepod community

Community Group 6 had rotifers, copepods, and the cladoceran *Diaphanosoma birgei* as indicator species. Sites belonging to this group had significantly higher than average biomass of post-nauplier copepods ($U = 135.5$, $\alpha < 0.01$).

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NMS ordination was able to account for 80.5% of the variance in zooplankton composition (Axis 2 = 41.9%, Axis 3 = 24.7%, and Axis 1 = 13.9%) based on 145 iterations with a final stress of 15.7. Joint-plots indicate that Axis 2 separates rotifers (on the negative end) from *Daphnia* (on the positive) while Axis 3 separates *Daphnia* and small rotifers from copepods and *Diaphasoma birgei* (Fig. 2.3; r-values for each taxa are provided in Appendix 1). This is consistent with the cluster analysis since small cladoceran (Group 1) and rotifer (Group 5) communities are located at the extreme left and *Daphnia* dominated (Group 3) communities at the extreme right of the ordination. Furthermore, rotifer (Group 5) and *Daphnia* communities (Group 3) are located at the bottom and copepod communities (Group 6) at the top of the ordination. There were no species positively correlated with the tertiary Axis 1, but littoral cladocerans *Ceriodaphnia* and *Alona gutatta* and cyclopoid copepods were negatively associated. Again this is consistent with the grouping analyses results as the highly variable, low-cladoceran Group 4 was separated from littoral cladoceran (Group 2) and copepod communities (Group 6) along this axis (data not shown).

Environmental factors affecting zooplankton community structure

Ordination joint-plot analyses

Fish and depth were positively associated with rotifer and small cladoceran communities and negatively associated with *Daphnia* communities according to the joint-plots of environmental variables with NMS Axis 2 (Fig. 2.4). *Daphnia* communities were also positively associated with SAV and negatively associated with chlorophyll *a* concentrations, although not as strongly as they were with fish and depth (correlations of $r^2 > 0.1$ between environmental variables and NMS axes are given in

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Appendix 1). Zygopteran and Gammaridae biomass were correlated with Axis 2 suggesting that predacious macro-invertebrates have a positive relationship with *Daphnia* communities and a negative relationship with small cladocerans and rotifers. However, stickleback abundance was significantly negatively co-correlated with Zygoptera (τ = -0.275, α <0.01) and Gammaridae (τ = -0.292, α <0.01) and Zygopertans were significantly positively correlated with SAV abundance (τ = 0.249, α < 0.01). The positive correlation of salinity with Axis 3 suggests that rotifer and *Daphnia* communities favour lower salinity environments compared to those dominated by copepods (Fig. 2.4). None of the environmental variables had coefficients of determination greater than 0.2 with the tertiary Axis 1 (Appendix 1).

CART Analysis

Bootstrap analyses indicated optimal CART model size was seven nodes (Fig. 2.5). For the groups that the CART model was able to describe, the overall misclassification rate was 22.2% based on jack-knifing, meaning the seven-node model was able to account for 77.8% of the variation in community type using the variables provided (Table 2.3).

According to the CART model, the most important factor determining zooplankton community structure was the abundance of sticklebacks in excess of 0.4CPUE. Since none of the lakes where fish were trapped had densities less than 0.4CPUE, this differentiation is considered as presence or absence of sticklebacks. The lakes with sticklebacks tended to have small-cladoceran (Group 1) communities while all other community types tended to be found in fishless conditions (Fig. 2.5).

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The primary variable discriminating zooplankton communities in the absence of sticklebacks were chlorophyll levels above and below 18μg/L. Lake-months with less than 18μg/L chlorophyll also had significantly higher SAV coverage than those above 18μg/L chlorophyll ($U = 141.5$, $\alpha < 0.01$). Low chlorophyll (<18μg/L), higher SAV sites tended to contain large/medium sized cladoceran dominated (Group 2 or 3) communities. High chlorophyll (>18μg/L) sites tended to have rotifer dominated (Group 5) or copepod dominated (Group 6) communities with the exception of littoral cladoceran (Group 2) communities in >0.11ppt salinity and >38μg/L total dissolved phosphorus conditions.

SAV ratings greater and less than 4.33 (or ~75% coverage) separated fishless, higher-SAV/low-chlorophyll (<18μg/L) sites. Sites with >~75% SAV coverage always had littoral cladoceran (Group 2) communities. Those with less SAV tended to have either littoral cladoceran (Group 2) or *Daphnia* dominated (Group 3) communities depending on the concentration of predacious water-boatmen (Corixidae).

Salinity levels greater and less than 0.11ppt differentiated fishless, high chlorophyll (>18μg/L) lake-months. Sites with salinity less than 0.11ppt tended to exhibit rotifer dominated (Group 5) communities while sites above 0.11ppt tended to exhibit crustacean dominated Group 6 or 2 communities. As mentioned earlier, the division between the copepod dominated (Group 6) and littoral cladoceran (Group 2)

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communities were attributed to higher levels of total dissolved phosphorus in sites dominated by littoral species.

Based on how closely the groups were oriented to each other in the NMS ordination (Fig. 2.3), we should expect that there was some overlap in the environmental conditions responsible for the formation of those groups. Misclassifications for each of the nodes in the CART model indicate that although sites with fish tend to have small cladoceran (Group 1) communities they can contain rotifer (Group 5) or copepod (Group 6) communities (Fig. 2.5;Table 2.3). Although fishless sites with low chlorophyll and SAV coverage <75% were differentiated based on the biomass of the predator Corixidae, both littoral cladoceran and *Daphnia* communities were found in high and low Corixid conditions.

The seven-node CART model identified environmental conditions characteristic of five of the groups, but failed to define parameters characteristic of Group 4 communities (Fig. 2.5). The highly variable, low cladoceran Group 4 sites were classified nine out of eleven times as being either littoral cladoceran (Group 2) or copepod (Group 6) communities, the two groups with which they overlapped in the NMS ordination (Fig. 2.3). Group 4 was also the only community not clearly differentiated by the first two NMS axes (Axes 2 and 3) (Fig. 2.3). Instead, this group was described by the tertiary Axis 1 that accounts for 13.3% of the overall variance in zooplankton composition. The strongest correlate of Axis 1 was the proportion of the SAV community composed of *Myriophyllum* (Appendix 1). Considering the close ties

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between Group 4 and the SAV associated littoral community (Group 2), it seems possible this low cladoceran communities' existence is dictated by the negative effects *Myriophyllum* has on Daphnidae species (Wetzel 1983). However, due to the relative weakness of the correlation ($r^2 < 0.2$), and the failure of the CART model to corroborate, this supposition is not easily defended. Add the failure to identify any significant indicator species for this group and it would appear the methods of measurement, the environmental variables, and/or the analyses used in this study were inadequate for defining the ~13% of zooplankton structure in WBF lakes represented by this group.

Phytoplankton composition and zooplankton community structure

For the most part, NMS overlays indicated that patterns in zooplankton community structure did not correspond with phytoplankton community structure (Fig. 2.6). The one exception was the differentiation of fishless, high chlorophyll Nodes 10 (rotifer Group 5) and 22 (copepod Group 6) sites. MRPP analyses indicated that the phytoplankton communities characteristic of these two CART nodes differ significantly ($A = 0.07$, $p = 0.03$). Dinophyta was a significant indicator of Node 10 (rotifer community) sites (IndVal number = 49.3, $\propto < 0.01$), but Node 22 (copepod community) sites had no significant phytoplankton indicators.

Discussion

When present, sticklebacks exerted the greatest influence of all environmental factors on zooplankton community structure by limiting the concentrations of medium and large cladocerans (e.g. *Daphnia*). However, the majority of western boreal forest (WBF) wetland lakes (isolated lakes of <2.0m depth) do not contain fish and, therefore,

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the relative importance of sticklebacks for contrasting zooplankton structure across the western boreal wetlands is limited. In fishless conditions, cladoceran dominance corresponded positively with high SAV/low chlorophyll conditions, not negatively with macro-invertebrate predator abundance as hypothesized. Salinity and phytoplankton composition played lesser roles in defining the environments associated with different zooplankton communities. A conceptual model outlining the conditions associated with the various zooplankton communities in western boreal forest (WBF) wetland lakes is given in Figure 2.7.

Both NMS and CART analyses indicated that stickleback abundance was the variable corresponding most strongly with zooplankton community structure. As predicted, communities composed of medium/large sized cladocerans were absent in the presence of sticklebacks. CART results also indicate there were fewer copepod-dominated communities in the presence of sticklebacks; however, the existence of some copepod dominated (Group 6) communities in fish bearing lakes suggests that the effect of sticklebacks on copepods is not as strong as it is on cladocerans. Variance of community types in stickleback bearing lakes may be associated with fish density (e.g. low stickleback concentration → copepod community), but the limited number of lakes with sticklebacks in my study makes detection of such trends using CART infeasible. A greater variety of zooplankton communities were present in fishless than in fish-bearing sites, seeming to indicate that sticklebacks limit the diversity of zooplankton communities that can exist. However, this too may be due to a lack of stickleback-bearing lakes (only four out of twenty-four lakes) in the study. If more sites with fish

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were examined it is possible that the number of zooplankton community types identified in the presence of sticklebacks would increase.

Contrary to my hypothesis, it appears that overall the role of macro-invertebrate predators in structuring zooplankton communities in wetland lakes of the WBF is relatively small. The positive correlation of zygoptera and gammarid macro-invertebrate predators with large cladocerans seems to support the findings of Carpenter et al. (1985) that macro-invertebrate predation favours large crustacean zooplankton. However, since both groups are negatively associated with fish the relationship between macro-invertebrate predators and *Daphnia* could be the result of either stickleback predation or competition between predators. Zygopterans rely on aquatic invertebrates for food and their absence in the presence of stickleback could be due to either a lower abundance of prey (Zimmer et al. 2000) or from direct predation by stickleback (Pierce et al. 1985). Furthermore, the positive correlation between zygopterans and daphnidae may also reflect the positive influence that SAV has on both families. Submersed vegetation has been found to positively effect many macro-invertebrates (including zygopterans) by providing habitat complexity (Crowder and Cooper 1982; Murkin and Ross 1999), variation in food resources (Zimmer et al. 2000), and possibly by decreasing predation pressure by fish (Zimmer et al. 2000). My study did not investigate the gut contents of the stickleback but Moodie (1986) found that during a four-year study gammarids were the most important food in the sticklebacks' diets by weight, followed by chironomidae and cladocerans. Therefore, it is reasonable to conclude that, like large *Daphnia*, gammarids were more abundant in our fishless ponds.

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CART analysis did not corroborate the importance of zygopteran or gammarid biomass for differentiating community types, but did identify corixidae (water-boatman) as distinguishing littoral cladoceran from *Daphnia* communities. Corixids are considered general feeders, gathering the majority of their food by sweeping it into their mouths using their fore tarsi (Jansson and Scudder 1972), but are known to survive longer when they feed on *Daphnia*, *Tubifex* and chironomid larvae (Zwart 1965). Therefore, as opposed to being the cause, the higher densities of water-boatman likely reflects a positive response of this macro-invertebrate predator to the abundance of its large prey *Daphnia*.

The importance of SAV for zooplankton structure seems obvious from the identification of a zooplankton community composed of littoral cladocerans. NMS joint-plot analysis suggests submerged macrophytes positively influence large/medium-sized cladocerans (including *Daphnia*) while negatively impacting rotifers. CART analysis corroborated this by identifying the existence of high SAV/low chlorophyll conditions as the key factor promoting medium/large cladoceran dominated communities. CART also indicates that sites above ~75% SAV coverage were the exclusive domain of littoral cladoceran (Group 2) communities. This result is consistent with previous findings that fringe species such as *Daphnia* are negatively effected by extreme plant concentrations and exhibit a unimodal relationship with SAV (van Donk and van de Bund 2002;Wetzel 1983).

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The importance of high- and low-chlorophyll conditions for differentiating cladoceran community types highlights the link between zooplankton and water clarity. The critical 18μg/L chlorophyll threshold defining the existence of cladoceran dominated communities corresponds to the 20μg/L chlorophyll level differentiating alternate SAV versus algae dominated states in western boreal lakes (Bayley & Prather 2003). With an ability to ingest a wider range of particles (Carpenter et al. 1985) and lower relative nutrient recycling rates (Paterson et al. 2002;Lehman 1984), medium/large cladoceran zooplankton can limit phytoplankton concentrations (Saunders et al. 2000;Jeppesen et al. 2002). However, the importance of zooplankton structure for the development of clear-water states in WBF wetland lakes relative to other factors (e.g. nutrients, settling, allelopathy) has yet to be determined. The next chapter explores environmental conditions associated with clear- and turbid-water conditions to assess the role zooplankton play in the formation of these contrasting states.

NMS analysis suggests higher salinity levels differentiate copepod dominated from *Daphnia* dominated lake-months. This is consistent with previous findings that *Daphnia* are sensitive to high salinity concentrations (Hall and Burns 2002), but was not expected as none of the lake-months approached the critical 1.0ppt level (Hall and Burns 2001;Jeppesen et al. 1994). It also contradicts the results of a separate enclosure experiment in one of the study lakes, which found that doubling the natural total salinity to 0.5-0.6ppt had no detectable impact on zooplankton community structure (Norlin & Bayley unpublished data). CART analysis did not concur that salinity was a meaningful variable preventing the development of *Daphnia* dominated (Group 3) communities. It

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did, however, indicate that salinity levels of greater and less than 0.11ppt distinguish crustacean dominated from rotifer dominated sites in fishless, high chlorophyll sites (Fig. 2.5). This suggests that instead of high levels of salinity effecting *Daphnia* survival there is a lower limit for the existence of copepod dominated communities. Little work has been done to identify minimal ion requirements for freshwater crustaceans, although Pennak (1989) suggested 0.01ppt as a lower limit for freshwater species. Although my study sites had salinities well above this lower limit, the pivotal concentration was 0.11ppt meaning that all sites lacking copepod dominated communities would have been below the global average salinity of freshwaters of 0.12ppt (Wetzel 1983). It may be that these low salinity conditions are less than optimal for copepods and *Diaphasoma birgei*, thereby providing a competitive advantage for rotifers.

Another possible explanation for the pattern separating crustacea from rotifers in the CART model is the tendency of Node 10 (rotifer community Group 5) sites to have high concentrations of dinoflagellate algae (e.g. *Ceratium*). Large algae such as *Ceratium* would be inedible for any of the crustacean species identified in the study. *Ceratium* may, therefore, have resulted in the development of a detrital food chain where organic matter from primary producers must first be decomposed by heterotrophic bacteria. This would likely favour zooplankton communities like those in Node 10 composed of micro-filtering rotifers capable of efficiently utilizing bacteria as a food source (Hillbricht-Ilkowska 1977).

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The weak correspondence between phytoplankton community structure and patterns in zooplankton composition suggests that phytoplankton composition is not a major factor determining zooplankton community structure. However, the possible restriction of crustaceans by high concentrations of inedible dinoflagelates suggests that in at least some cases the type of the phytoplankton available can influence zooplankton community structure. Phytoplankton structure may also be important in fishless sites of >18μg/L chlorophyll and >38μg/L total dissolved phosphorus where littoral cladocerans (Group 2) dominate. In two of these sites blooms of the large colonial algae *Aphanizomenon* formed. The large amount of vegetative matter in the water column resulting may resemble conditions experienced by zooplankton in dense SAV beds, thereby explaining the existence of littoral species. However, neither the presence of *Aphanizomenon* blooms nor the concentrations of blue-green nitrogen fixers were selected as a distinguishing factor in the CART model. Thus, my results fail to explain the significance of higher dissolved phosphorus levels for differentiating zooplankton community types.

The selection of water depth in the NMS joint-plot analysis as a key factor influencing zooplankton structure is likely due to its association with fish survival and plant development. Depth of the water column is positively correlated with sticklebacks ($\tau = 0.379$, $\alpha < 0.01$), likely reflecting the suitability of lakes as habitat during the harsh northern Alberta winters. Depth is also negatively co-correlated with the development of SAV ($\tau = -0.156$, $\alpha = 0.04$) and, thereby, the preferential effect macrophytes have on large/medium sized cladocerans.

