University of Alberta

Fish assemblages and their influence on waterfowl of shallow lakes in the Boreal Plains Ecozone in Alberta

by

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Abstract

Shallow lakes in the Boreal Plains Ecozone of Alberta, Canada are naturally productive systems that provide important breeding and moulting habitat for waterfowl. Many lakes also support fish, which can compete with waterfowl for macroinvertebrate food resources. To examine fish assemblages and their influence on waterfowl density, species richness, and community composition, I studied 63 lakes in this ecozone. Lakes were classified into 3 groups based on fish assemblage; fishless lakes, lakes with only small-bodied fish and lakes with large-bodied fish. Fish assemblage was best discriminated by lake depth, dissolved organic carbon, total phosphorus and total nitrogen, environmental parameters that influence hypoxic conditions that lead to fish kills. Waterfowl density was greatest in shallow, productive and fishless lakes. Environmental characteristics were more important determinants of waterfowl density and composition than were fish. Fish assemblage contributed independently to a small but significant proportion of the variation in breeding waterfowl, and certain waterfowl species were linked to a specific fish assemblage group.

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Chapter 1

Introduction

Shallow lakes are important aquatic systems that provide habitat for a variety of wildlife species. Fish and waterfowl are two important groups of vertebrates in aquatic systems and both fishing and waterfowl hunting are important economic and social activities in many regions of North America. However, loss and degradation of shallow lake and wetland systems across North America are major conservation concerns (Melinchuk 1995). Understanding the dynamic interactions between fish and waterfowl is essential for effective conservation and management of both groups.

The fish assemblage in a given lake is the product of continental, regional, lake type, and local filters that act in series (Tonn 1990). In North America, piscivory and a small number of abiotic factors, including maximum depth, area, and isolation, have been found to be most important to fish assemblage structure in small lakes (Tonn and Magnuson 1982, Robinson and Tonn 1989). In turn, fish assemblage can play an important role in shaping the ecology of shallow lakes through top down processes and can influence clear-turbid trophic state dynamics (Scheffer et al. 1993, 2001, Hanson and Butler 1994) thereby influencing many other taxa including zooplankton (Romo et al. 2004, Norlin et al. 2005), macroinvertebrates (Zimmer et al. 2001, 2002, Hornung and Foote 2006), and waterfowl (Hanson and Butler 1994). Nearly all wildlife habitat and aspects of native plant biodiversity that humans value are favoured by the clear trophic state (Norris 2006) and many efforts to improve poor lake conditions by reducing nutrient loads have failed due to a lack of consideration of the fish assemblages present and their influence on clear-turbid state dynamics (Jeppesen et al. 2007). It is therefore essential to understand the regional fish assemblages, factors associated with fish assemblages and how they relate to clear-turbid state dynamics to successfully manage these aquatic systems. Furthermore, climate change and other anthropogenic disturbances can impact fish assemblage structure by increasing water temperature (Matulla et al. 2007), storm induced habitat change (Han et al. 2007), drought frequency and duration (Magalhaes et al. 2007), and decreasing water quality (Danz et al. 2007). Conservation of environmental conditions most important to fish assemblage type will help mitigate negative effects of climate change and other anthropogenic disturbances on fish and their aquatic habitat.

Fish can directly or indirectly influence waterfowl. Fish can compete with waterfowl for macroinvertebrate prey (Eadie and Keast 1982, DesGranges and Rodrigue 1986, Giles 1994, Strand et al. 2008) and fish presence in shallow lakes has been linked to decreased use by waterfowl (Eadie and Keast 1982, Giles 1994, Hanson and Butler 1994, Norris 2006) and declines in reproductive success for many species of waterfowl (DesGranges and Rodrigue 1986, Mallory et al. 1994, Cox et al. 1998). Decreased availability of amphipods for lesser scaup (*Aythya affinis*), a species experiencing significant continental decline (Anteau and Afton 2004), has been linked to size-selective predation of amphipods by fishes (Strand et al. 2008). Brook stickleback (*Culea inconstans*) presence can alter foraging patterns in Blue-winged Teal (*Anas discors*) (McParland and Paszkowski 2006), indicating that fish can also influence behavioural patterns in waterfowl. By increasing turbidity, fish can have indirect negative effects on submerged aquatic vegetation and macroinvertebrate resources, critical aspects of waterfowl habitat (Giles 1994, Hanson and Butler 1994, Zimmer et al. 2002). Increased fish rearing in shallow lakes in Minnesota resulted in decreased habitat quality for waterfowl (Norris 2006). Continued continent-wide habitat loss poses a major threat to waterfowl and competing demands for remaining wetlands and lakes requires that careful conservation planning and management be employed that incorporates the direct and indirect connections between fish and waterfowl.

The southern portion of the Boreal Plains Ecozone, more commonly referred to as the Boreal Transition Zone (BTZ), is characterized by mixedwood forests, shrub and grassland habitats, shallow lakes, and wetland complexes (Ducks Unlimited Canada 2004). Encompassing proportionately more total wetland area than either the prairie or parkland ecozones (Ducks Unlimited Canada 2004), the BTZ provides important breeding and moulting habitat for many species of waterfowl. More than 4.1 million breeding ducks use the BTZ annually (Ducks Unlimited Canada 2004). Industrial activities, including forestry, extraction of oil, gas, minerals and peat, agriculture, recreational and residential development, have drastically increased in the BTZ and this growth threatens the quality and abundance of wetlands and shallow lakes (Ducks Unlimited Canada 2004). In addition to many historical projects in the BTZ, Ducks Unlimited Canada (DUC) has recently undertaken a large number of projects in the region managed under the North American Waterfowl Management Plan (NAWMP). Given the potential for competition between waterfowl and fish and the influence that fish can have on shallow lake condition, understanding the relationship between the two taxa is important for selection of priority habitat for waterfowl.

To examine the fish assemblages in shallow BTZ lakes and their influence on waterfowl, I studied the fish, waterfowl, and environmental characteristics of 63 shallow lakes during the summers of 2006 and 2007. In chapter 2, I examine the relationship between fish, nutrients and agricultural development, to assess the factors most important to fish assemblage structure. Chapter 3 addresses the influence of fish assemblage on waterfowl species richness, densities, and community composition and the relative importance of biotic and abiotic factors to waterfowl. Chapter 4 provides general conclusions and suggests directions for future research.

The results of this project will contribute to current DUC wetland-waterfowl modeling initiatives and will help guide priority habitat for waterfowl conservation. By doing so, this project will contribute to the fulfillment of two key strategic directions for DUC in the BTZ region: retention of key natural habitats and delivery of enhancement activities that result in land use change for improved waterfowl habitat (Ducks Unlimited Canada 2004). Furthermore this project complements related research initiatives in the BTZ region on the relationships between waterfowl, lake and landscape characteristics (Dr. S. Bayley, University of Alberta and Dr. J. Thompson, Ducks Unlimited Canada) and the factors governing turbid and clear states in BTZ shallow lakes. Increased understanding of fish assemblages, the factors related to their structure and their influence on waterfowl in the BTZ is essential to management of these important aquatic systems.

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Chapter 2

Fish assemblages of shallow lakes in the southern Boreal Plains Ecozone in Alberta

2.1 Introduction

Numerous studies on fish communities indicate that lakes of a region support a small number of fish assemblage types rather than random sets of the regional species pool (Tonn and Magnuson 1982, Robinson and Tonn 1989, Jackson et al. 1992, Jackson et al. 2001, Mehner et al. 2005). Tonn (1990) proposed that the fish assemblage present in a given lake is the product of a series of filters acting at a particular spatial and temporal scale. The structure of a fish assemblage in a given lake is determined by evolutionary and geological factors (continental filters), climate, geomorphology, and dispersal barriers (regional filters), general limnology, distribution of resources and species-limiting biotic interactions (lake type filters), and disturbance, isolation and biotic interactions (local filters). These filters act in a hierarchical manner; for an individual lake, only fish species that have made it past continental, regional and lake type filters will be in the species pool on which local filters act. Therefore, the spatial and temporal scale examined will influence which biotic and abiotic factors are most important to fish (Jackson et al. 2001).

In North America, pisciviory and a small number of abiotic factors, including maximum depth, area and isolation, have often been found to be important to fish assemblage structure (Tonn and Magnuson 1982, Eadie and Keast 1984, Robinson and Tonn 1989). Piscivores such as northern pike (*Esox lucius*) can significantly reduce (Findlay et al. 2000) and even exclude minnow populations (Robinson and Tonn 1989) that cannot outgrow the size limitations of their predators nor possess antipredator devices such as spines (Tonn and Magnuson 1982). Robinson and Tonn (1989) found a nearly perfect negative association between component species of fathead minnow (*Pimephales promelas*)/brook stickleback (*Culea inconstans*) assemblages and those of northern pike/yellow perch (*Perca flavescens*) assemblages in boreal Albertan lakes. Small-bodied fish species are generally more tolerant of low oxygen levels than large-bodied fishes (Robb and Abrahams 2003). Hypoxic (low oxygen) conditions are frequent in winter in small northern lakes and this can result in the loss of an entire fish population from a lake by winterkill (Danylchuk and Tonn, 2003). Thus low winter oxygen levels are a major determinant of fish assemblage type (Tonn and Magnuson 1982). Deep lakes or those with significant inflows possess oxygen-rich water that can support large-bodied fishes, including piscivores, that are less tolerant of low oxygen conditions. Low winter oxygen in nutrient rich shallow lakes can exclude large-bodied fish and allow more tolerant minnow species to be released from predation pressure. Repopulation of fish to lakes after winterkill events is dependent on hydrologic connections to other aquatic environments with fish populations. Hence, a lake's isolation or connection to a regional hydrological system can thus also be an important factor determining fish assemblage composition (Tonn and Magnuson 1982, Conlon 2002).