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The importance of fish for zooplankton structure means activities increasing migration (e.g. ditching → increased connectivity) or winter survivorship (e.g. impounding water → increased under-ice water depth) of sticklebacks will likely significantly impact the structure and possibly the variety of zooplankton communities throughout WBF wetlands. Moreover, activities affecting the development of the SAV-dominated/clear-water states described by Bayley and Prather (2003) will likely alter the zooplankton community structure and functional ecology of WBF shallow-water lakes. Abundant fossil fuel and fiber resources characteristic of the WBF mean that human development and resource extraction will undoubtedly continue in the western boreal. Hopefully such knowledge of the ecological factors influencing biologic productivity will help us to avoid significantly impacting the function of these important wetland ecosystems.

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Tables and Figures:

Rotifers

Taxa	Group
Asplanchna sp.	Predatory Rotifers
Trichocerca multicrinis	
T. longiseta	
Ascomorpha sp	<140μm<5%*
Bdelloidea	
Monommata sp	
Cephelodella sp	
Anuraeopsis fissa	
Macrochaetus sp.	
Ploesoma sp.	>140μm<5%*
Squatinella sp.	
Stephanocerus sp.	
Tylotrocha sp.	
Trochosphaera sp	
Synchaeta sp.	
Brachionus sp.	Not grouped
Conochilus sp.	
Euchlanis sp.	
Filinia longisitae	
Keratella cochlearis	
Keratella quadrata	
Lecane spp.	
L. lunaris	
Lepadella sp.	
Mytillina sp.	
Notholca sp.	
Polyarthra sp.	
Testudinella sp.	
Trichocercae rousselti	
Trichotria tetractis	

Cladocera

Taxa	Group
Alona spp.	Chydoridae
Allonella nana	
Disparalona sp.	
Pleuroxus sp	
Alona guttata	A.gut/Chyd.
Chydorus sp	
Daphnia rosea	*Daphnia sp.*
D. pulex	
Macrothricidae	Benthic sp.
Eurycercus sp.	
Moinodaphnia sp.	
Diaphanosoma birgei	Not grouped
Bosmina longirostris	
Simocephalus vetulus	
Ceriodaphnia quadrangula	
Polyphemus pediculus	

Copepoda

Taxa	Group
Skistodiaptomus oregonensis	Calanoid
Calanoid copepodites	
Diacyclops bicuspidatus	Cyclopoid
Paracyclops fimbriatus	
Cyclopoid copepodites	
Copepod Nauplii	

Table 2.1: Zooplankton taxa collected during study. * < or >140μm<5% are species greater or less than 140μm in size who appeared in less than 5% of the samples collected.

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Group	**N**	**Cladocera**	**Copepoda**	**Rotifera**
#1 Small cladoceran	9	**Bosm(43.1)***		**>140<5%(39.8)*, Euch(35.8)***, Poly(29.2)
#2 Littoral cladoceran	33	**Chyd(39.7)*, A.gut(31.1)*, Ceriod(35.4)***, Benthic(9.1)	Naup(19.4)	**Mytl(43.1)***, Leped(23.2), Lecane(22.1), L.lunari(16.2), Noth(8.3), Tricho(6.7)
#3 Daphnia	13	**Polyph(53.9)*, Daph(31.7)***, Simoc(21.8)		
#4 (No name)	11			K.quad(19.8)
#5 Rotifer	8			**T.rous(63.9)*, Test./Po(59.7)*, Predrots(47.6)***, <140<5%(29.5), K.coch(30.6)
#6 Copepod	9	**Diaph(41.8)***	**Cyctot(30.5)***, Caltot(20.4)	Conoch(24.1), F.long(21.7), Brach(9.7)

Table 2.2: Zooplankton community types and Indicator species. Shows the number of sites (N) and indicator species values for each community type. * Indicates significant at 99% confidence based on Monte-Carlo test (1000 permutations)

	One	Two	Three	Five	Six	Misclassification Rate
One	8	0	1	0	0	1/9
Two	0	27	4	0	2	6/33
Three	0	1	11	0	1	2/13
Five	1	1	1	5	0	3/8
Six	2	2	0	0	5	4/9
					Overall =	16/72 (or 22.2%)

Table 2.3: Confusion matrix for CART model based on jack-knifing. Shows the number of lake-months of each zooplankton community type (rows) that were correctly and incorrectly classified (columns) as well as the overall misclassification rate.

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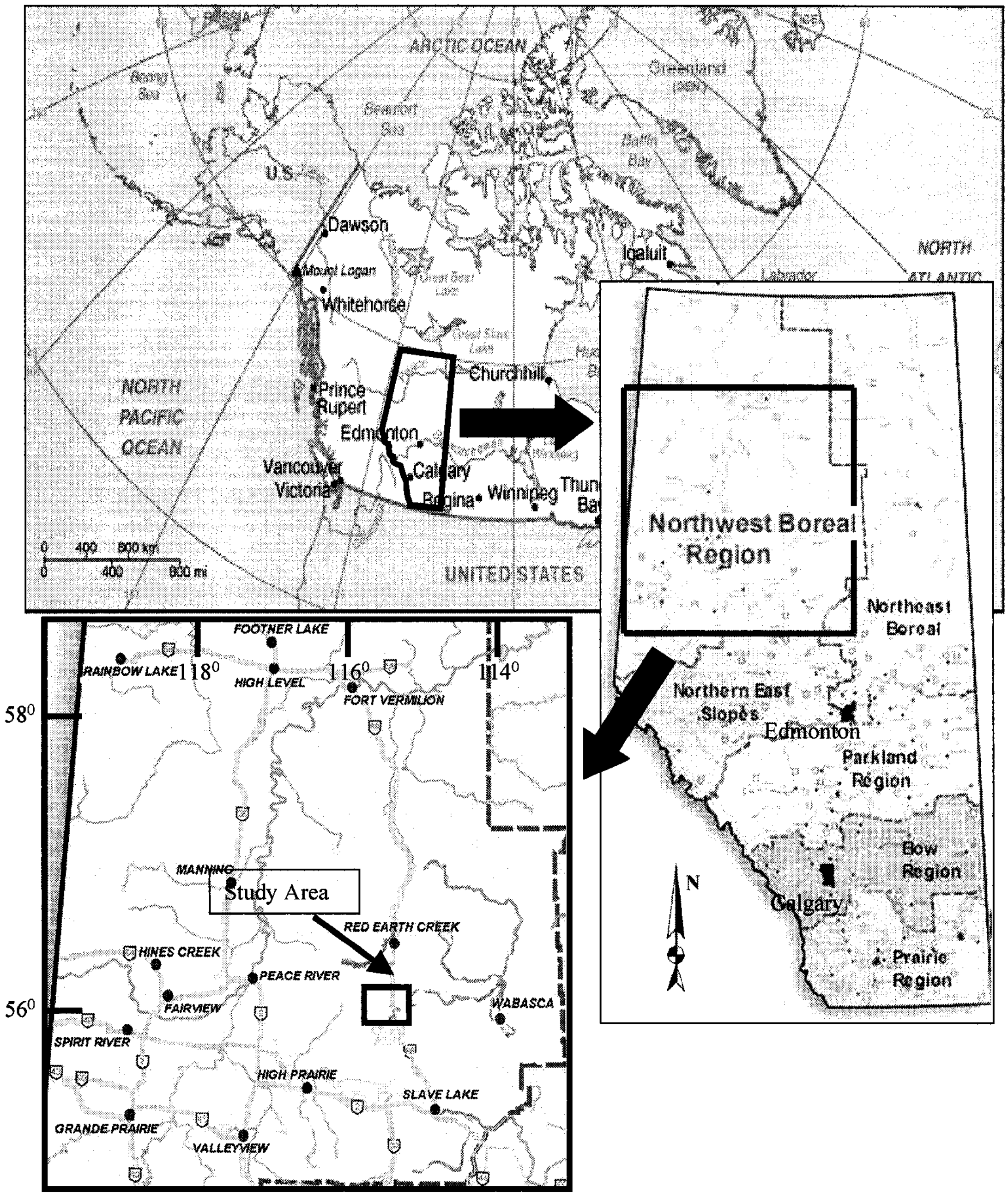

Fig. 2.1: Location of HEAD Project Utikuma Lake study area in Alberta, Canada.

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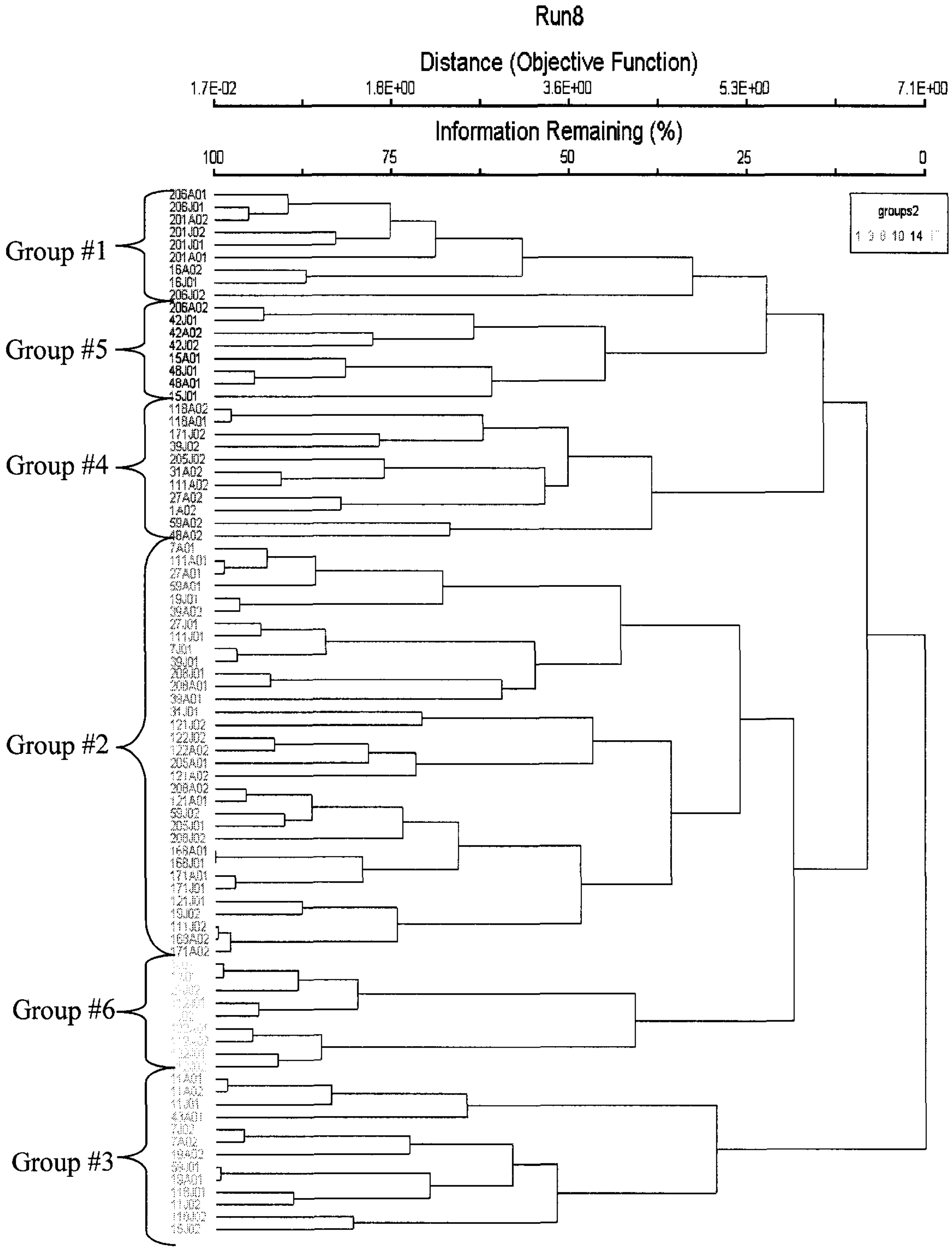

Fig. 2.2: Cluster dendrogram of lake-months based on zooplankton biomass. Using Sorensen distance measure and flexible-beta clustering, six different community types are distinguished. Percent chaining for the solution was 2.24%.

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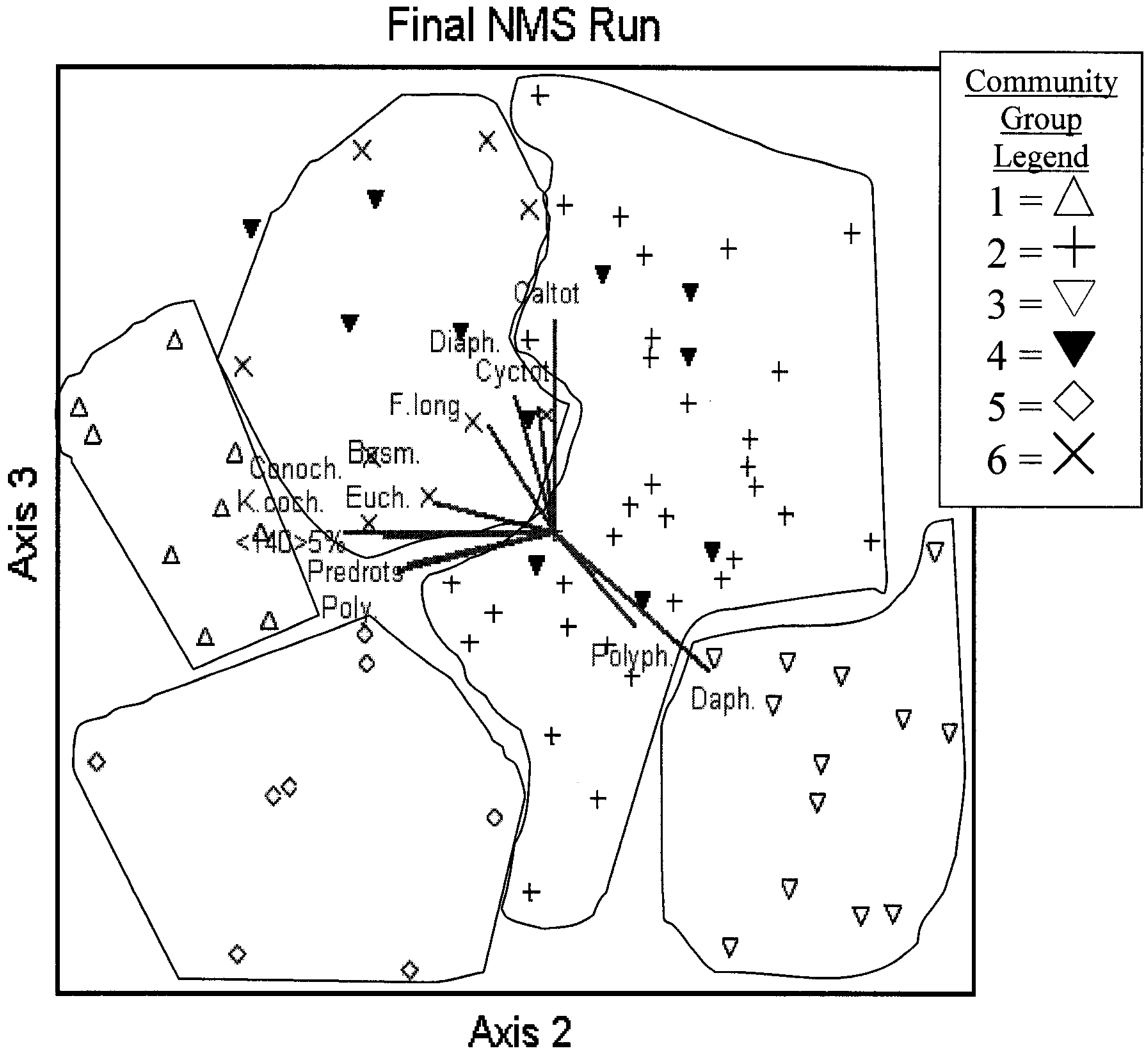

Fig. 2.3: NMS ordination of 2001/2002 sites based on zooplankton species' biomass. The five groups clearly differentiated by Axis 2 (41.9%) and Axis 3 (24.7%) are outlined. Only species exhibiting a coefficient of determination >0.20 are shown in the associated joint-plot.

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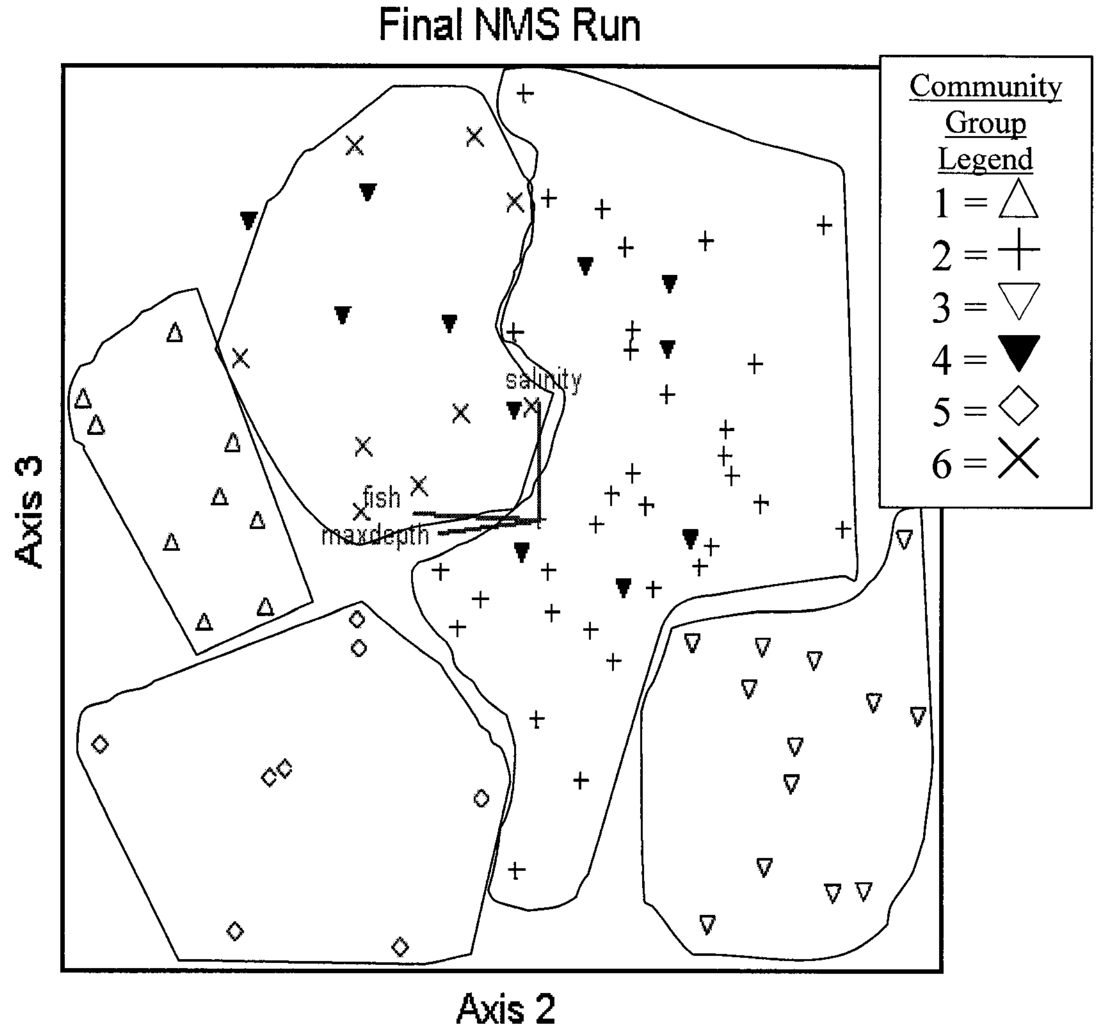

Fig. 2.4: Joint-plot showing importance of sticklebacks, salinity, and depth. The five groups clearly differentiated by the two most important axes are outlined. Only variables exhibiting a coefficient of determination >0.20 with either of the axes are shown in the joint-plot.

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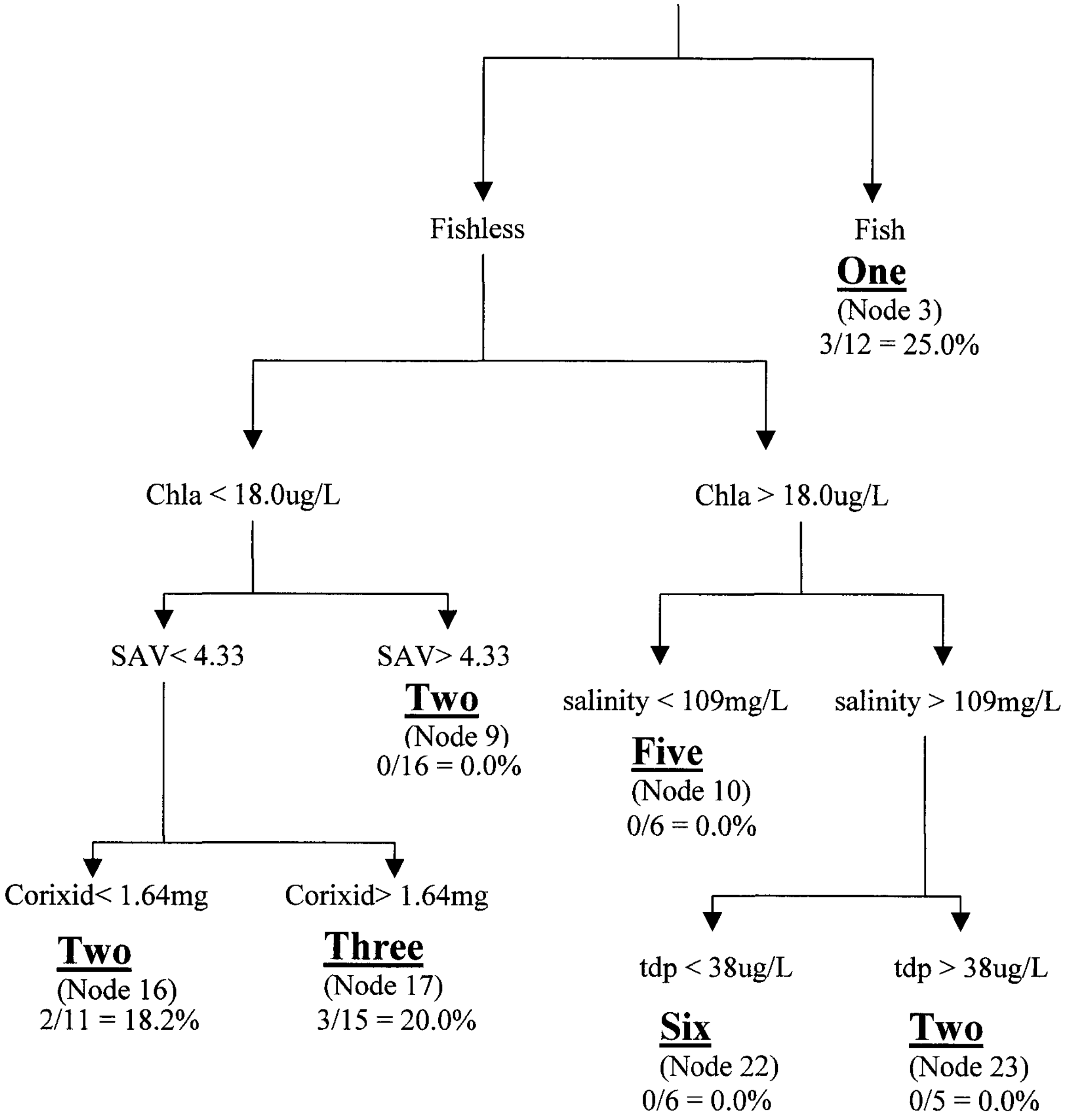

Fig. 2.5: Pruned CART model delineating the conditions associated with each zooplankton community. Numbers (One → Six) correspond with groups described in community analyses (Table 2.2). The higher a variable is in the tree, the more important it is for differentiating communities. Node number and misclassification rates are provided for each end group.

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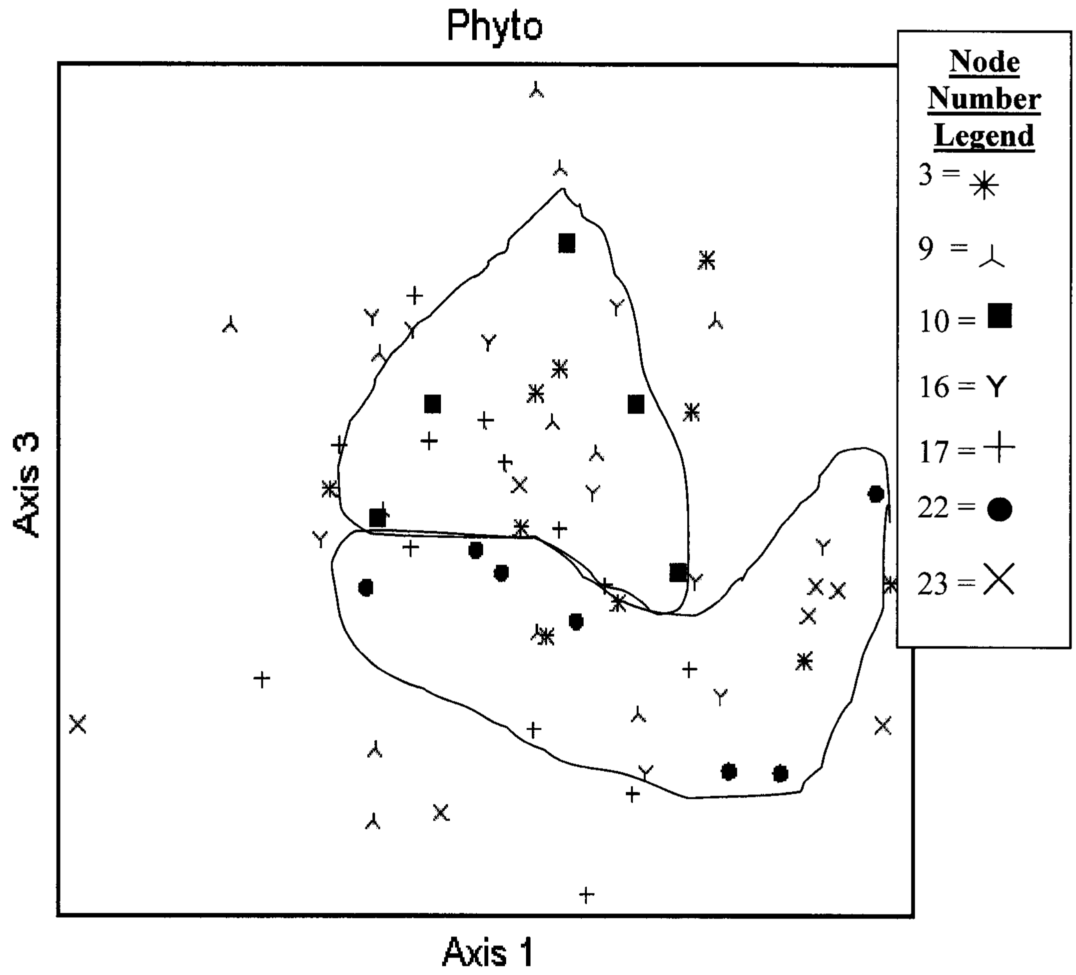

Fig. 2.6: NMS ordination of sites based on phytoplankton community structure overlaid with CART node number. Only pattern observed was differentiation of Node 10 (rotifer communities) and 22 (copepod communities) across Axis 3. This suggests that the differentiation of these two community types may be due to differences in phytoplankton community structure.

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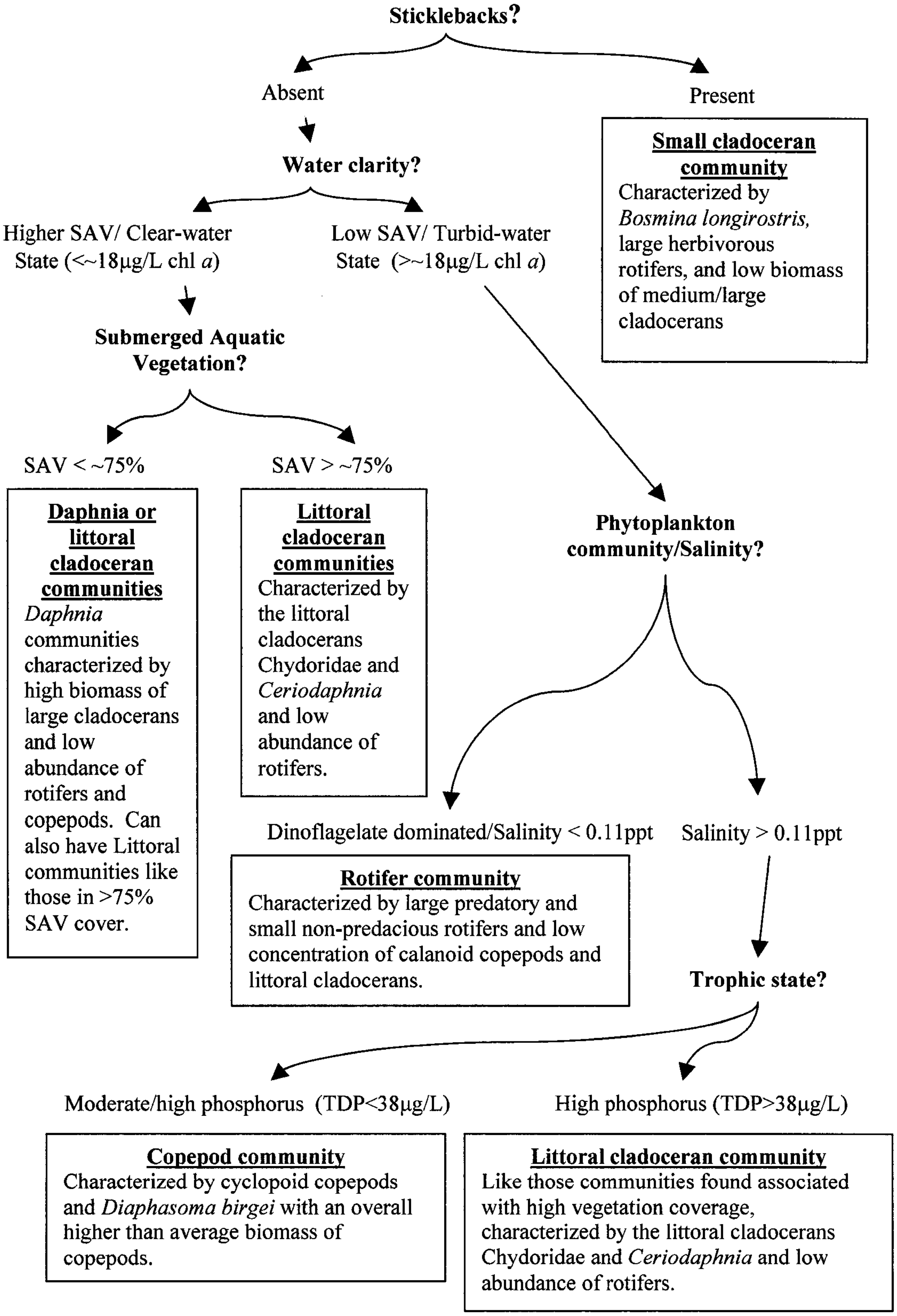

Fig. 2.7: Conceptual model outlining the environmental conditions associated with each zooplankton community type. Figure is based on findings of Cluster, Ordination, CART, and Phytoplankton analyses. Variables located highest in tree are the most important for differentiating zooplankton community types.