Fish play a particularly important role in shaping the ecology of shallow lakes through top-down processes (Zimmer et al. 2001, Romo et al. 2004, Hanson et al. 2005). Numerous studies in diverse regions have documented reductions in zooplankton biomass (Moss et al. 2004, Romo et al. 2004, Stephen et al. 2004) and changes in zooplankton community composition by planktivorous fish (Stephen et al. 2004, Vakkilainen et al. 2004, Norlin et al. 2005). Reduction of grazing zooplankton by planktivorous fish can lead to increases in phytoplankton (Findlay et al. 2004, Romo et al. 2004) and a turbid algal dominated state (Hanson et al. 2005) through trophic cascade mechanisms (Carpenter et al. 1985). Biomanipulation of lakes has taken advantage of these relations either through the removal of planktivorous fish or the addition of piscivorous fish to reduce predation on grazing zooplankton, reduce algal biomass and return systems to a clear and desirable state (Hanson and Butler 1994) with increased invertebrate abundance and increased waterfowl use of wetlands (Hanson and Butler 1994).

The southern portion of the Boreal Plains Ecozone in Alberta, more commonly referred to as the Boreal Transition Zone (BTZ), is characterized by mixedwood forests, shrub and grassland habitats, shallow lakes, and wetland complexes (Ducks Unlimited Canada 2004). The area is experiencing rapid increases in agricultural, commercial, and residential development (Ducks Unlimited Canada 2004). Shallow lakes in the BTZ region are important for wildlife and support an abundance of waterfowl, waterbirds, and invertebrates. BTZ lakes are naturally nutrient rich (Prepas 1983) and many lakes in the region are turbid. Factors governing turbid and clear states in the region are being examined in a related project by Dr. S. Bayley (University of Alberta). Recreational fishing occurs in lakes that support northern pike and walleye (*Sander vitreus)* populations and in a number of lakes in the region that are stocked with rainbow trout (*Oncorhynchus mykiss*). Many lakes in the area are thought to be fishless or to contain minnow or stickleback species only. To date, however, few fish communities in the BTZ have been examined and the factors related to different fish assemblages have not yet been identified. The objective of this study was to examine the relationship between fish assemblages and the environment in the BTZ and how fish assemblages may be affected by a changing land use regime. I studied a total of 63 shallow lakes in the BTZ of Alberta to determine the fish assemblages that exist in the region, the environmental parameters that are most related to fish community structure, and specifically how nutrient concentrations and agricultural activity in the landscape affect fish assemblages.

I hypothesized that in the BTZ, fish assemblages would be similar to those found in the boreal region of Alberta (Robinson and Tonn 1989, Conlon 2002); many lakes would be fishless, that a second group of lakes would have brook stickleback and fathead minnow species only and that a third group of lakes would be characterized by northern pike presence in combination with other large-bodied fish species. Because winterkill is an important factor determining fish assemblages in northern lakes (Tonn and Magnuson 1982, Robinson and Tonn 1989), I hypothesized that depth and connectivity would be the most important parameters determining fish community structure. Because high nutrient loads to lakes, including those related to agriculture and lakeshore development, can increase winter oxygen depletion (Babin and Prepas 1985), I hypothesized that the number of fishless lakes would increase with increased agricultural development surrounding the lakes.

2.2 Methods

2.2.1 Description of study sites

The study lakes are located in the BTZ of central Alberta, Canada (53°5'N, 112°4'W to 56°7'N, 119°7'W) and distributed among four sub-regions near the communities of Grande Prairie (11 lakes), Grimshaw (4 lakes), Barrhead (16 lakes) and Athabasca (32 lakes) (Figure 2.1). The surrounding landscape is a mixture of mixedwood forest and agricultural lands used for pasture and hay production. The study lakes are shallow, alkaline, and naturally eutrophic, with mean total phosphorus concentrations of 330.21 μg/L (median 186.05 μg/L, August 2006 sampling) (Table 2.1). The study lakes have abundant submerged aquatic vegetation and many are surrounded by a fringe of emergent marsh vegetation. Typical for the region, the study lakes have few if any permanent inlet or outlet streams and connectivity to the regional drainage system is low. Annual precipitation in 2006 ranged from 414.8 mm (Grande Prairie weather station) to 482.3 mm (Athabasca weather station), with most of it falling between May and August (Environment Canada 2007). The study lakes were selected from a cohort of 125 lakes sampled in 2005 by Dr. S. Bayley (University of Alberta) and Dr. J. Thompson (Ducks Unlimited Canada), who are examining relationships among waterfowl, lake, and landscape characteristics. The study lakes were selected to establish gradients in waterfowl density, lake depth, lake area, and agricultural development surrounding the lake.

2.2.2. Sampling methods

Fish

The fish assemblages in 28 study lakes were sampled from May-August 2006. Fish were sampled using a combination of minnow traps, gill nets, and fyke nets. Fish sampling was based on the protocol described by Tonn et al. (2003), an Alberta based modification of the Nordic survey protocol (Nyberg and Degerman 1988). Eighteen unbaited Gee minnow traps were set on each of two subsequent nights at random locations on all lakes to establish fish presence and to sample small-bodied fishes. Lakes where small-bodied fish were present were sampled further with either fyke or gill nets to assess the presence and identify the large-bodied fishes. Lakes where no fish were caught in minnow traps were considered fishless and were not sampled further. Even though northern pike can survive in lakes without forage fish (Venturelli and Tonn 2006), the maximum depth in all fishless lakes sampled was well under 6 m, the depth determined by Conlon (2002) as the minimum maximum depth necessary to support northern pike in the boreal regions of Alberta. Therefore, I considered it reasonable to deem shallow lakes without any small-bodied species as being fishless. Fyke nets were used on nine lakes where gill netting was not permitted, or considered inappropriate or one of the following reasons:

1) lakes were stocked with rainbow trout

2) lakes were breeding sites for trumpeter swan (*Cygnus buccinator)*

3) lakes contained very high densities of nesting waterfowl and waterbirds (*Gaviidae* and *Podicipedidae*).

Multi mesh survey gill nets were used on all fish-bearing lakes other than those in the above 3 categories. Gill nets were 30 m by 1.5 m and mesh size ranged from 5 mm to 55mm. A comparison of catchability between fyke nets and gill nets was done on lake

190. All fish caught were identified and enumerated. Fork length, total length, and fish mass were measured for subsets of 150 fish (length) and 50 fish (mass). Length–mass regressions and length-frequency distributions for each lake were used to determine the mass of the remaining fish. If less than 150 individuals of a species were caught on a lake, all fish caught were measured. All fish caught in one gear unit (one minnow trap, one gill net) were measured to avoid non-random picking of fish for length and mass measurements. For example, if mass measurements were begun on fish in a minnow trap containing more than fifty fathead minnows, mass measurements were carried out on all fathead minnows in that minnow trap. Data on the presence-absence of fish species for two additional lakes was obtained from Earle (2007) (lake 448) and McGregor (2003) (lake 43) and used in all analyses that used species presence - absence data. Water quality and lake landscape data for these two lakes were also collected in 2006.

During the 2006 sampling, I also obtained water quality and lake landscape data from a second set of 33 lakes. Data on fish occurrence in these lakes were obtained in June 2007 by setting 10 Gee minnow traps overnight in each lake. Data from these additional 33 lakes were included in the analyses to examine whether total phosphorus, total nitrogen, maximum depth, trophic state, chlorophyll a and percentage agriculture differed among fish assemblages. Because no quantitative fish data were collected, these lakes were not used in ordination and CART analyses. Of these 33 lakes, 28 were fishless and 5 lakes contained fathead minnow and/or brook stickleback species. Although unbalanced, this distribution of fish assemblages was not surprising, given the characteristics of the lakes. In particular, the fishless lakes in this set were exceptionally shallow (mean maximum depth = 112.1 cm; compared to fishless lakes sampled in 2006 mean maximum depth = 173.8 cm). Even the small-bodied fish lakes sampled in 2007 were very shallow (mean maximum depth = 124.3 cm) compared to the mean maximum depth of small-bodied fish lakes sampled in 2006 (312.9 cm).