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Chapter 3. The importance of zooplankton community structure and sticklebacks for maintaining clear-water states in western boreal wetland lakes.

Introduction

Previous studies of shallow lakes in western Canada (Bayley and Prather 2003; Jackson 2003) have made a distinction between shallow clear-water lakes with relatively low chlorophyll ($<15\text{-}20\mu g\ L^{-1}$) levels and lakes with dense phytoplankton blooms and turbid-waters. These differences in algal abundance could be the result of contrasting nutrient concentrations (Hann and Goldsborough 1997; Carpenter et al. 1998) or the development of inedible species of algae (Hillbricht-Ilkowska 1977;Ghadouani et al. 1998). They could also be the consequence of lakes developing submerged aquatic vegetation (SAV) that limits phytoplankton biomass by assimilating phosphorus (primarily via epiphytic algae) (Engelhardt & Ritchie 2001), allelopathy (Jasser 1995), and/or limiting mixing (Barko and James 1998).

According to studies conducted primarily in Europe, top-down control of phytoplankton by herbivorous zooplankton is another factor capable of governing the existence of clear- over turbid-water states (Jeppesen et al. 2002). The relationship between zooplankton and water clarity is not simply a matter of total grazing pressure, but is a result of differences in food size-selection and physiology between zooplankton species (Pace 1984;Carpenter et al. 1996). Some zooplankton communities are believed to produce clear-water states due in part to their ability to graze a wider range of particles. Herbivores (e.g. *Daphnia*) capable of consuming both small (e.g. bacteria)

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and large (e.g. algae >50μm) particles create a more efficient link in the food-web since more material is transferred directly into secondary production instead of becoming detritus (Havens 1999). Although variation in food size utilization has typically been associated with zooplankton girth (Lougheed and Chow-Fraser 1998;Burns 1968), not all zooplankton of the same size are capable of ingesting the same range of food particles (Bogdan and Gilbert 1984). Therefore, species as well as size needs to be accounted for when considering a communities grazing capacities (Havens 1998;Sommer et al. 2003).

In addition to being limited with respect to the size of food they can consume, communities composed of smaller zooplankton tend to recycle nutrients at a faster rate than communities composed of larger zooplankton, thereby facilitating a higher level of algal productivity (Queimalinos et al.1998). Much of the recent literature pertaining to nutrient recycling by zooplankton has focused on differences in nutrient requirements between species. In particular, *Daphnia*'s relatively high phosphorus retention has been identified as a possible explanation for this groups association with clear-water states (Elser et al. 2002). It has also been postulated that by altering the ratio of available nitrogen to phosphorus (N:P) in the water column *Daphnia* inhibit blooms of grazer resistant, nitrogen-fixing cyanobacteria (Elser 1999). Like most shallow eutrophic water-bodies, nutrient loading in western boreal wetland lakes is probably dominated by internal processes (Moss 1998); therefore, recycling of nutrients from organic sources is likely to be of particular importance for phytoplankton growth in these shallow lakes.

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In many systems, predation by fish on larger zooplankton and macro-invertebrates has been credited for the differences in zooplankton community structure leading to alternate clear- and turbid-water states (Carpenter et al. 1985;Jeppesen et al. 1999). Due to a combination of harsh winter conditions and shallow water, the majority of these shallow (<2.0m), isolated wetland lakes in northern Alberta's western boreal forest (WBF) contain only brook stickleback (*Culea inconstans*), if any fish at all (Conlon 2002). I found that when sticklebacks are present, all large crustaceans (>~400μm) are suppressed and large/medium sized cladoceran communities are absent in these shallow lakes (Chapter 2). If zooplankton communities dominated by medium/large crustaceans create the clear-water conditions with which they are associated, we would expect that the introduction of sticklebacks would lead to the development of turbid states (Sarvala et al. 2000). However, recent work focusing on small shallow systems suggests that predation from the complex macro-invertebrate predator communities that form in the absence of fish can also inhibit cladoceran zooplankton (Burks et al. 2002;Sutor et al. 2001). In fact Wissel et al. (2000) predicts that in shallow lakes, intermediate densities of planktivorous fish minimizing macro-invertebrate predator abundance may be required for stable water-clearing cladoceran zooplankton communities to develop.

According to the previous chapter, the most important factor differentiating medium/large cladoceran dominated communities from other zooplankton communities in fishless WBF wetland lakes was chlorophyll *a* levels <18μg L^{-1} (Chapter 2). This corresponds to the 20μg L^{-1} chlorophyll *a* threshold defining alternate states in WBF

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lakes (Bayley and Prather 2003) and suggests that zooplankton community structure may play a role in the development of contrasting clear- and turbid-water conditions. However, the question of how important top-down control by zooplankton is for maintaining clear-water in these fishless wetland lakes relative to bottom-up processes (e.g. nutrient limitation) has yet to be explicitly addressed. Furthermore, although sticklebacks significantly alter zooplankton community structure (Chapter 2), it is not clear what effect their presence has on the balance between clear- and turbid-water conditions in shallow WBF lakes. The primary objectives of this study were to:

1) identify the factors associated with clear- versus turbid-water conditions in fishless WBF wetland lakes and
2) evaluate the association between sticklebacks and water clarity.

It was hypothesized that:

1) zooplankton community structure would be the most important factor differentiating clear- and turbid-water conditions, consistent with the theory that top-down control of phytoplankton by zooplankton dictates the existence of alternate states and
2) sticklebacks would be associated with high chlorophyll levels and turbid-water states due to the exclusion of zooplankton communities dominated by medium/large sized cladocerans.

Methods

Site Description

The study lakes were the same as those described in Chapter 2 located in northern Alberta, Canada, approximately 300km north of Edmonton near Utikuma Lake

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(Fig. 3.1). Deep glacial till covers the study area with gray Luvisols and Brunisols in the uplands and organic deposits (peatlands) in the depressions being the predominant soil types. The twenty-four study lakes were distributed along a 45km long transect running northwest to southeast (from $115^{0}42'$W $56^{0}07'$N to $115^{0}09'$W $55^{0}57'$N) and spanning outwash plain (dominated by sands), moraine (with more depressions) and lacustrine plain (flat areas with extensive peatlands underlain with clay) landforms. A minimum of six lakes were located in each landform type with an elevation change of approximately 645m to 630m from the transect top to bottom.

Located in the central mixed wood subregion of the boreal forest natural region, the area typically receives an annual precipitation of 503mm (Environment Canada 2002a). However, during the study, precipitation was much lower at around 288mm in 2001 and 376mm in 2002 (Environment Canada 2002b). The lakes are exposed to long, cold winters with average daily mean temperatures in January of -14.5^{0}C (Environment Canada 2002a) and ice typically does not leave even the smallest lake until late April or mid May. Despite a mean annual temperature of only 1.7^{0}C, the lakes experience mean daily air temperatures of 15.6^{0}C during July (Environment Canada 2002a) allowing for periods of high biologic productivity.

The study lakes were small, with an average surface area of approximately 7.0ha (median 3.4ha), and shallow, with an average mean depth of 59cm (min. 7.7cm, max. 101cm), especially during drought conditions in 2002. Western boreal wetland lakes are typically eutrophic (Bayley and Prather 2003) and in this study the total phosphorus

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(TP) levels ranged from mesotrophic to hyper-eutrophic with an average of 102μg L^{-1} TP (min. 28μg L^{-1}, max. 413μg L^{-1}, and median 68μg L^{-1}). Despite the eutrophic conditions, the lakes appeared not to be nitrogen limited with an average total nitrogen to total phosphorus (TN:TP) ratio of 37:1 and a minimum value for all lake-months of 17:1.

Sampling schedule

Each of the twenty-four study lakes were sampled once during July and August in 2001 and in August in 2002, with the exception of three lakes which were too shallow to obtain a reliable sample from in 2002. In each lake samples were collected from five randomly selected sites, size permitting, with data collected from each site subsequently averaged for the lake. Daytime samples were used since diurnal sampling of fish and fishless lakes indicated no significant difference in composition or abundance between zooplankton samples collected during daylight hours and those collected at peak darkness (data not shown). The resulting unit of measure for the survey was lake-month and reflects the conditions in each lake during July or August in 2001 or 2002. A total of fifty-five lake-months of data from twenty different lakes were available for analyses of factors affecting alternate states in fishless lakes. Eight lake-months of data from four fish bearing lakes were available to assess the influence of sticklebacks.

Defining turbid- and clear-water states

Clear-water states were defined as those having chlorophyll values < 15μg L^{-1} chlorophyll *a* with turbid sites being those >20μg L^{-1} based on the levels identified by Bayley and Prather (2003), Timms and Moss (1984), and Chapter 2. Chlorophyll *a*

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concentration for each lake-month was determined following the methods outlined in Chapter 2.

Environmental factors impacting water clarity

Twelve variables were assessed to describe the abiotic conditions for each of the lake-months (Appendix 3). Turbidity was determined in the field using a Turner Designs Aquafluor Turbidimeter. Conductivity, pH, and temperature were measured in-situ using a Hyrolab Quanta field probe. Salinity was calculated by summing the eight major ions (Ca^{++}, Mg^{++}, Na^{+}, K^{+}, HCO_3^{-}, CO_3^{2-}, SO_4^{2-}, Cl^{-}) (Wetzel 1983); ion concentrations were determined following the methods outlined in Bayley and Prather (2003). Total nitrogen (TN), inorganic nitrogen, and dissolved organic carbon (DOC) values for the ponds were also determined following the methods outlined in Bayley and Prather (2003). Samples for chemical analyses were prepared within 48 hours of collection with total phosphorus (TP), total dissolved phosphorus (TDP), and soluble reactive phosphorus (SRP) determined following the methods of Bierhuizen and Prepas (1985).

Depth of water was determined by lowering a secchi disk onto the flocculent sediments and measuring the distance from the top of the disk to the surface of the water. The location of each measurement was recorded using a GPS then, using a staff gauge near shore as a reference, all measurements were standardized and the maximum and mean depth for any date calculated based on the depth at the staff gauge.

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To describe algal communities, phytoplankton samples were collected from the same water used for zooplankton samples and identified and enumerated following the Utermöhl method (Lund et al. 1958). Phytoplankton community structure was defined based on the concentration (number of cells per milliliter) of 14 different taxonomic groups (Appendix 3).

Fish presence and abundance was determined twice in each lake from June to August in 2001 using a minimum of ten Cuba Minnow Traps placed at 5-10m intervals along a stretch of shoreline (W.M. Tonn personal communication). The traps were left overnight then the number, species, and length of each fish was recorded before they were released. Severe drought conditions in 2002 made trapping of seven lakes impractical, but the remaining 17 ponds were trapped at least once during July/August. Results were recorded as fish per trap per night or Catch Per Unit Effort (CPUE).

SAV abundance was recorded as one of five classes: (1) 0% cover, (2) 0-5% cover, (3) 5-25% cover, (4) 25-75% cover, or (5) >75% cover (Bayley and Prather 2003). In cases where SAV coverage was thought to be low or zero and visibility was poor, visual estimates were confirmed by raking the bottom. For computational purposes each class was designated by a whole number 1-5 (Bayley and Prather 2003). Proportion of total biomass composed by each species was determined from samples collected at twenty random sites in each lake during August in 2001 and 2002 using standardized 1.00m x 0.38m rakes of the bottom. SAV were separated and identified to

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species using the keys of Burland (1989) and Moss (1983). Separated samples were then dried at 64^0C for a minimum of 48hrs and total dried biomass calculated as g/m^2.

Predacious macro-invertebrate abundance for all lake-months and zooplankton composition and biomass in fish bearing sites was assessed following the methods in Chapter 2 (a list of macro-invertebrate predators is provided in Appendix 3) . Zooplankton community type for each lake-month was obtained from Chapter 2 (Table 3.1).

Analyses

Approach

To determine what factors were correlated with clear- and turbid-water conditions, the biotic and abiotic environments characteristic of each condition were compared using a combination of univariate and multivariate analyses. Little was known regarding the processes controlling the development of clear- versus turbid-water states in these systems; therefor, I was unable to make assumptions regarding which environmental variables must be accounted for and which could be assumed unimportant. As a result, the number of possible conditions (e.g. combinations of high and low nutrient, physical parameter, and predator states) that needed to be accounted for was incredibly large. Further confounding the issue, many of the factors identified in classical literature as being capable of influencing phytoplankton abundance tend to change drastically between months of the same year in shallow, small lakes (Bennion and Smith 2000). Given the large number of conditions I wished to account for in my analyses and the variability in environmental conditions between July and August, I

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chose to treat the samples collected in each month as individual cases (see Appendix 2 for a thorough discussion of lake-month as a sample unit). Although the number of combinations of factors I could include in the analyses was increased using lake-month as a sampling unit, the variance for some factors was artificially lowered relative to what was observed at a lake-year temporal scale. The significance of this is that I could not utilize analyses requiring the strict assumption of sample independence (e.g. in the generation of a p-value). Therefore, I chose to compare clear- and turbid-water lakes-months using an exploratory classification and regression tree (CART) algorithm. CART analysis provided an automated method of identifying environmental factors most useful for differentiating turbid- from clear-water conditions. Nested two-way stepwise regression was applied to identify the factors that best correlated with chlorophyll in the fish-bearing study lakes. Relationships between biota and chlorophyll concentrations in these lakes were then assessed on a case by case basis to discern if a relationship existed between fish predation, zooplankton community structure, and water clarity.

Factors affecting the development of clear- versus turbid-water states

The physical characteristics of the turbid- and clear-water states were compared by averaging variables in lake-months of each type and determining significant difference using Mann-Whitney U tests. Phytoplankton communities associated with clear- versus turbid-water in fishless sites were compared using Non-metric Multi-Dimensional Scaling (NMS) (Mather 1976;Kruskal 1964) and Multiple Response Permutation Procedure (MRPP) (Zimmerman et al. 1985). The NMS was run with a Sorensen distance measure, a random starting configuration, 40 runs with real data, and

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50 runs of randomized data with a probability of finding the same solution by chance of 0.02. Dimensionality was determined based on the point of diminishing returns on the Scree-plot and the additional percent of the original space represented by each axis. Final stability was defined as 1×10^{-5} standard deviations over the last 15 iterations. MRPP was run using Sorensen distance measure and weighted based on $n_i/\sum n_i$.

CART structural model analysis was used to identify which of the fifty-two environmental variables best differentiated clear- and turbid-water sites (see Appendix 3 for list of variables and transforms applied). Non-parametric CART analysis avoided the problems associated with the use of conventional linear model statistics (McCune and Grace 2002). CART also allowed for the identification of different combinations of variables that may result in high chlorophyll concentrations (De'ath 2002). Prior to analyses, environmental data was standardized based on n_i/n_{imax}, where n_i was the value for the lake-month and n_x the max value for all lake-months (McCune and Grace 2002). Minimum group size to be split was set at ten. Optimal CART model size was determined using cost-complexity pruning based on ten step boot-strapping; optimal tree size was the smallest tree within one standard deviation of the lowest overall misclassification rate (Urban 2002). The validity of the model was assessed via a confusion matrix and overall misclassification rate based on jack-knifing (Urban 2002).

The impact of sticklebacks on water clarity

The factors having the strongest correlation with chlorophyll *a* levels in sites with sticklebacks were identified using a two-way step-wise regression of normalized environmental variables nested within lakes. The relationship between sticklebacks,

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zooplankton community structure, and water-clarity was assessed in two of the four fish bearing lakes where drastic changes in chlorophyll concentration were documented.

NMS and MRPP were all performed using PC-ORD for Windows version 4.14. The CART model was created in S-Plus 6 for windows with the TREE analyses pack provided by Ripley (1997). Mean values and Mann-Whitney U tests were calculated in SPSS 10.0 for windows. Nested step-wise regression analyses and nested regression modeling was carried out in S-Plus 6 for windows.