Given the shallow depths of the 2007 set of lakes, it was not surprising that the majority of these lakes were fishless and that large-bodied fish species were absent. Shallow lakes in northern Alberta have winter ice depths ranging from 0.5 to 0.7 m (Bayley et al. 2007). These ice levels and shallow depths are associated with winter anoxia, fish winterkills and mostly fishless lakes (Conlon 2002, Danylchuk and Tonn 2003). Furthermore, given the isolation and lack of connectivity of the shallow lakes and because the probability of local fish species extinction in such lakes is expected to be higher than the probability of a new species arriving Magnuson et al. (1998), it was unlikely that small-bodied fish would have colonized the lakes in 2007 and resulted in a different fish assemblage between 2006 and 2007. Finally, the fish species present in lake 448 during the 2007 sampling were in agreement with the more thorough sampling by Earle (2007). Hence, I believe it appropriate to include the 33 additional sites in the data set, despite the fact that fish status was established a year after the environmental parameters were collected.

Environmental Parameters

I measured or calculated a total of 35 environmental parameters for all study lakes. Water samples were collected from study lakes in both May and August and analysed in the University of Alberta Biogeochemistry lab using techniques described in Bayley and Prather (2003) to determine 23 water quality parameters; dissolved oxygen [DO], turbidity, total phosphorus [TP], total dissolved phosphorus [TDP], soluble reactive phosphorus [SRP], total nitrogen [TN], ammonium nitrogen [$NH4^+$], total dissolved nitrogen [TDN], nitrite +nitrate [NO_2^- +NO_3^-], sodium [Na^+], chloride [Cl^-], sulphate [SO_4^-], dissolved organic carbon (DOC), magnesium [Mg^{2+}], silicon [Si], potassium [K^+], calcium [Ca^{2+}], carbonate, bicarbonate, alkalinity, chlorophyll *a*, color, and total dissolved solids (TDS). Specific conductivity and pH and were measured in the field using a Hydrolab MiniSonde 5. Estimated cover and density of submersed aquatic vegetation (SAV) were determined based on Bayley and Prather (2003). Visual assesment (Bayley et al. 2007) was used to designate each lake as either "clear" or "turbid". Maximum depth for each lake was estimated from a minimum of 25 depth soundings along 2-5 transects measured with a calibrated weighted rope at the time of fish sampling. Secchi depth was measured in the field at the time of water chemistry sampling. Area and perimeter were calculated by DUC using digital versions of the National Topographic Survey Maps (NTS) (1:50,000 scale) and DUC's Landsat-based habitat inventory for sites that did not appear on the NTS maps. The percentage of agricultural development in the 1.6 km radius surrounding the wetland lake was calculated from Prairie Farm Rehabilitation Administration (PFRA) data (Agriculture and Agri-food Canada 1995). These data were verified using aerial photos of the study lakes taken during the 2006 and 2007 waterfowl surveys.

Two landscape level metrics of surface water connections, lake isolation and connectivity as defined by Conlon (2002), were evaluated from aerial photos (1:20,000 or 1:30,000) and verified using maps (1:70,0000-1:100,000) and field notes. I created a third metric; modified lake connectivity, an extension of Conlon's 2002 connectivity metric. Lakes were assigned to 4 categories based on their connectivity to the regional drainage system: those with permanent inlets and outlets, those with intermittent connections, those connected to isolated wetland complexes, those with neither inlets nor outlets.

2.2.3 Statistical analysis:

Identification of fish assemblages in BTZ lakes

To identify lake types based on fish assemblages that existed in the study lakes, I used Non-metric Multi-dimensional Scaling (NMS, PC-ORD v 5.0). NMS is an ordination technique well suited to ecological community data and does not assume linear relationships among variables (McCune and Grace 2002). NMS was performed on fish count data from 13 shallow lakes where fish were present and count data was available. Fishless shallow lakes were considered one lake type and were not included in this analysis. Three fish species walleye (*Sander vitreus*), spottail shiner (*Notropis hudsonius*) and iowa darter (*Etheostoma exile*) were each present in one lake only and these species were removed from the analysis. Average fish counts/trap/hour for each species for each lake were relativized using the general relativization (PC-ORD v 5.0) by species. Relativization of fish counts was necessary to account for different gear types. Brook stickleback, fathead minnows, and yellow perch counts were all based on sampling from minnow traps, while northern pike and cisco (*Coregonus artedi*) counts were based on sampling from gill nets, and rainbow trout counts were based on sampling from fyke nets. Thus, the relativized count for each species is a proportion of the total count for that species across all lakes using one gear type. NMS was run in auto pilot mode using the Sorenson distance measure, a random starting configuration, 250 runs with real data, 250 runs with randomized data. Final stability was defined as $1x10^{-7}$ standard deviations over the last 15 iterations. Dimensionality was determined by comparing the final stress values of the best solution for each dimensionality. Associations between fish community and environmental characteristics for both May and August sampling periods were examined using graphical joint plots and overlays of the NMS analysis. All quantitative environmental variables except pH were log(x+1) transformed prior to analysis.

Environmental differences between fish assemblages

Multi-Response Permutation Procedures (MRPP, PC-ORD v 5.0), a non-parametric multivariate procedure for testing differences among groups, was used to evaluate whether lake environmental characteristics differed between different fish assemblages; fishless, small bodied-fish, and large-bodied fish lakes. MRPP was performed using Bray–Curtis/Sorenson distance measure. Environmental data from August was used in the analysis and all quantitative environmental variables except pH were log(x+1) transformed prior to analysis. The analysis was performed using the original 30 lake dataset and the full 63 lake dataset. However, because environmental data was not available for two lakes that dried up in August, the analyses were run with n=28 and n=61.

I used non-parametric Kruskal-Wallis tests and subsequent Mann-Whitney tests for pair-wise comparisons to further examine how environmental variables of interest, trophic state, total phosphorus, total nitrogen, maximum lake depth, chlorophyll a, and the percentage of agricultural development in the surrounding landscape, differed among the different fish assemblages (SPSS v.14). August 2006 environmental data from 61 lakes were analysed because August sampling was considered to best represent overall variation in wetland lake environment characteristics. In shallow lakes in Alberta, both vegetative state and zooplankton abundance are reset each spring and by late summer distinct environmental conditions and clear and turbid states are present (Bayley et al. 2007). Non-parametric tests were used since data did not meet assumptions of normality and homogeneous variance even after transformations. The Benjamini-Hochberg method for controlling False Discovery Rate was used to account for multiple comparisons (Roback and Askins 2004, Waite and Campbell 2006).

The environmental characteristics that best discriminated fishless shallow lakes, small-bodied fish lakes and large-bodied fish lakes were evaluated by non-parametric Classification and Regression Trees (CART) modeling techniques, which are suitable for complex ecological data that contain non-linear relationships, interactions, and missing values (De'ath and Fabricius 2000, Urban 2002). CART models use a recursive approach whereby data is repeatedly split into more homogeneous groups using combinations of explanatory variables (De'ath and Fabricius 2000, Urban 2002). To evaluate which May environmental parameters were most associated with each fish assemblage, seven environmental variables that were both highly correlated with fish assemblages (r^2>0.3) in NMS ordination joint plots and were considered biologically meaningful were selected for inclusion as explanatory variables in the CART model; total nitrogen, total phosphorus, secchi depth, chlorophyll *a*, maximum depth, region, and dissolved organic carbon. For analysis of August environmental data, total nitrogen, total phosphorus, secchi depth, chlorophyll *a*, maximum depth, region, dissolved organic carbon, and turbidity were selected. The number of explanatory variables was reduced to minimize model overfitting and avoid selecting biologically unmeaningful variables as important because they are statistically correlated with other variables. The original thirty study lakes sampled in 2006 were grouped by the response variable fish assemblage; fishless lakes, small-bodied fish lakes, or large-bodied fish lakes. In May, n=30, and August, n=28, because August environmental data were not available for two lakes that dried up. These data sets were selected because environmental data from both May and August were available for analysis. Optimal CART model size was based on cost-complexity pruning and CART model validity was evaluated by misclassification rates based on jack-knifing. CART models were run in S-PLUS 7.0 for windows using the S-PLUS tree (tree) and 10-fold cross-validation (cv.tree) functions.

2.3 Results

Overall, nine fish species were found in the sixty-three study lakes (Table 2.2). Over half of the study lakes were fishless. Eight lakes contained brook stickleback only, seven lakes contained brook stickleback and fathead minnows. Three lakes contained northern pike together with other large-bodied fish species, such as cisco, yellow perch and walleye and small-bodied fish species spottail shiner and Iowa darter. In one of these lakes, lake 43, northern pike coexisted with brook stickleback and fathead minnow. Because count data were not available for lake 43, it was not included in NMS analyses. Two lakes contained rainbow trout together with combinations of yellow perch, brook stickleback and fathead minnow. Overall fish species diversity was low, with an average 2.2 species per lake where fish were present.

2.3.1 Fish assemblage structure

NMS ordination accounted for 78.8% of the variation in fish community structure (32.5%. Axis 1, 19.2% Axis 2, 27.1% Axis 3) based on 148 iterations with a final stress of 5.03 (Figure 2.2). Lakes with northern pike and those with rainbow trout were separated by axes 1 and 3 from lakes with brook stickleback only and those with brook stickleback and fathead minnows. Axis 3 also distinguished lakes with brook stickleback only from lakes with both fathead minnow and brook stickleback. Axis two (not shown) separated lakes with northern pike from all other lakes. Lakes with either northern pike or rainbow trout were grouped together as large-bodied fish lakes. Lakes with brook stickleback only or brook stickleback and fathead minnow were grouped together as small-bodied fish lakes. Patterns in fish assemblage structure revealed by NMS were consistent with those from preliminary agglomerative clustering analyses.

2.3.2 Environmental differences between fish assemblages

May maximum depth (Zmax), secchi depth, and the Athabasca region were positively correlated ($r^2 > 0.30$) with the presence of large-bodied fish based on the NMS joint plot analysis (Figure 2.3). Total nitrogen, total phosphorus, chlorophyll *a*, color, DOC and turbidity are negatively correlated with the presence of large-bodied fish and positively correlated with the presence of small-bodied fish only. Using August environmental parameters in the joint plot gave very similar results (Figure 2.4): maximum depth (Zmax), secchi depth, and the Athabasca region were positively correlated ($r^2 > 0.30$) with the presence of large-bodied fish and negatively correlated with the presence of small-bodied fish only. Total nitrogen, total phosphorus, total dissolved nitrogen, and ammonium were negatively correlated with the presence of large-bodied fish presence and positively correlated with the presence of small-bodied fish only. DOC was correlated with brook stickleback presence.

MRPP analyses and subsequent pairwise comparisons demonstrated that the environmental characteristics differed between fishless lakes, small-bodied fish lakes, and large-bodied fish lakes using both the original 30 lake and the expanded 63 lake datasets. Environmental differences between fish assemblages, based on August sampling data, were significant ($p<0.01$, MRPP test statistic $T=-10.88$, $A= 0.130$, $n= 62$), ($p<0.01$ MRPP test statistic $T=-5.95$, $A= 0.085$, $n= 30$). All pairwise comparisons differed in environmental characteristics ($p< 0.01$) except the 30-lake small-bodied fish lakes vs. large-bodied fish lakes, $p=0.02$.

Total phosphorus, total nitrogen, and maximum depth differed among fish assemblages ($p<0.01$). There were no differences in chlorophyll *a* concentration ($p=0.70$), or the percentage of agriculture in a 1.6 km radius surrounding the study lake ($p=0.13$) among fish assemblages. Although a greater percentage of fishless lakes were clear compared to small-bodied fish lakes, the difference was not significant ($p=0.12$) (Table 2.3). Subsequent pair-wise comparisons revealed that total nitrogen was significantly greater in fishless lakes than in either small-bodied fish lakes or large-bodied fish lakes. Total nitrogen was greater in small-bodied fish lakes than large-bodied fish lakes (Figure 2.5a). Total phosphorus was lower in large-bodied fish lakes than in either fishless or small-bodied fish lakes; the latter two groups did not differ (Figure 2.5b). Maximum depth was greater in large-bodied fish lakes than in either fishless or small-bodied fish lakes, and greater in small-bodied fish lakes than fishless lakes (Figure 2.5c).

CART modeling techniques were used to investigate environmental differences among fish assemblages and to determine which environmental characteristics best distinguished the fish assemblages. Cost-complexity pruning and boostrap analyses indicated that a 3 node model was best using both May and August environmental data. Using May data, lake depth was the most important variable discriminating the 3 fish assemblages (Figure 2.6). Lake depths greater than 6.14 m discriminated large-bodied fish lakes whereas lakes under 6.14 m in depth were either fishless lakes or small-bodied fish lakes. Subsequently, DOC greater than 29.6 mg/L best discriminated fishless lakes from small-bodied fish lakes. Overall misclassification rate for this model was 5/30 or 16.6 % and model residual mean deviance was 22.62/27 or 0.84.

Using August environmental data, total nitrogen was the most important variable distinguishing fish assemblage (Figure 2.7). Total nitrogen concentration above 3340 μg/L discriminated fishless lakes from the other two lake types. Similar to May analyses, lake depth in excess of 5.20 m best discriminated large-bodied fish shallow lakes from small-bodied fish shallow lakes. The overall misclassification rate for the model was 3/28 or 10.7% and the model residual mean deviance was 12.46/24 or 0.52.

2.4 Discussion

2.4.1 Fish assemblages in BTZ lakes

In addition to shallow fishless lakes, which represent the majority of lakes sampled, two distinct fish assemblages were identified, characterized by small-bodied fishes and large-bodied fishes, respectively. These assemblages are similar to those identified in the boreal region of Alberta (Robinson and Tonn 1989, Paszkowski and Tonn 2000, Tonn et al. 2003), and in Wisconsin (Tonn and Magnuson 1982) and are consistent with work in other regions that indicate a small number of fish assemblages in lakes rather than random sets of regional species (Jackson et al. 1992, 2001, Mehner et al.

2005). Similar to other studies in Alberta (e.g. Robinson and Tonn 1989), my study lakes had an overall low diversity of fish species (mean 2.2 species/lake). The low fish species diversity in Alberta has been attributed to its isolation from major glacial refugia and the severe conditions of the region (e.g., low oxygen during winter) (Robinson and Tonn 1989).

2.4.2 Important processes structuring fish assemblages in the BTZ

Maximum depth was, as predicted, the most important factor distinguishing large-bodied fish lakes from other assemblages. This is consistent with other findings in both North America (Paszkowski and Tonn 2000) and Europe (Mehner et al. 2005). Because shallow lakes will experience a proportionately greater winter oxygen depletion than deeper lakes (Welch et al. 1976, Barica and Mathias 1979), shallow lakes will tend to exclude large-bodied fish that are physiologically less tolerant of low oxygen (Robb and Abrahams 2003) than minnows and sticklebacks. The maximum depth thresholds identified by CART modeling to distinguish large-bodied fish lakes from small-bodied fish lakes (6.14 m using May data and 5.20 m using August data) were very similar to Conlon's (2002) 6 m depth threshold for 102 boreal lakes, above which piscivore presence was predicted. Conlon (2002) also found significant overlap between piscivore lakes and cyprinid only lakes where maximum depth ranged from 3 to 6 m and suggested that winterkill is highly variable at this depth zone. There was little overlap between the two fish assemblage types in my study, but only 5 of the 63 lakes studied had a maximum depth between 3 and 6 m. Of these 5 lakes, 3 had small-bodied fish and 2 were fishless.

Similar to Robinson and Tonn (1989) and Tonn et al. (2003) my study lakes exhibited a negative association between northern pike and brook stickleback/fathead minnow assemblages. Piscivory by northern pike has been identified as a dominant process structuring fish assemblages in small lakes across North America (Tonn and Magnuson 1982, Jackson et al. 2001), often resulting in the exclusion of predation-intolerant minnow species (Robinson and Tonn 1989, Jackson et al. 1992). Piscivory and hypoxic conditions related to lake morphological features such as maximum lake depth work together to maintain distinct assemblage types. In deep lakes with northern pike, predation appears to exclude fathead minnows and sticklebacks, whereas in shallow lakes, predators such as northern pike are excluded because of intolerance to low oxygen. However, in 2 of my large-bodied fish lakes northern pike were absent, and instead, the lakes were characterized by stocked rainbow trout that coexisted with fathead minnow and brook stickleback. Piscivory by rainbow trout is limited to larger sized individuals (Haddix and Budy 2005). Thus, limited piscivory by rainbow trout may allow for coexistence with fathead minnow and brook stickleback. In BTZ lakes, rainbow trout stocked lakes are somewhat intermediate between the small-bodied fish lakes and the northern pike dominated lakes. Examining the influence of stocked rainbow trout on small-bodied fish communities was not within the scope of this study but is an important research area given the demand for sport fishing in central Alberta and the potential of rainbow trout additions to influence fish community dynamics.

Small-bodied fish lakes were significantly deeper than fishless shallow lakes. Lower oxygen levels or even freeze-out in the most shallow lakes more often than not exclude even small-bodied fish. Interestingly, however, it was increased nutrient concentrations, specifically total nitrogen or DOC, that distinguished fishless lakes from small-bodied fish lakes. DOC levels in May were highly correlated with total nitrogen, so DOC's inclusion in the final May CART model likely reflects the importance of total nitrogen. Alberta lakes tend to be nutrient rich, much more so than Wisconsin or Ontario lakes (Riley and Prepas 1984), and lakes the BTZ region had very high total phosphorus and nitrogen concentrations (Table 2.1). High nutrient concentrations in lakes can lead to increased oxygen depletion (Barica 1975, Babin and Prepas 1985) and associated fish kills; the high nutrients in many BTZ lakes combined with shallow depths, may therefore have led to reduced winter oxygen levels to levels intolerable to even minnows and sticklebacks, resulting in the high proportion of fishless lakes (68.3%). Interestingly, nutrient enrichment can also increase the recruitment of young fathead minnows by increased food availability, growth and survival (Grant and Tonn 2002). At what point is nutrient enrichment too much? This is difficult to determine since the occurrence of a winterkill event is highly variable and dependent on many factors, including lake levels and climate (Danylchuk and Tonn 2003). Furthermore, fathead minnow populations in winterkill prone lakes have also shown faster growth rates and spawned earlier in the season (Danylchuk and Tonn 2006), indicating that species living in these highly variable lakes are capable of adapting to these disturbances.