Results

Factors affecting the development of clear- versus turbid-water states in fishless lakes

Turbid-water lake-months (>20μg L^{-1} chlorophyll *a*) had significantly higher total macro-invertebrate predator biomass ($U = 300.0$, $\propto <0.05$), total phosphorus ($U = 185$, $\propto < 0.01$), and total nitrogen ($U = 327.0$, $\propto < 0.05$) levels and lower SAV coverage ($U = 141.5$, $\propto < 0.01$) than clear-water lake-months (<15μg L^{-1} chlorophyll *a*) (Table 3.2). Although total nutrient levels were higher in the turbid sites, the amount of available phosphorus (soluble reactive phosphorus) and inorganic nitrogen ($NO_3 + NH_4$) did not differ significantly between the two conditions ($U = 251.5$, $\propto = 0.70$ and $U = 303.0$, $\propto = 0.95$ respectively).

NMS ordination indicated that phytoplankton community structure did not differ between turbid- and clear-water sites, as there was complete overlap between lake-

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months exhibiting both conditions (Fig. 3.2). The 3-dimensional NMS solution was determined from 112 iterations with a final stress of 13.8 and represents 85.0% of the total variance in phytoplankton composition (Axis 1 = 21.8%, Axis 2 = 14.1%, Axis 3 = 49.1%). The results of the NMS analysis were supported by MRPP which found no significant difference between the phytoplankton communities of turbid- and clear-water sites (A = 0.006, $\propto = 0.15$).

CART analysis indicated that the most important factor differentiating turbid- from clear-water sites was SAV concentrations above and below a cover rating of 2.3 (Fig. 3.3). This rating corresponds to a percent cover of 5-25%; henceforth, a conservative estimate of 25% coverage is used to identify the amount of SAV required for differentiating turbid- from clear-water states as indicated by the CART model. With SAV coverage greater and less than 25% as the sole factor considered, we are able to account for 81.8% of the variance between turbid- and clear-water states (Table 3.3). The next most important variable for differentiating turbid- from clear-water states was zooplankton community structure with total phosphorus concentrations as a tertiary factor (Fig. 3.3). Cost complexity (data not shown) and jack-knifing analyses (Table 3.3) indicate that the addition of zooplankton community structure as a variable does not significantly improve the model's overall predictive ability. These further steps do, however, indicate the importance of zooplankton community structure and nutrient concentrations for the existence of high-SAV/clear-water states.

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A conceptual model outlining the conditions required for the development of clear- over turbid-water states is provided in Fig. 3.4. The probability of either state existing (as determined from the CART analysis) is provided for each step in the model.

The impact of sticklebacks on water clarity

Three of the four fish-bearing lakes studied contained the small cladoceran dominated zooplankton communities identified as being typical of lakes with sticklebacks (Chapter 2). Stepwise linear regression of chlorophyll *a* concentrations nested within lake indicates that the only factors significantly correlated with chlorophyll concentrations in these three sites were stickleback density (t-value = 4.67, $\propto < 0.01$) and SAV coverage (t-value = -3.24, $\propto = 0.02$). Stickleback density (as CPUE) was identified as the factor having the strongest correlation with chlorophyll concentrations in these sites ($r^2 = 0.81$, $F_{2,7} = 15.3$, $\propto < 0.01$) (Fig. 3.5). This relationship appeared not to be co-correlated with SAV coverage (i.e. SAV and sticklebacks were not correlated;r = -0.29, $\propto = 0.42$) which was identified previously as being the most important factor differentiating clear-water states in fishless systems.

In one of these three lakes, Study Lake 201, a massive drop in stickleback captured from 95 to 0.2CPUE occurred between August 2001 and July 2002 (Fig. 3.6). Corresponding with this decrease in planktivorous fish abundance was an increase in species richness of herbivorous cladocerans (from 2 to 7 species) and calanoid copepod biomass (12.1 to 38.1μg L^{-1}) and a decrease in rotifers (277 to 178μg L^{-1}). Over this same period chlorophyll *a* dropped from 29.2 to 7.15μg L^{-1} despite virtually no change in phosphorus concentrations (46.3 vs. 45.6μg L^{-1} TP and ~3.1 vs. 3.3μg L^{-1} SRP

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respectively). At the same time SAV coverage was able to increase to ~10%, it's highest level recorded in this lake during the study.

The remaining stickleback bearing lake, Study Lake 1, had a zooplankton community dominated by copepods, not by small cladocerans. In this lake the relationship between stickleback density and chlorophyll *a* appears to be negative (Fig. 3.7), contrary to the pattern seen in the other three fish-bearing sites. During the summer of 2001, the stickleback population in Study Lake1 increased from undetectable levels in June to 52CPUE by August (Fig. 3.8). Corresponding with this increase in fish abundance was a decrease in the average biomass of invertebrate predators collected per sweep from 55mg in July to 3.2mg in August (due primarily to a decrease in the Amphipod *Hyallela azteca* from 51mg to undetectable levels). At the same time, the micro-filtering cladoceran *Bosmina longirostris* increased from 64.8μg L^{-1} in July to 628μg L^{-1} by August, resulting in a zooplankton community dominated by calanoid copepods and *Bosmina* similar to that which existed in Lake 201 during its clear state in July 2002. These changes in the animals of Lake 1 corresponded with a drop in chlorophyll *a* from 22.1 to 5.76μg L^{-1}, despite an increase in phosphorus from 47.9 to 71.3 L^{-1} TP and nitrogen from 1.04 to 8.63mg L^{-1} TN over the same period.

Discussion

The effects of zooplankton and SAV on alternate clear- and turbid-water states

Contrary to what was hypothesized, SAV coverage of >25%, not zooplankton community structure, was identified as the factor best differentiating clear- from turbid-

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water conditions in the lakes studied. Although zooplankton structure was not the most important factor differentiating alternate states, it was identified by CART analysis as being an important factor associated with water clarity within those sites of >25% SAV coverage. This suggests that SAV associated zooplankton could be a key mechanism by which SAV maintains clear-water conditions. The CART model also suggests that the clear-water conditions associated with high (>25%) SAV and cladoceran dominated zooplankton communities become less stable as phosphorus concentrations reach hyper-eutrophic levels >138μg L^{-1} TP (Fig. 3.4).

One would expect some correlation to exist between water clarity and the abundance of SAV given that one of the factors often limiting SAV growth is light availability (Muylaert et al. 2003;Gulati and van Donk 2002). However, consistent with the findings of Sondergaard and Moss (1998), the selection of SAV above any of the other fifty environmental variables suggests macrophytes are strongly linked to the existence of clear- over turbid-water conditions. Although zooplankton community structure was not the key factor differentiating alternate states as predicted, zooplankton associated with SAV appear to play an important role in the development of clear-water conditions. The next step in the CART model indicates that most (96.5%) of high SAV lake-months with cladoceran-dominated zooplankton communities were clear while the majority (56%) of lake-months with non-cladoceran-dominated communities were turbid (Fig. 3.4). This is consistent with other studies which have identified herbivorous invertebrates as a SAV facilitated top-down mechanism maintaining the clear-water condition (Stephen et al. 1998;Lau and Lane 2002). SAV encourages the development

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of these efficient grazing medium/large sized cladoceran dominated communities in fishless systems by providing epiphytic algae as an alternate food source during periods of low phytoplankton abundance (Burks et al. 2002;Jeppesen et al. 2002). Increased macrophyte abundance also tends to decrease the number of rotifers in the water column (Duggan 2001), thereby increasing the relative proportion of the zooplankton community dominated by herbivorous crustacean zooplankton.

Due to the many mechanisms available to SAV for suppressing phytoplankton development (e.g. phosphorus uptake, allelopathy) determining the proportion of clearing that can be directly attributed to SAV-associated zooplankton was difficult. As much as 60% of the variance in alternate states could be attributed to SAV associated zooplankton based on the number of sites under the zooplankton node in the CART model, less misclassifications. However, although SAV-associated cladoceran communities ensure clear-water conditions in >96% of the cases studied, their absence did not necessarily result in a high probability of there being a turbid-water state. This indicates that a water-clearing zooplankton community is not necessarily required for clear conditions and, thus, the amount of variance attributable to zooplankton was likely less than 60%. This interpretation is consistent with Jeppesen et al.'s (2002) conclusion that although zooplankton grazing is an important (and perhaps a key) mechanism by which SAV suppress phytoplankton, they are only part of the means by which SAV maintain the clear-water state. Identification of other factors (SAV and non-SAV associated) affecting clear-water states in this study was prevented by the small number of high SAV/turbid-water lake-months and the CART rules regarding minimum node

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size for splitting. In fact, the small number of high SAV/high chlorophyll sites was likely responsible for the increase in relative misclassification with the addition of the third node in the jack-knifing analysis (i.e. the removal of turbid, high SAV sites has a disproportionate impact on the model structure). In order to make a meaningful estimate of the proportion of variance attributable to SAV associated zooplankton, more data from turbid-water sites with >25% SAV coverage is needed.

The results of this study also fail to tell us what specific role the zooplankton associated with these clear-water conditions play. *Daphnia* dominated communities likely directly impact phytoplankton as this species has been identified in other studies as being capable of suppressing chlorophyll levels (Meijer et al. 1999). Littoral cladoceran communities contain species capable of suppressing phytoplankton too (e.g. *Ceriodaphnia*) (Hann and Goldsborough 1997), but the zooplankton in this group also service macrophytes (e.g. by grazing epiphytic algae) and may be indicative of the functional health of the SAV complex. The importance of zooplankton for the establishment of SAV was also not considered in this study, although it may be important considering the recovery of macrophytes in Pond 201 in 2002. If spring clear-water phases resulting from zooplankton grazing (e.g. Talling 2003) prove to be important in the establishment of SAV, the relative significance of zooplankton for the existence of alternate states in western boreal lakes may be greater than suggested by the results of this study.

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Role of nutrients and phytoplankton community structure in regulating alternate states

Nutrient concentrations limiting phytoplankton growth from the bottom-up does not appear to be a key process directly regulating the existence of alternate states in these western boreal wetland lakes. Although total phosphorus and nitrogen concentrations in the water column were significantly higher in turbid- compared to clear-water conditions (TP, U = 185, $\propto < 0.01$; TN, U = 327.0, $\propto < 0.05$), the amount of biologically available phosphorus (SRP) (U = 251.5, $\propto = 0.70$) and nitrogen (NO_3 + NH_4) (U = 303.0, $\propto = 0.95$) were not (Table 2.2). The differences in total nutrient concentrations could reflect the greater amount of nutrients bound up in algae in turbid sites. However, since biologically available constituents (e.g. SRP) assimilated by algae could be replaced (e.g. from nutrient rich, flocculent sediments (Ogilvie and Mitchell 1998)) , functionally there may be little difference in nutrients between turbid- and clear-water lake-months. CART analysis supports this interpretation by not selecting any of the variables describing nutrients as being primary for differentiating turbid- from clear-water sites. However, CART does find that within lakes of >25% SAV coverage, those lake-months with >138μg L^{-1} TP had a higher probability of being turbid (Fig. 3.3). This likely indicates that as absolute nutrient concentrations reach hyper-eutrophic levels, the processes by which SAV maintains water-clarity become less effective and, as was observed by Muylaert et al. (2003), the clear-water state becomes less stable. Although this threshold corresponds to the 128μg L^{-1} TP level identified by Jeppesen et al. (1999) as being critical for shallow-water lakes in Europe, my conclusions are based on observations from only six lake-months. Therefore, data from a greater number of

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turbid/high SAV lakes would be required to validate this interpretation. Further study of the relative stability of clear-water conditions as a function of nutrient concentration is required to get a better idea as to what phosphorus thresholds exist for alternate states in these lakes.

NMS ordination (Fig. 3.2) and MRPP ($A = 0.006$, $p = 0.15$) of phytoplankton in non-fish-bearing sites indicate that the phytoplankton communities associated with turbid- and clear-water sites do not differ significantly. This suggests that the development of less-edible phytoplankton species was relatively unimportant in the evolution of alternate turbid- and clear-water states. CART model analysis supports this conclusion by not selecting any of the phytoplankton community structure variables to differentiate clear- and turbid-water states.

The impact of sticklebacks on water clarity

As predicted, stickleback concentrations were positively associated with chlorophyll levels in the majority of the fish bearing lakes studied. However, the small-cladocerans and calanoid copepods that thrive in low-stickleback, low-macro-invertebrate predator environments appear capable of suppressing chlorophyll and clearing the water column. From this I conclude that in these four lakes, despite the effect that sticklebacks have on zooplankton communities (Chapter 2), only in high concentrations do they encourage the development of turbid-water conditions.

Based on the conclusion that zooplankton community type is important for SAV to maintain the clear-water state, I expected that suppression of medium/large

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cladoceran zooplankton by sticklebacks (Chapter 2) would negatively impact water-clarity. This hypothesis is supported by the strong positive correlation between stickleback density and chlorophyll in the three stickleback bearing lakes with small cladoceran dominated zooplankton communities ($r^2 = 0.81$, $F_{2,7} = 15.3$, $\propto < 0.01$). Observations from one of these lakes (Study Lake 201) suggest, however, that a community dominated by the small, micro-filtering cladoceran *Bosmina longirostris* and the macro-filtering calanoid copepod *Skistodiaptomus oregonensis* are able to affect a change in water clarity (Fig. 3.6). This agrees with the findings of Bukaveckas and Shaw (1998) that the removal of large cladocerans (e.g. *Daphnia*) is not crucial for top-down control of phytoplankton because smaller cladocerans are able to compensate for their loss. It is also consistent with the finding of Sommer et al. (2003) that communities composed of both micro-filtering and macro-filtering (e.g. calanoid copepods) species' are capable of efficiently filtering the water column.

In contrast to the other fish bearing lakes that had small cladoceran dominated communities, a negative relationship between stickleback density and chlorophyll existed in Study Lake 1 (Fig. 3.7). This appears have been the result of sticklebacks suppressing predatory macro-invertebrates thus allowing the invertebrate predator sensitive *Bosmina longirostris* (Sutor et al. 2001) to increase in numbers (Fig. 3.8). Consistent with Wissel et al. (2000), these findings suggest that low levels of sticklebacks that limit macro-invertebrate predators may actually encourage the development of water-clearing zooplankton communities. The results also implicitly support the findings of others that in some cases macro-invertebrates are capable of

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affecting changes in water clarity through trophic cascades (Burks et al. 2002;Sutor et al. 2001).

Overall, the results of this study support the hypothesis that SAV and its associated zooplankton are crucial for the maintenance of alternate clear- over turbid-water states, even in fishless shallow lakes. Based on these findings, one would predict that practices weakening top-down control of phytoplankton by inhibiting SAV growth (e.g. increased water depth) or altering zooplankton structure (e.g. pesticide use) would increase the propensity of turbid-water states throughout the WBF wetlands. However, activities (e.g. ditching) that spread stickleback, thereby eliminating medium/large sized cladoceran dominated communities, may only promote turbid-water conditions in cases where stickleback densities become high.

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Tables and Figures

Group	N	Cladocera	Copepoda	Rotifera
#1 Small cladoceran	9	**Bosmina**		**>140<5%*, Euchlanis,** Polyarthra
#2 Littoral cladoceran	26	**Chydoridae, Alona guttata, Ceriodaphnia,** Benthic species	Nauplii	**Mytillina,** Lepedella, Lecane, L.lunaris, Notholca, Trichotria
#3 Daphnia	8	**Polyphemus, Daphnia,** Simocephalus		
#4 (No name)	8			Keratella quadrata
#5 Rotifer	7			**Trichocercae rousselti , Testudinella sp. , Predatory rotifers,** <140<5%*, Keratella cochlearis
#6 Copepod	6	**Diaphasoma**	**Cyclopoids,** Calanoids	**Conochilus sp.,** Filinia longisitae, Brachionus sp.

Table 3.1: Zooplankton community types and Indicator species from Chapter 2. Shows the community types identified in Chapter 2 along with their indicator species and number of lake-months (N) belonging to each. * <>140µm<5% are species greater and less than 140µm in size who appeared in less than 5% of the samples collected. Zooplankton taxa in bold are significant indicators at 99% confidence based on Monte-Carlo test (1000 permutations).