Nevertheless, because of the importance of nutrient concentrations for distinguishing fishless from fish-bearing lakes, I expected that the land use surrounding a lake would also be related to fish assemblage. This was not, however, the case, as the percentage of agriculture in the 1.6 km radius surrounding the lake did not differ among fish assemblages. Most of the agricultural land surrounding my study lakes, however, was for hay production or light pasture, land uses associated with lower nutrient loading than crop production (Harmel et al. 2006). If agriculture intensity or agricultural practices in the region change and increase nutrient loads to the lakes, the influence of agriculture on fish assemblages may increase.

Contrary to my predictions, lake isolation was not important to fish assemblage structure despite the importance of fish immigration and recolonization routes to fish assemblages in Alberta (Tonn et al. 1995, Conlon 2002,). Most of my study lakes were predominantly isolated and very few had permanent inlets or outlets. Intermittent streams may be important recolonization routes in the BTZ. Robinson and Tonn (1989) observed the recolonization of northern pike and white sucker by intermittent streams following a period of heavy rain, suggesting that intermittent streams are indeed important recolization routes for isolated lakes of Alberta. Because accurately identifying intermittent streams was difficult, this parameter may be poorly represented by the data. Still, the greater importance of maximum depth and nutrient variables, which are associated with the extinction of fish populations, compared to lake isolation and variables associated with fish recolonization is, however, consistent with Magnuson et al. (1998), who concluded that variables associated with fish extinction would generally be more important than isolation variables in predicting fish richness and composition because in small lakes, the probability of extinction is likely higher than the probability of a new species arriving. Accordingly, the fish assemblage sampled at a given point in time will reflect the stamp of extinction variables more strongly than variables associated with recolonization, such as isolation or hydrological connectivity; this was indeed the case in the BTZ study lakes.

2.4.3 Does fish presence promote the turbid trophic state?

Although fishless lakes exhibited a slightly higher percentage of clear lakes than either the small-bodied fish or large-bodied fish lakes, contrary to expectations based on alternate stable state theory (Scheffer et al. 1993, 2001), this difference was not significant. Thus, my results remain inconclusive regarding the relationship between fish presence and trophic state in naturally eutrophic shallow lakes. The high percentage of fishless lakes that were turbid was likely related to the overall high nutrient concentrations (TN and TP) in BTZ lakes. Fishless lakes had significantly higher concentrations of total nitrogen than the other two fish assemblage types and increased nitrogen in particular has been linked to the loss of submerged aquatic vegetation and the development of the turbid trophic state (Bayley and Prather 2003, James et al. 2003, Gonzalez et al. 2005). Additionally, the combination of high total phosphorus and total nitrogen concentrations may have contributed to an exceptionally high percentage of turbid lakes since water quality and biomass of submerged macrophytes have been shown to decrease more with dual nutrient (TP, TN) treatments than single nutrient treatments (Gonzalez et al. 2005). Phosphorus, often a limiting nutrient in shallow lake systems and an important determinant of the turbid state (Hargeby et al. 2007, Jeppesen et al. 2005, Bayley et al. 2007), was also extremely high in the BTZ region (median 186 µg/L, mean 330 µg/L) compared to studies in the prairie pothole region (110 µg/L mean, Zimmer et al. 2001) and in the boreal region (median 46.4 µg/L, Paszkowski and Tonn 2000; median 39.2 µg/L in clear lakes and 122.5 µg/L in turbid lakes, Bayley et al. 2007). Extremely high TP across all of my study lakes may have increased the frequency of the turbid state because high TP promotes algal growth and the turbid state (Jeppesen et al. 2005). Mean

TP in my BTZ study lakes was greater than the TP threshold for the transition between from the clear to turbid state in lakes with high SAV density (275 µg/L) (Bayley et al. 2007). The influence of high TP may have overshadowed any biotic contributions by fish to turbid state predominance. These results support other studies (e.g., Stephen et al. 2004) in suggesting that nutrient concentrations or bottom up processes are more important to clear/turbid state dynamics than biotic influences of fish particularly at very high nutrient loads. They also support Bayley et al. (2007)'s conclusion that shallow lakes in areas of harsh conditions, such as the boreal and BTZ regions of Alberta, are regulated by nutrients.

2.4.4 Conclusion:

Environmental factors that influence hypoxic conditions that lead to fish kills, including depth and nutrient concentrations, were the most important parameters influencing fish assemblages in the BTZ region of Alberta. Low fish diversity, a high number of shallow fishless lakes, and the importance of extinction-related variables reflect the hydrological isolation of BTZ lakes and the severity of the regional climate. The high proportion of turbid lakes in the BTZ was likely related to high nutrient concentrations, which minimized the relationship between trophic state and fish presence. Although the percentage of agriculture surrounding a lake did not significantly influence fish assemblage, increases in agricultural practices that increase nutrient loads to lakes may affect fish assemblages and trophic states in the future given the importance of nutrients to fish assemblages.

Table 2.1 Nine environmental characteristics of particular interest to shallow lake ecology in 61 study lakes in 2006.

Environmental Variable	Mean	Median	Maximum	Minimum
Total phosphorus (µg/L)	332.21	186.05	3605.00	12.63
Total nitrogen (µg/L)	4183.25	3535.00	12800.00	923.00
Soluble reactive phoshorus (µg/L)	163.46	19.66	3165.4	1.48
Chlorophyll *a* (µg/L)	56.63	16.84	633.98	0.37
Maximum depth (cm)	228.82	121.50	1880.00	7.00
Secchi depth (cm)	60.32	53.83	232.33	4.67
Turbidity (NTU)	14.32	2.50	229.70	0
Submerged Aquatic Vegetation *	3.72	4.00	5	1
DOC (mg/L)	45.92	43.13	127.7	1

*Submerged Aquatic Vegetation abundance described by a 1-5 scale defined in Bayley and Prather (2003)

Table 2.2 Fish species present in my study lakes in 2006

Common Name	Scientific Name	Species Code	Number of Lakes
Small bodied fish			
Fathead minnows	*Pimephales promelas*	FTMN	8
Brook stickleback	*Culea inconstans*	BRST	16
Spottail shiners	*Notropis hudsonius*	SPSH	1
Iowa Darter	*Etheostoma exile*	IWDA	1
Large bodied fish			
Northern pike	*Esox lucius*	NRPK	3
Cisco	*Coregonus artedi*	CISC	2
Rainbow trout	*Oncorhynchus mykiss*	RNTR	2
Yellow perch	*Perca flavescens*	YLPR	3
Walleye	*Sander vitreus*	WALL	1

Table 2.3 Comparisons of total nitrogen, total phosphorus, maximum depth, chlorophyll *a*, trophic state, and percentage agriculture by fish assemblage, n=61. Differences among fish assemblages were calculated for each environmental characteristic using a Kruskal-Wallis test. Pairwise comparisons between fish assemblages were made for total phosphorus, total nitrogen and maximum depth, characteristics that demonstrated significant differences among fish assemblage. Bolded p-values are significant based on Benjamini-Hochberg method for controlling the False Discovery Rate.

	TP	TN	Max Depth	State	Chl *a*	% ag
Kruskal-Wallis test for difference among fish assemblages	**.006**	**.0005**	**.0005**	.116	.695	.132
Fishless vs. small-bodied	.174	**.007**	**.004**	-	-	-
Fishless vs. large-bodied	**.001**	**.0005**	**.0005**	-	-	-
Small-bodied vs. large-bodied	**.019**	**.015**	**.0005**	-	-	-

Table 2.4a Confusion matrix for pruned May CART model based on jack-knifing, which shows the number of lakes of each fish assemblage type (rows) that were correctly or incorrectly classified (columns) as well as the overall misclassification rate.

	Fishless lakes	Small-bodied fish lakes	Large-bodied fish lakes	Misclassification Rate
Fishless lakes	13	2	0	3/15
Small-bodied fish lakes	1	8	1	2/10
Large-bodied fish lakes	0	5	0	0/5
Overall Misclassification				5/30

Table 2.4b Confusion matrix for pruned August CART model based on jack-knifing, which shows the number of lakes of each fish assemblage type (rows) that were correctly or incorrectly classified (columns) as well as the overall misclassification rate.

	Fishless lakes	Small-bodied fish lakes	Large-bodied fish lakes	Misclassification Rate
Fishless lakes	12	1	0	1/13
Small-bodied fish lakes	1	8	1	2/10
Large-bodied fish lakes	0	5	0	0/5
Overall Misclassification				3/28

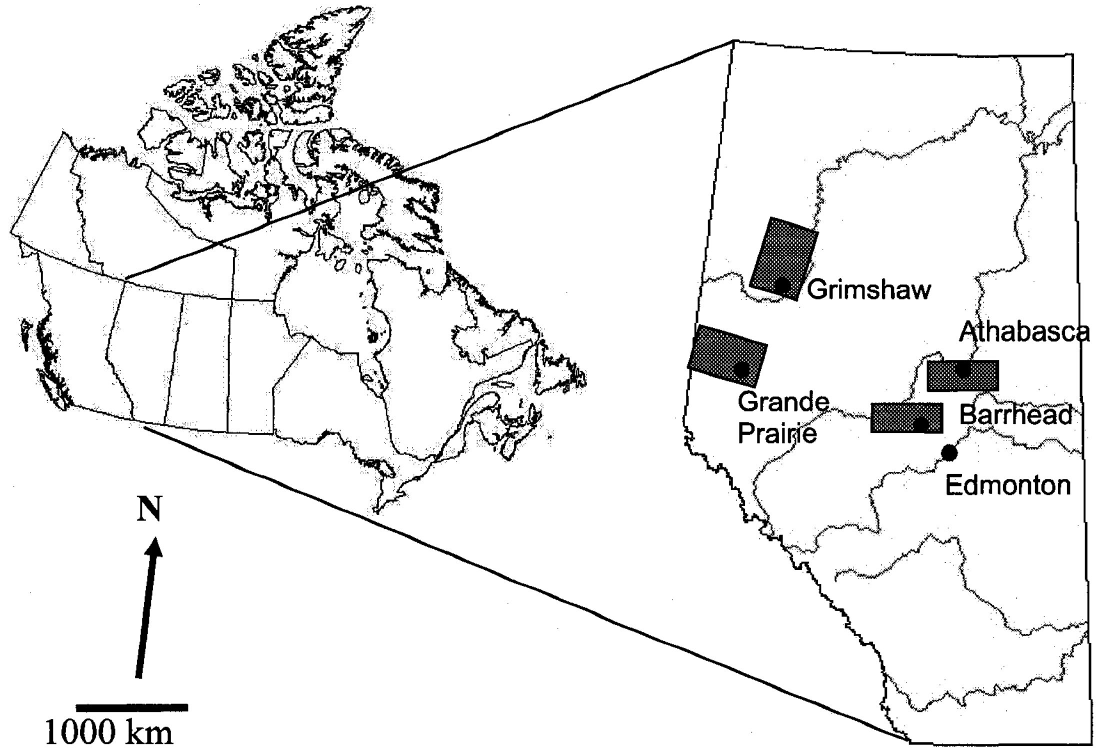

Figure 2.1 Location of four Boreal Transition Zone sub-regions in Alberta, Canada. Study shallow lakes are located within the shaded areas. Black dots are nearby communities.

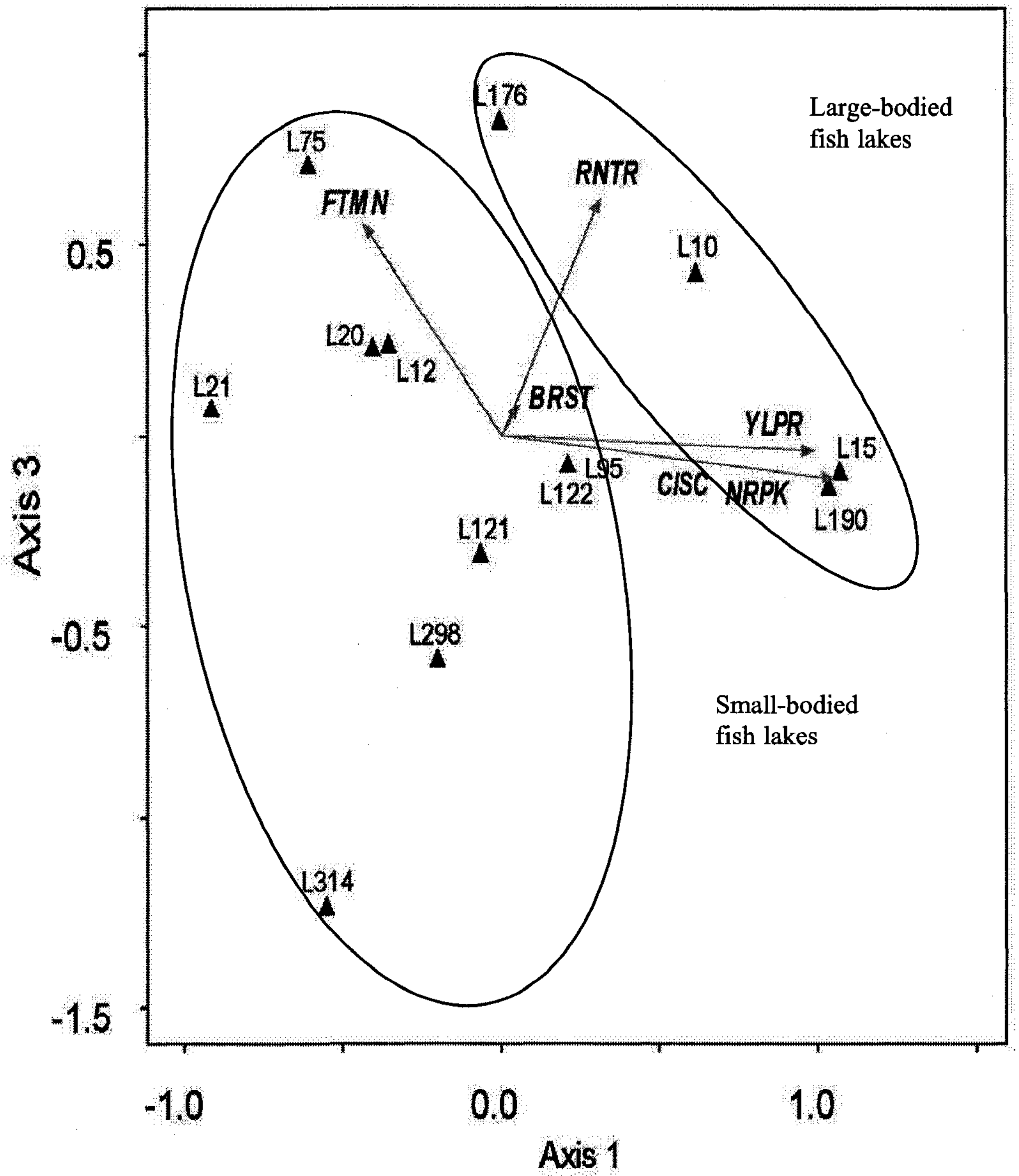

Figure 2.2 NMS ordination joint plot of fish assemblages based on relativized fish species counts from 13 fish bearing study lakes. Triangles represent lakes and lake ID codes are given for each lake. Triangles closer together are similar in fish species composition and the relative abundance of species present. Grey lines are species vectors, the angles and lengths of which represent the direction and strength of the relationship of the species to the ordination axes. Ellipses were added to highlight the two fish assemblage types (see text).