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Variable	**Turbid-water State (>20μg L^{-1} chl *a*)**	**Clear-water State (<15μg L^{-1} chl *a*)**
Average Depth	68.5cm	63.3cm
Chlorophyll *a***	57.5μg L^{-1}	6.18μg L^{-1}
Dissolved Organic Carbon	53.7μg L^{-1}	56.8μg L^{-1}
Inorganic Nitrogen	194μg L^{-1}	203μg L^{-1}
Macro-invertebrate Predators*	219mg L^{-1}	120mg L^{-1}
pH	8.11	8.25
Salinity	188mg L^{-1}	177mg L^{-1}
Soluble Reactive Phosphorus	7.36μg L^{-1}	8.33μg L^{-1}
Submerged Vegetation**	2.11(~5% coverage)	3.71(~30% coverage)
Total Nitrogen*	4.01mg L^{-1}	3.24mg L^{-1}
Total Phosphorus**	162μg L^{-1}	86.6μg L^{-1}
Turbidity**	8.28NTU	3.29NTU
Zooplankton species richness	12.0	12.2

Table 3.2: Average values for environmental variables in turbid- and clear-water lake-months. *Denotes significant difference at 95% confidence; ** denotes 99% confidence. A complete list of predacious macro-invertebrates is provided in Appendix 3.

Two-Node Classification Tree		
	Turbid	Clear
Turbid	14	6
Clear	4	31
Overall Misclassfication		10/55 = 18.2%

Three-Node Classification Tree		
	Turbid	Clear
Turbid	14	1
Clear	7	11
Overall Misclassfication		8/33 = 24.2%

Table 3.3: Confusion Matrices for Two- and Three-Node alternate state CART models. Provides the number of times turbid and clear sites (rows) were classified as turbid or clear (columns). Results suggest that adding zooplankton as a factor decreases the number of turbid sites misclassified as clear, but overall misclassification rate increases. This may be due to the lower number of three-node solutions available for this data set.

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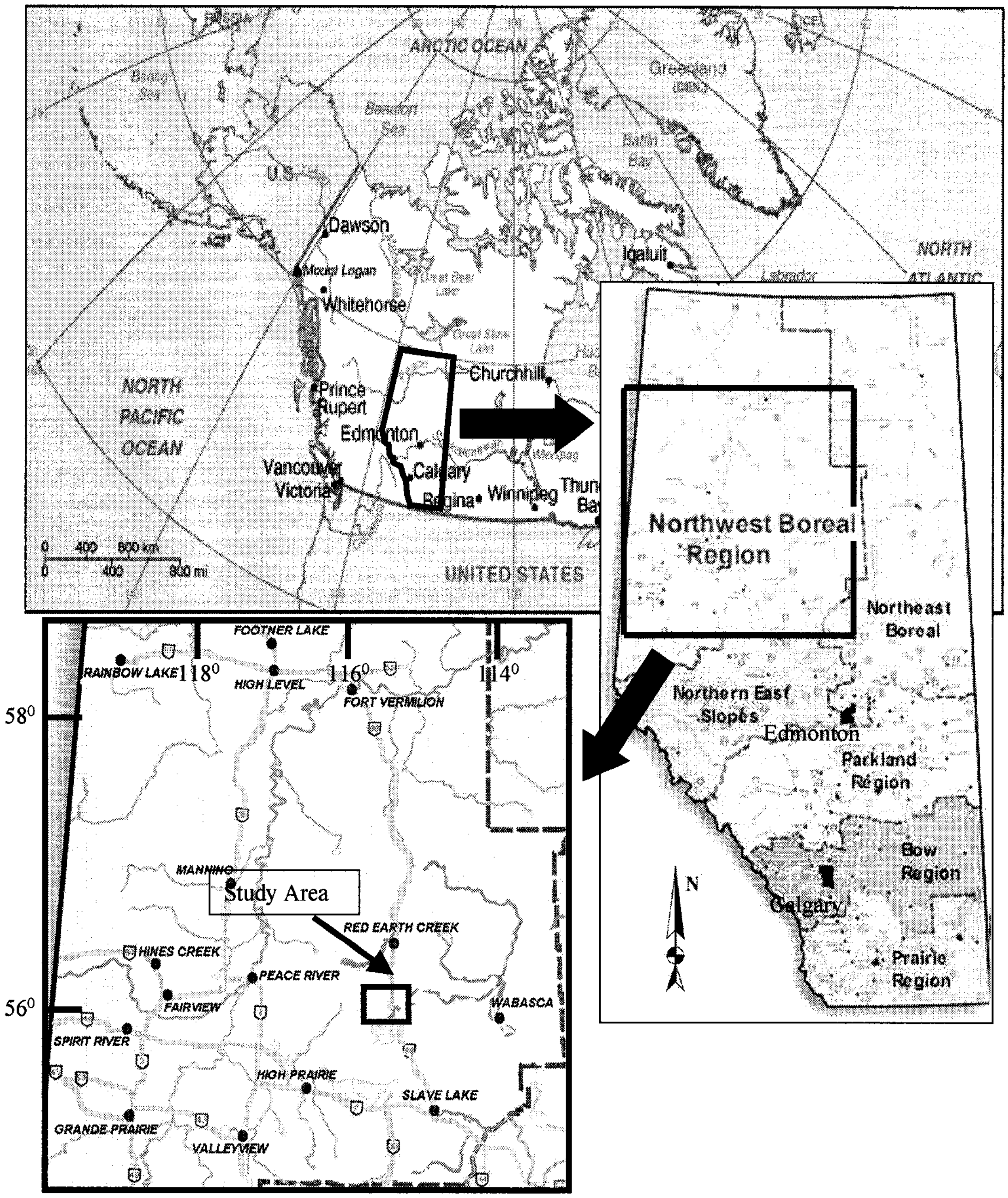

Fig. 3.1: Location of HEAD Project Utikuma Lake study area in Alberta, Canada.

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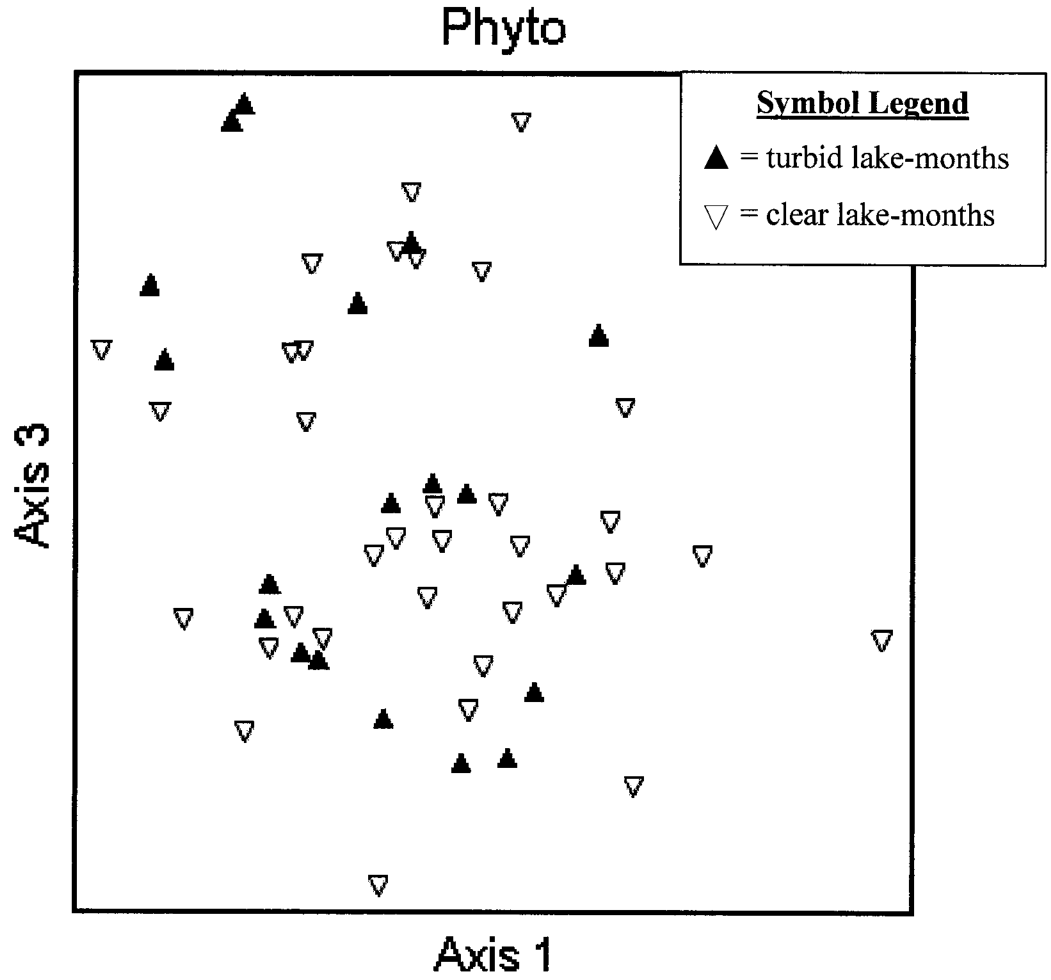

Fig. 3.2: NMS ordination of sites based on phytoplankton counts. Overlap of clear- and turbid-water lake-months indicates no difference in community composition.

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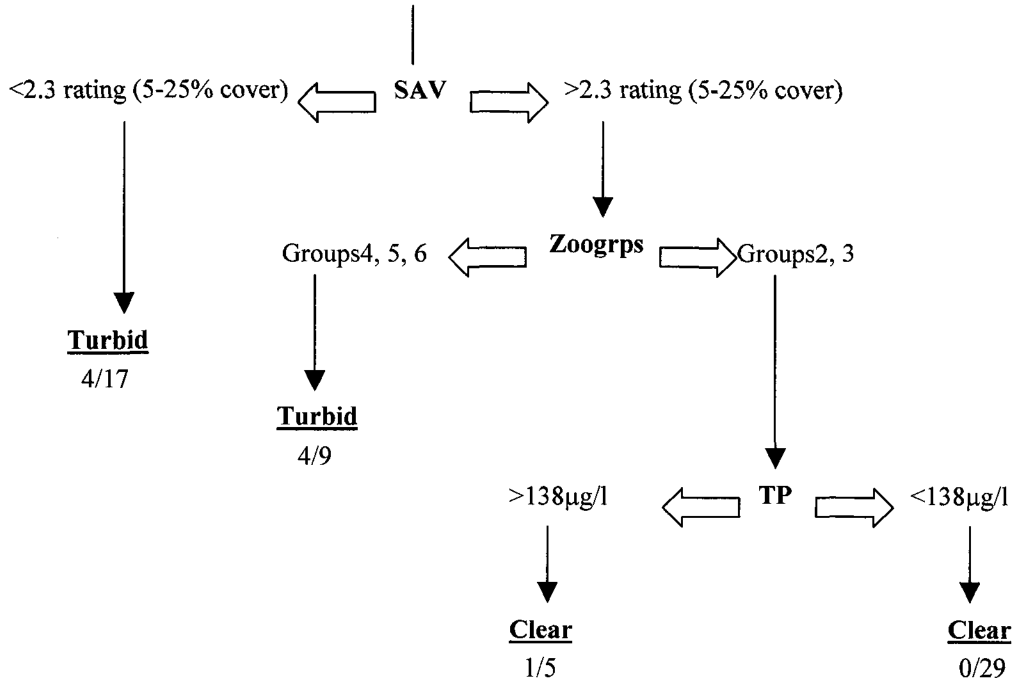

Fig. 3.3: CART model delineating the conditions associated with turbid- and clear-water lake-months. The number of misclassifications (impurities) is given for each node.

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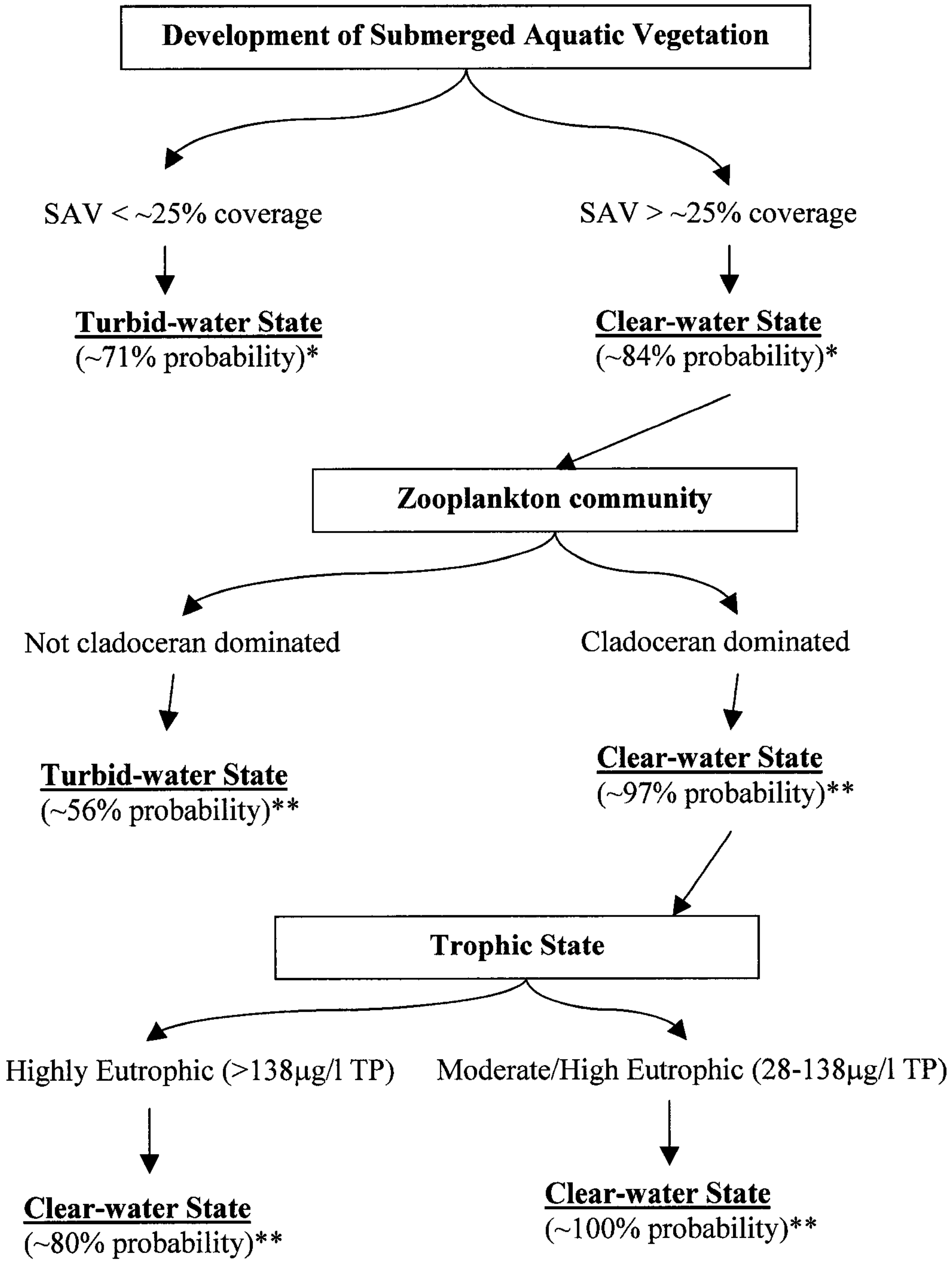

Fig. 3.4: Conceptual model of the controls on clear- vs. turbid- water states in western boreal, shallow wetland lakes. This summarizes the factors associated with turbid- and clear-water states in the non-fish-bearing ponds studied. Factors located highest in the tree are most important and those at bottom the least important for differentiating clear- from turbid-water conditions. * based on cross-validated, 2-node CART model; ** based on un-validated 5-node CART model.