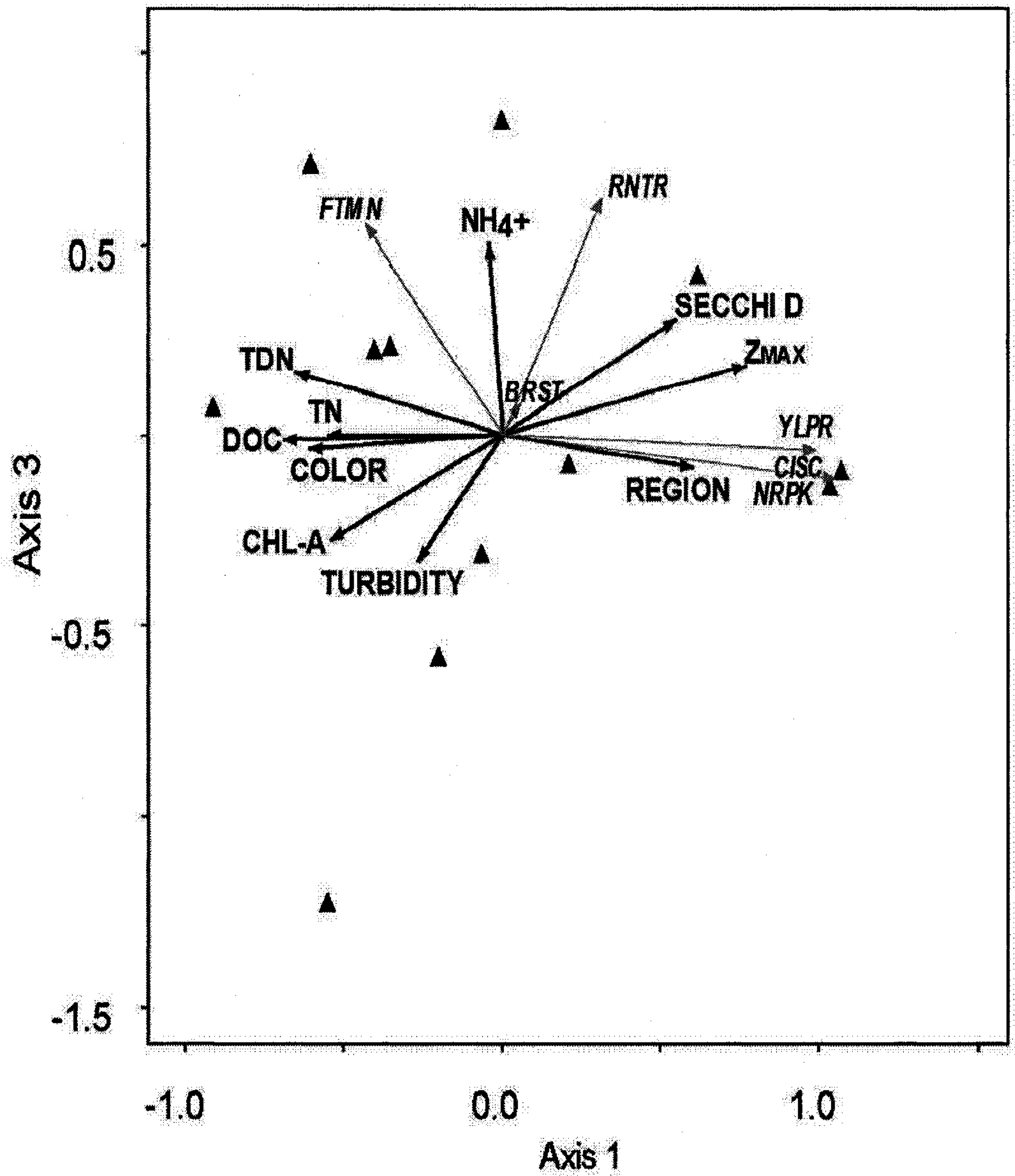

Figure 2.3 NMS ordination joint plot of fish assemblages based on relativized fish species counts from 13 fish bearing study lakes showing the May environmental characteristics most associated with small bodied fish and large bodied fish assemblages. Triangles represent lakes, lines are joint plot vectors, the angles and lengths of which represent the direction and strength of the relationship of the species (grey) or environmental factors (black) to the ordination axes. R^2 cutoff = 0.3 for environmental vectors.

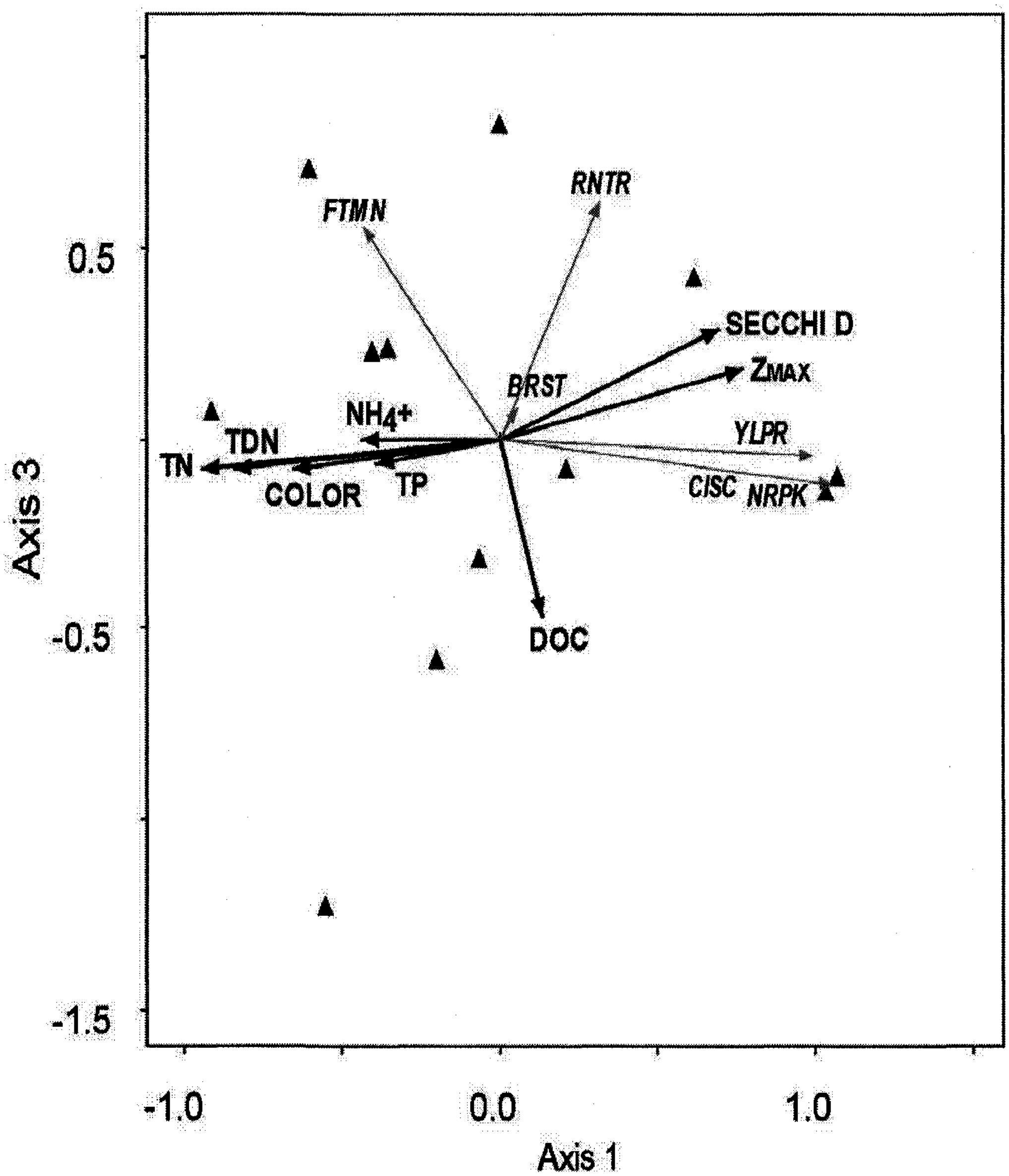

Figure 2.4 NMS ordination joint plot of fish assemblages based on relativized fish species counts from 13 fish bearing study lakes showing the August environmental characteristics most associated with small bodied fish and large bodied fish assemblages. Triangles represent lakes, lines are joint plot vectors, the angles and lengths of which represent the direction and strength of the relationship of the species (grey) or environmental factors (black) to the ordination axes. R^2 cutoff = 0.3 for environmental vectors.

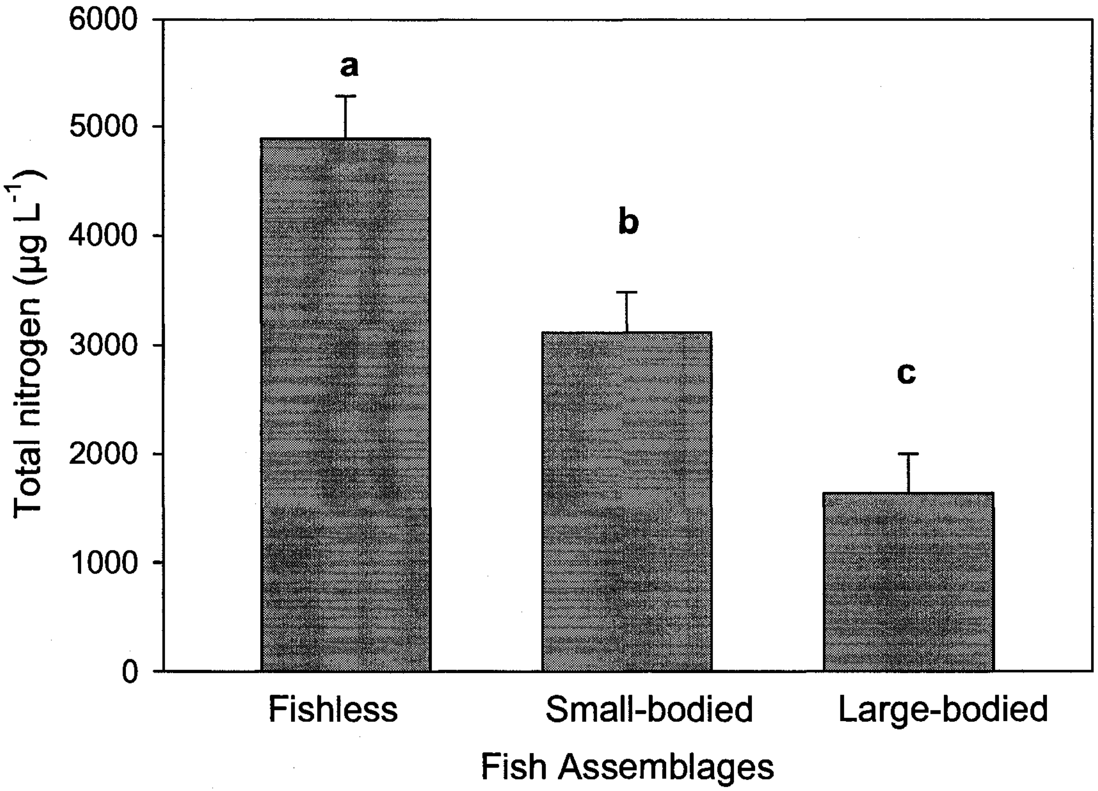

Figure 2.5 a Mean total nitrogen concentrations for lakes grouped according to their fish assemblage type. Letters indicate significant differences based on Mann-Whitney pairwise comparisons of lake types. Bars indicate standard error. Fishless lakes n=41, small-bodied fish lakes n=15, large-bodied fish lakes n=5.