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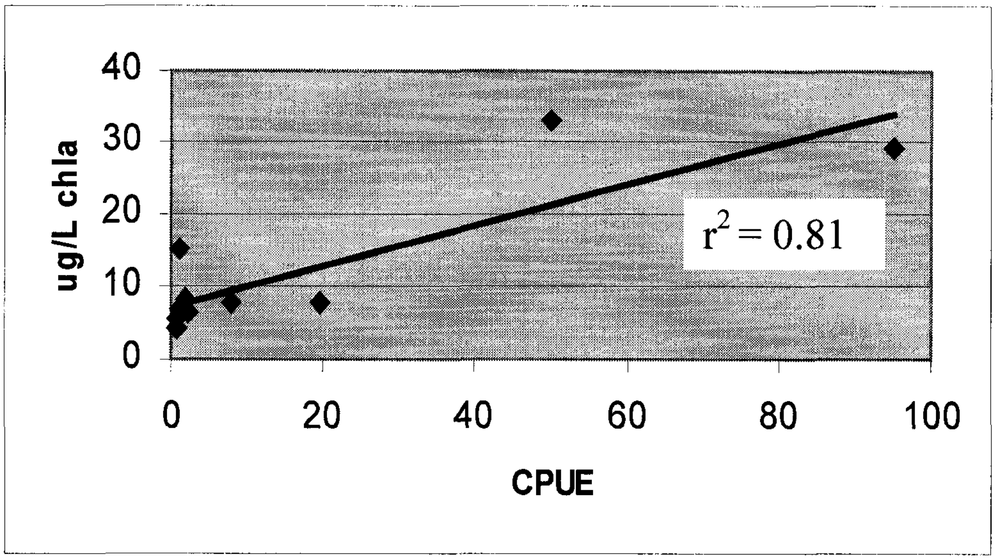

Fig. 3.5: Nested regression of stickleback and chlorophyll concentrations in sites containing small cladoceran dominated zooplankton communities. Stickleback CPUE accounts for approximately 81% of the variation in chlorophyll within these lake-months ($r^2 = 0.81$, $F_{2,7} = 15.26$, $\alpha < 0.01$).

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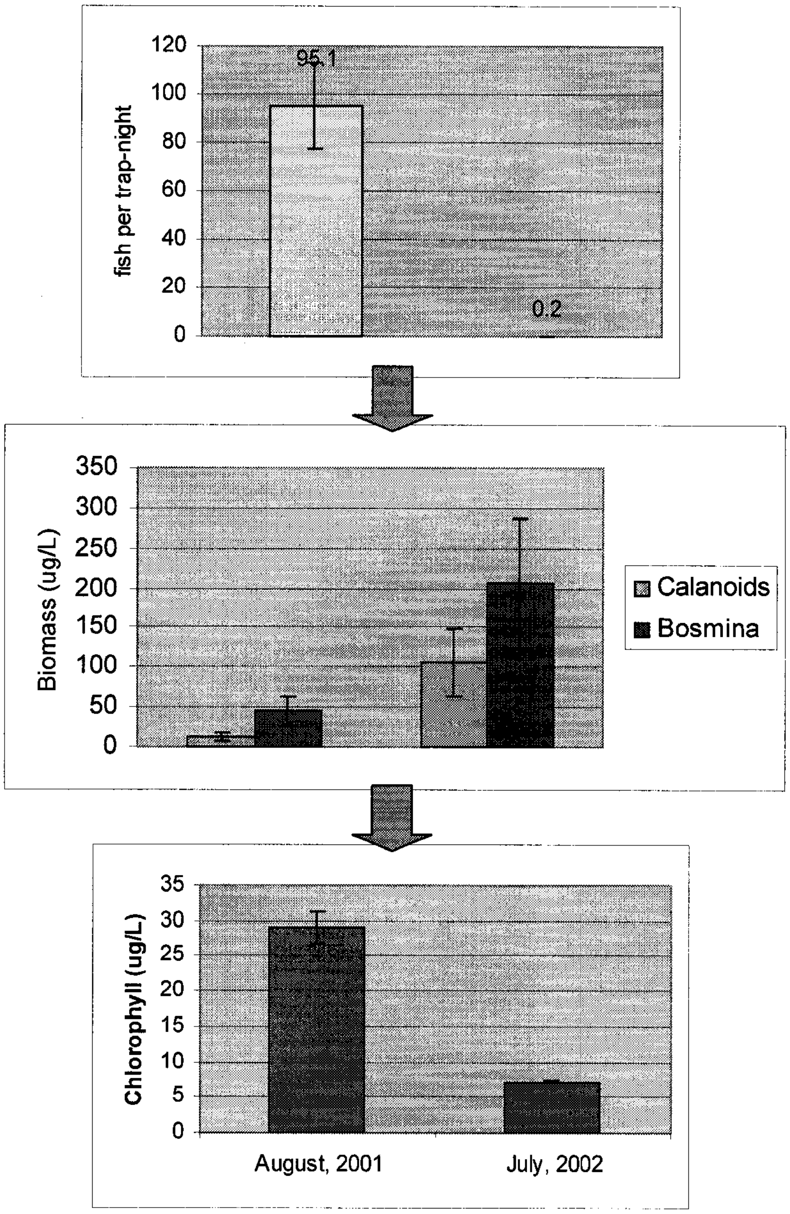

Fig. 3.6: Effects of decreased stickleback concentrations in Lake 201 between August, 2001, and July, 2002. A severe drop in stickleback abundance corresponds with a recovery of calanoid copepods resulting in a *Bosmina*/calanoid dominated zooplankton community and a change from a turbid- to a clear-water state. Stickleback and chlorophyll error bars represent 95% confidence limits. Zooplankton biomass error bars represent 40% standard error of abundance estimates.

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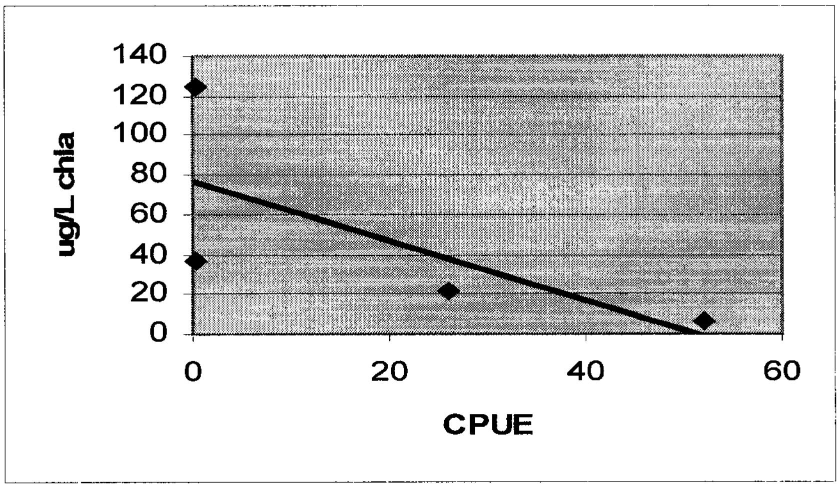

Fig. 3.7: Stickleback and chlorophyll concentrations in Lake 1. A significant correlation does not exist, but the trend indicates that stickleback concentrations are negatively correlated with chlorophyll levels.

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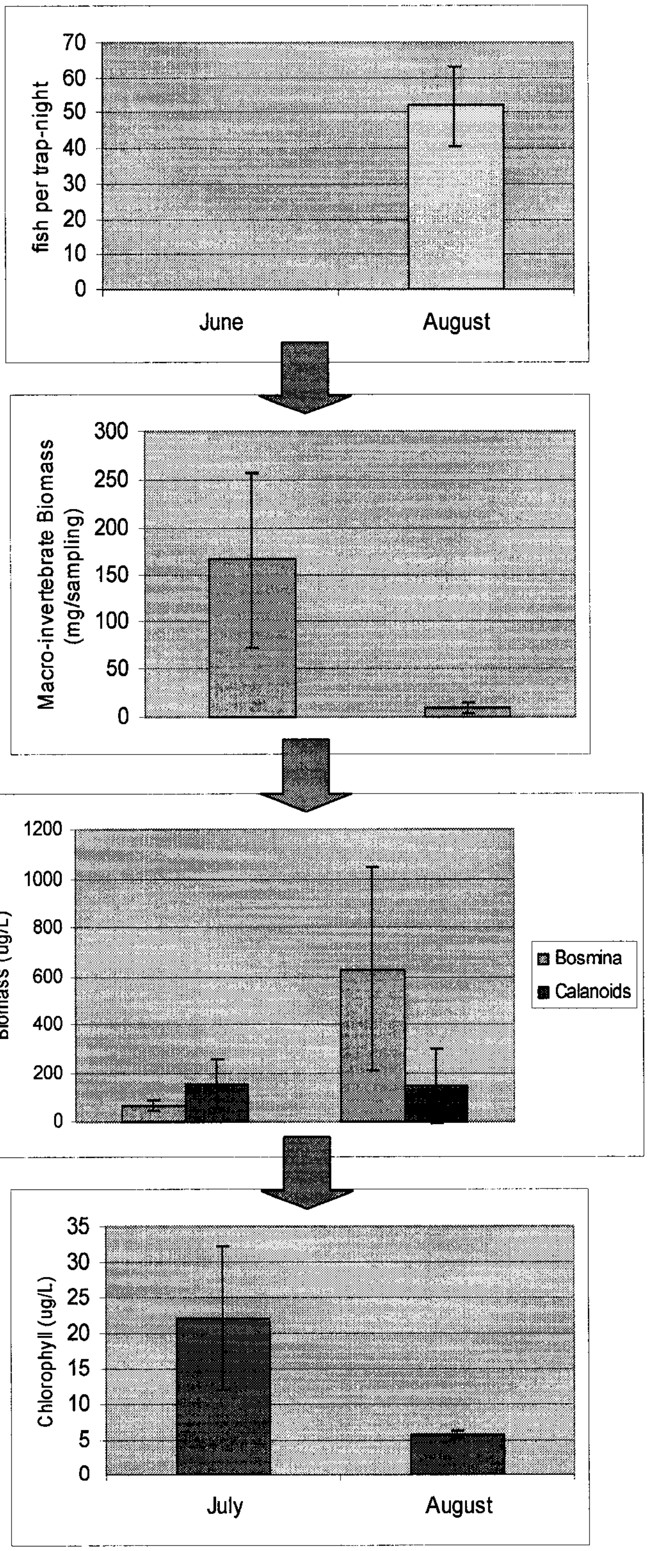

Fig. 3.8: Effects of increased stickleback concentrations in Lake 1. Appearance of sticklebacks leads to a reduction in macro-invertebrate predators, an increase in *Bosmina*, and a clearing of the water column. Error bars represent 95% confidence limits.

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Chapter 4. Conclusions

The results of this work reflect the importance of submerged aquatic vegetation (SAV) for the function of wetland lakes in the western boreal forest (WBF). I conclude that disturbances restricting the growth of SAV in these shallow lakes (e.g. impounding water and increasing depth), in addition to seriously altering the zooplankton community structure, will alter the balance between alternate states across the WBF. Thus, although practices that impact natural bottom-up processes (e.g. nutrient loading) may not directly affect water clarity in these lakes, they may indirectly determine alternate states by influencing the development of submerge macrophytes.

Due to the apparent importance of SAV associated zooplankton for maintaining water clarity, I further predict that activities restricting the development of cladoceran dominated zooplankton communities (e.g. pesticide use) would increase the propensity for turbid water conditions. However, to fully comprehend the importance of zooplankton in the balance between alternate states, we need to understand their role in the establishment (e.g. through spring clear-water phases) and maintenance (e.g. through epiphytic grazing) of high SAV concentrations in WBF wetland lakes. My results highlighting the importance of SAV associated invertebrates are consistent with the majority of studies from shallow European lakes (Jeppesen et al. 2002). Therefore, future research and policy development for the management of WBF wetland lakes should integrate the theories outlined by these works (e.g. the Alternate Stable States Hypothesis (Scheffer and Jeppensen 1997)).

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As is the case in other small water bodies, the most important factor influencing zooplankton community structure in WBF wetland lakes is the presence/absence of zooplanktivorous fish. However, contrary to the theories developed based on findings from deeper systems (e.g. the Trophic Cascade Hypothesis (Carpenter et al. 1985)), the presence of vertebrate planktivores (sticklebacks) did not necessarily result in an increase in turbidity. This seems to give credence to the findings of Wissel et al. (2000) and Bukaveckas and Shaw (1998) and implies that in at least some cases macro-invertebrate predators can influence water clarity. Therefore, I suggest that future research and policy development for management of fish populations and their possible impacts on water clarity in western boreal wetlands consider Wissel et al. (2000)'s Optimal Biomass Hypothesis.

In addition to characterizing the previously undocumented zooplankton communities in western boreal wetland lakes, the results of this study suggest that top-down processes (SAV and its associated zooplankton) are the primary factors dictating the existence of alternate states in these systems. In concert with studies focusing on bottom-up processes that determine potential productivity and macrophyte growth, this knowledge will help us to better understand what controls the rate and form of biologic productivity in WBF wetlands. Comprehension of these processes will be crucial in our efforts to preserve the functions performed by these valuable northern ecosystems and the wildlife (e.g. water birds) they support.

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Appendix 1: Environmental variables and NMS ordination axes correlates.

Physical Parameters			
Code	**Variable**	**Unit of Measure**	**Transform**
avdepth	Average Depth	cm	None
cond	Conductivity	mS/cm	None
doc	Dissolved Organic Carbon	µg/L	None
InorgN	Inorganic Nitrogen (NO_3+NH_4)	µg/L	ln
maxdepth	Maximum Depth	cm	None
ph	pH	pH units	None
salinity	Salinity	mg/L	None
lntdp	Total Dissolved Phosphorus	µg/L	ln
tn	Total Nitrogen	µg/L	None
lntntp	Total Nitrogen:Phosphorus	not applicable	ln
lntp	Total Phosphorus	µg/L	ln

Table A1.1: Physical parameters included in analyses

Code	Organism/Group	Unit of Measure	Transform
Predators			
anisop	Anisoptera	mg/sampling	ln(x+1)
chaob	*Chaoborus sp.*	mg/L	ln(x+1)
corix	Corixidae	mg/sampling	ln(x+1)
dytiscid	Dytiscidae	mg/sampling	ln(x+1)
fish	*Culea inconstans*	Fish/trap/night (CPUE)	ln(x+1)
gammar	*Gammarus lacustris*	mg/sampling	ln(x+1)
gerrid	Gerridae	mg/sampling	ln(x+1)
gyrini	Gyrinidae	mg/sampling	ln(x+1)
hyall	*Hyalella azteca*	mg/sampling	ln(x+1)
hirud	Hirudinea	mg/sampling	ln(x+1)
hydroph	Hydrophilidae	mg/sampling	ln(x+1)
mites	Arachnida	mg/L	ln(x+1)
totpred	Total Predators	mg/sampling	ln(x+1)
zygop	Zygoptera	mg/sampling	ln(x+1)
Submerged AquaticVegetation (SAV)			
allisma	*Alisma gramineum*	% of total biomass	ln(x+1)
cerato	*Ceratophyllum demersum*	% of total biomass	ln(x+1)
chara	*Chara sp.*	% of total biomass	ln(x+1)
myro	*Myriophyllum exalbescens*	% of total biomass	ln(x+1)
ppect	*Potamogeton pectinatus*	% of total biomass	ln(x+1)
pprae	*P. praelongus*	% of total biomass	ln(x+1)
ppus	*P. pusillus*	% of total biomass	ln(x+1)
prich	*P. richardsonii*	% of total biomass	ln(x+1)
pvagin	*P. vaginatus*	% of total biomass	ln(x+1)
pzost	*P. zoteriformis*	% of total biomass	ln(x+1)
sav	Total SAV	% cover code	None
ranun	*Ranunculus circinatus*	% of total biomass	ln(x+1)

Table A1.2: Variables used to describe predators and vegetation in sample sites.

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Appendix 1 (continued)

Taxonomic Group	Unit of Measure	Transform
Aphanizomenon bloom	Presence/absence	None
Bacillariophyta	Cells/ml	ln(x+1)
Chlorophyll *a*	µg/L	ln
Chlorophyta-CELLS	Cells/ml	ln(x+1)
Chlorophyta-COLONY	Cells/ml	ln(x+1)
Chlorophyta-FILAMENT	Cells/ml	ln(x+1)
Chroococcales	Cells/ml	ln(x+1)
Chroococcales-COLONY	Cells/ml	ln(x+1)
Chroococcales-large Colony	Cells/ml	ln(x+1)
Chrysophyceae	Cells/ml	ln(x+1)
Cryptophyceae	Cells/ml	ln(x+1)
Dinophyta	Cells/ml	ln(x+1)
Euglenophyceae	Cells/ml	ln(x+1)
Microcystis	Cells/ml	ln(x+1)
Nostocales	Cells/ml	ln(x+1)
Oscillatoriales	Cells/ml	ln(x+1)

Table A1.3: Variables used in analyses to describe phytoplankton community.

Variable	Axis 2	Axis 3	Axis 1
lntdp	0.149	—	—
zygop	0.130	—	—
gammar	0.114	—	—
Myrio	0.101	0.117	-0.166
SAV	0.100	—	—
Totpred	0.092	—	—
Allisma	-0.122	—	—
avdepth	-0.128	—	—
lnchla	-0.151	—	—
maxdepth	**-0.238**	—	—
Fish	**-0.299**	—	—
Salinity	—	**0.242**	—
cond	—	0.173	—
lntp	—	0.117	—
gerrid	—	—	0.108
Pzost	—	—	0.105

Table A1.4: NMS axis-environmental variable coefficients of determination. Only those variables with coefficients of $r^2>0.1$ are displayed with those >0.2 in bold.

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Appendix 2: The use of lake-month as a sampling unit

The major focus of my work was to determine: 1) which environmental variables were responsible for the development of different zooplankton communities and, 2) the relative importance of zooplankton for maintaining clear-water states in western boreal wetland lakes. However, since little was known regarding the processes controlling zooplankton community structure or alternate high- and low-phytoplankton conditions, I was unable to make assumptions regarding which variables must be accounted for and which could be assumed unimportant. As a result, the number of possible conditions that needed to be accounted for was incredibly large. For example, considering only total nitrogen (TN), total phosphorus (TP), inorganic nitrogen, and total dissolved phosphorus (TDP), there is a total of 2^4 different combinations of variables which could exist in the presence of clear- or turbid-water conditions (i.e. ↓ or ↑ TP + ↓ or ↑ TN + ↓ or ↑ TPD + ↓ or ↑ inorganic N). If we consider twenty observations of each condition as a minimum to make statistically meaningful comparisons between conditions using classical parametric statistics, the minimum number of observations required would be 320. Since during this study I included a total of fifty-two different variables as possible factors influencing the development of clear- and turbid-water states and different zooplankton community types (2^{52} possible conditions for comparing turbid versus clear; 6^{52} for comparing different zooplankton community types), the use a classic comparison of means approach was infeasible.

Further confounding the issue, many of the factors identified in classical literature as capable of determining algal productivity changed drastically between

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months of the same year (Figures A2.1 and A2.2). For example, in Lake 27 in 2002, chlorophyll concentrations increased from 6.93μg/L in July to 28.2μg/L in August while total nitrogen (TN) concentrations increased by 1250μg/L. During 2001 in Lake 205, chlorophyll concentrations remained unchanged between July and August (7.3 and 7.9μg/L respectively) but the abiotic environment change drastically. TP (+236μg/L), TDP (+145μg/L), TN (four times greater), and inorganic nitrogen (+15μg/L) were higher in August as compared to July (Figure A2.1). Accounting for such variances in environmental conditions associated with a change (or no change) in water clarity (or differences in zooplankton community structure) was essential to my study objectives.

Given the large number of conditions I wished to account for in my analyses and the variability in environmental conditions between July and August within individual lakes, I chose to consider the samples collected in each month as individual cases. The drawback to this approach was that although the number of combinations of factors I could include in the analyses was increased, the variance for some factors was artificially lowered relative to what was observed at a lake-year temporal scale. For example, TP concentrations varied less between lake-months than they did between lake-years (coefficient of variations of 26.9% (±8.3%) versus 62.9% respectively). The significance of this is that I could not utilize analyses requiring the strict assumption of sample independence (e.g. in the generation of a p-value). Therefore, I chose to address the question of how the turbid- and clear-water lake-months (or lakes-months with different zooplankton community types) conditions differed using a CART algorithm with the validity of the output tested using a jackknifing procedure. This exploratory

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approach did not require the strict assumption of discrete sampling units while being capable of describing the multitude of combinations of different variables (e.g. ↓ or ↑ nutrients + ↓ or ↑ macro-invertebrate predators + ↓ or ↑ macrophyte abundance) which could result in a similar state of water clarity or zooplankton community structure. However, when attempting to extrapolate the results from these analyses, one must remember that the number of sample sites observed was only twenty-four and twenty for Chapters 2 and 3 respectively.

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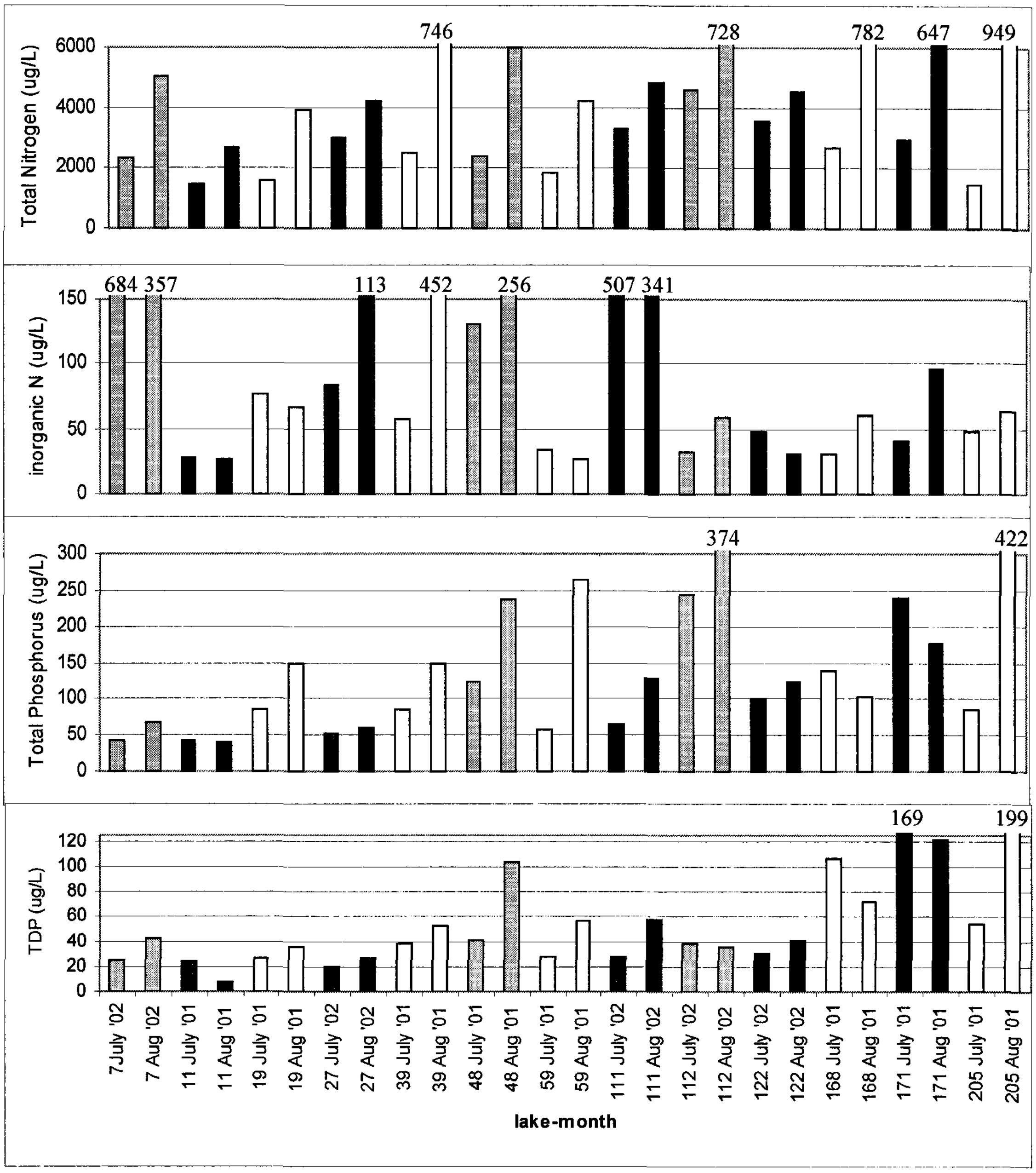

Fig. A2.1: Variance of nutrient conditions between months. Shows the variability in some of the key nutrient measures between months during the same year. Twenty-six lake months are shown representing 31% and 47% of lake-months used in Chapter 2 and Chapter 3 analyses respectively.

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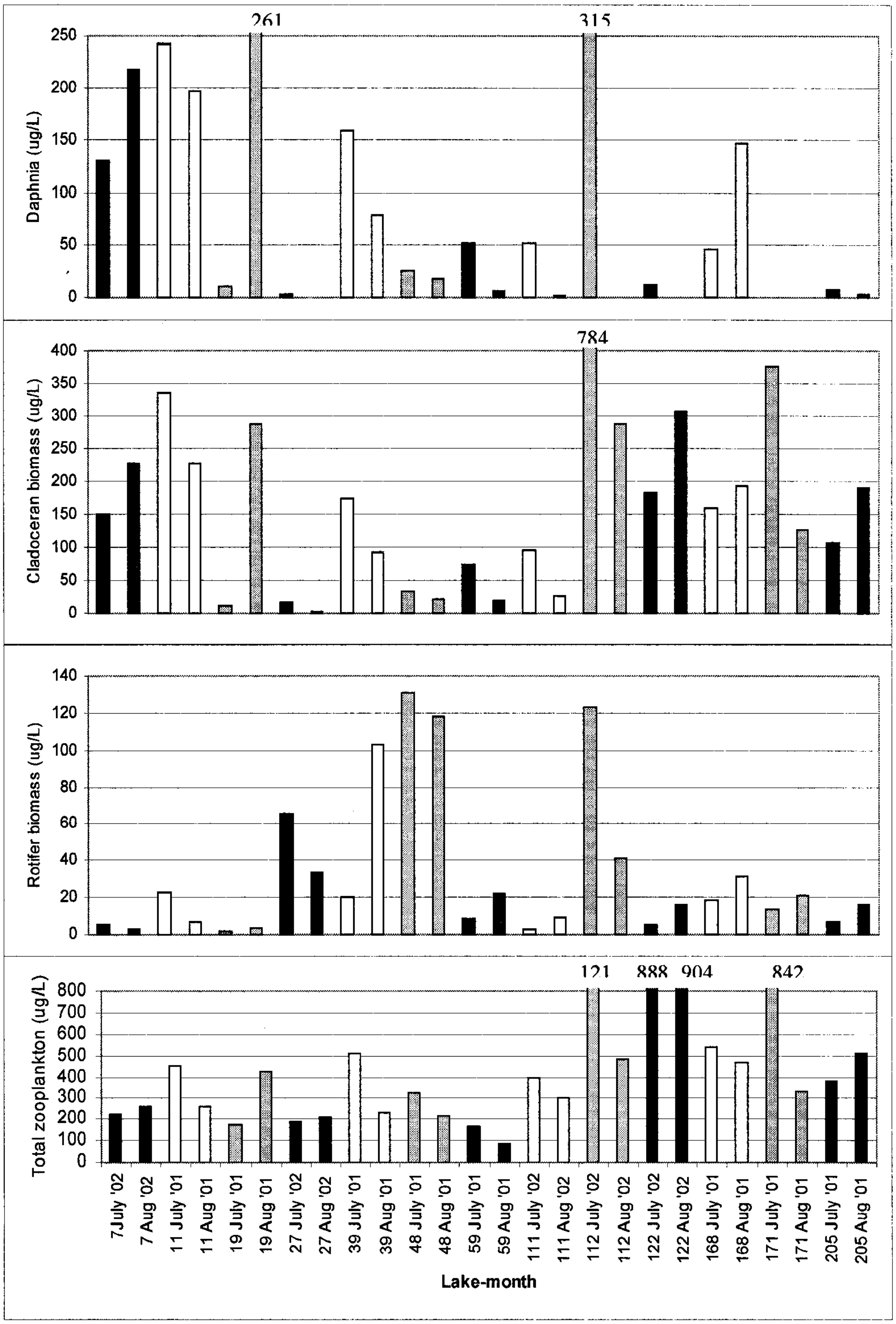

Fig. A2.2: Variance in zooplankton densities between months. Shows the variability in zooplankton between months during the same year. Twenty-six lake months are shown representing 31% and 47% of lake-months used in Chapter 2 and Chapter 3 analyses respectively.

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Appendix 3: Environmental factors included in CART analysis

Abiotic Variables		
Name	**Unit of Measure**	**Transform**
Average Depth	cm	None
Conductivity	mS/cm	None
Dissolved Organic Carbon	µg/L	None
Inorganic Nitrogen (NO_3+NH_4)	µg/L	ln
Maximum Depth	cm	None
pH	pH units	None
Salinity	mg/L	None
Submerged Vegetation	% cover	None
Total Dissolved Phosphorus	µg/L	ln
Total Nitrogen	µg/L	None
Total Nitrogen:Phosphorus	None	ln
Total Phosphorus	µg/L	ln
Phytoplankton		
Aphanizomenon bloom	Presence/absence	None
Bacillariophyta	Cells/ml	ln(x+1)
Chlorophyta-CELLS	Cells/ml	ln(x+1)
Chlorophyta-COLONY	Cells/ml	ln(x+1)
Chlorophyta-FILAMENT	Cells/ml	ln(x+1)
Chroococcales	Cells/ml	ln(x+1)
Chroococcales-COLONY	Cells/ml	ln(x+1)
Chroococcales-large Colony	Cells/ml	ln(x+1)
Chrysophyceae	Cells/ml	ln(x+1)
Cryptophyceae	Cells/ml	ln(x+1)
Dinophyta	Cells/ml	ln(x+1)
Euglenophyceae	Cells/ml	ln(x+1)
Microcystis	Cells/ml	ln(x+1)
Nostocales	Cells/ml	ln(x+1)
Oscillatoriales	Cells/ml	ln(x+1)
Predators		
Anisoptera	mg/sampling	ln(x+1)
Chaoborus sp.	mg/L	ln(x+1)
Corixidae	mg/sampling	ln(x+1)
Dytiscidae	mg/sampling	ln(x+1)
Culea inconstans	Fish/trap/night (CPUE)	ln(x+1)
Gammarus lacustris	mg/sampling	ln(x+1)
Gerridae	mg/sampling	ln(x+1)
Gyrinidae	mg/sampling	ln(x+1)
Hyalella azteca	mg/sampling	ln(x+1)
Hirudinea	mg/sampling	ln(x+1)
Hydrophilidae	mg/sampling	ln(x+1)
Arachnida	mg/L	ln(x+1)
Total Predators	mg/sampling	ln(x+1)
Zygoptera	mg/sampling	ln(x+1)
Macrophyte species		
Alisma gramineum	% of total biomass	ln(x+1)
Ceratophyllum demersum	% of total biomass	ln(x+1)
Chara sp.	% of total biomass	ln(x+1)
Myriophyllum exalbescens	% of total biomass	ln(x+1)
Potamogeton pectinatus	% of total biomass	ln(x+1)
P. praelongus	% of total biomass	ln(x+1)
P. pusillus	% of total biomass	ln(x+1)
P. richardsonii	% of total biomass	ln(x+1)
P. vaginatus	% of total biomass	ln(x+1)
P. zoteriformis	% of total biomass	ln(x+1)

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