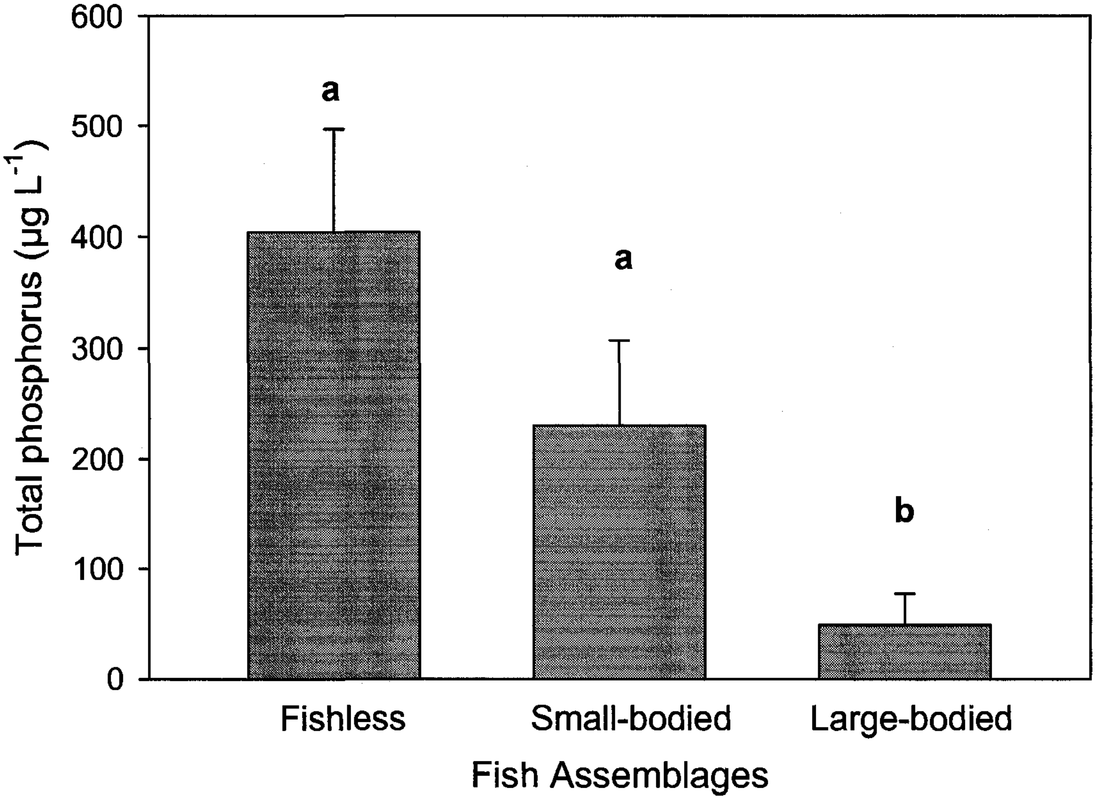

Figure 2.5 b Mean total phosphorus concentrations for lakes grouped according to their fish assemblage type. Letters indicate significant differences based on Mann-Whitney pairwise comparisons of lake types. Bars indicate standard error. Fishless lakes n=41, small-bodied fish lakes n=15, large-bodied fish lakes n=5.

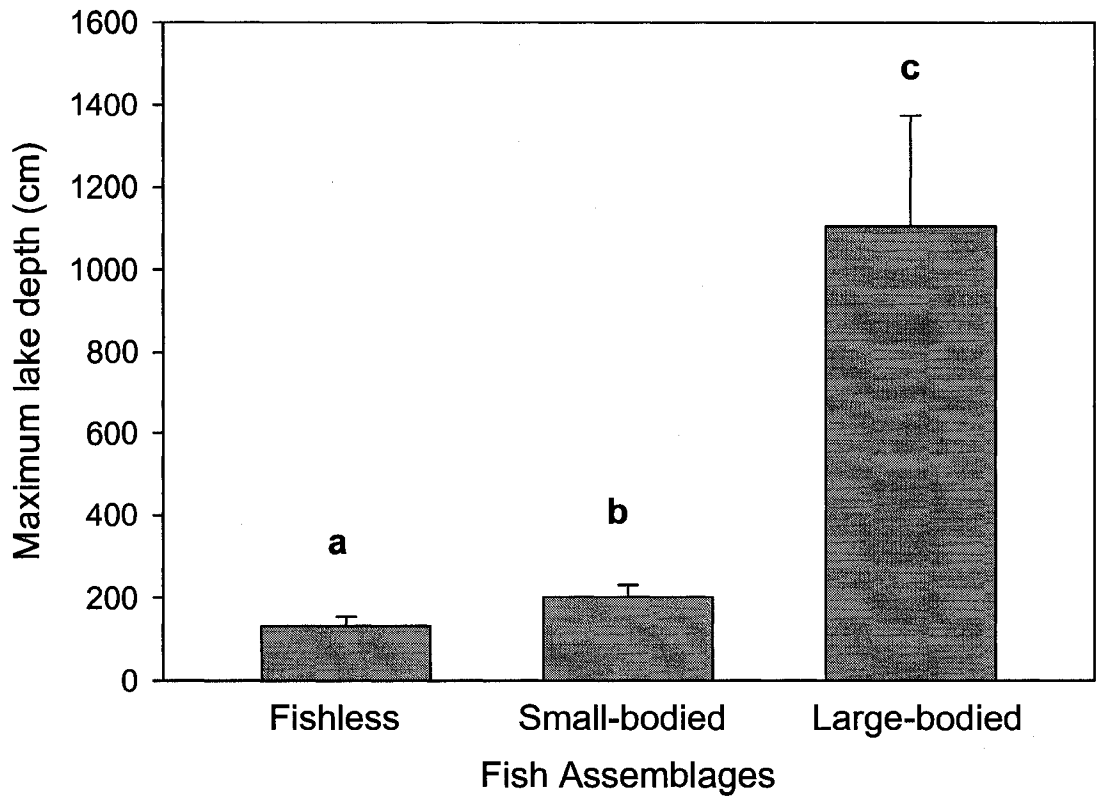

Figure 2.5c. Mean maximum depth for lakes grouped according to their fish assemblage type. Letters indicate significant differences based on Mann-Whitney pairwise comparisons of lake types. Bars indicate standard error. Fishless lakes n=41, small-bodied fish lakes n=15, large-bodied fish lakes n=5.

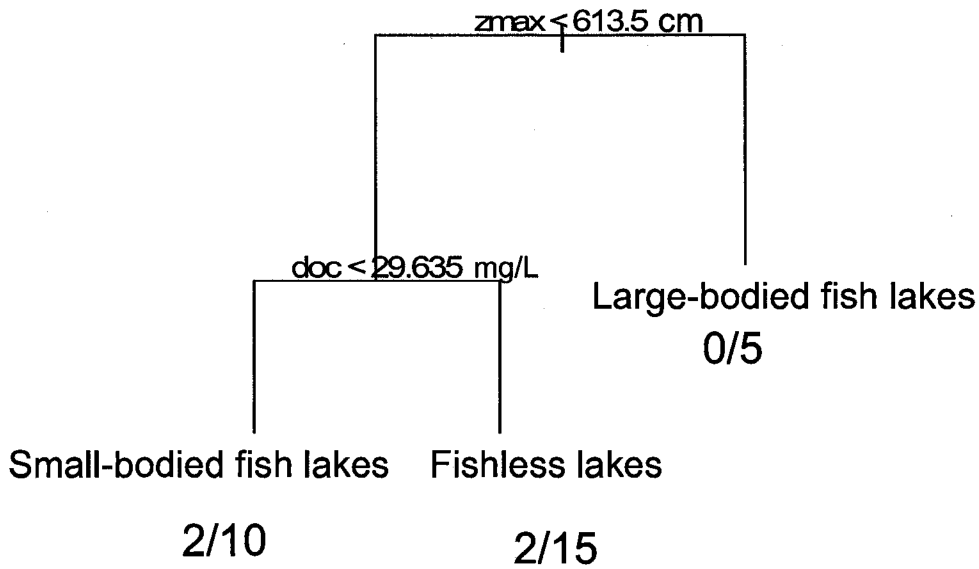

Figure 2.6 Pruned CART Model showing May environmental parameters that best discriminate lakes according to their fish assemblages. Misclassification rates shown below fish assemblage type.

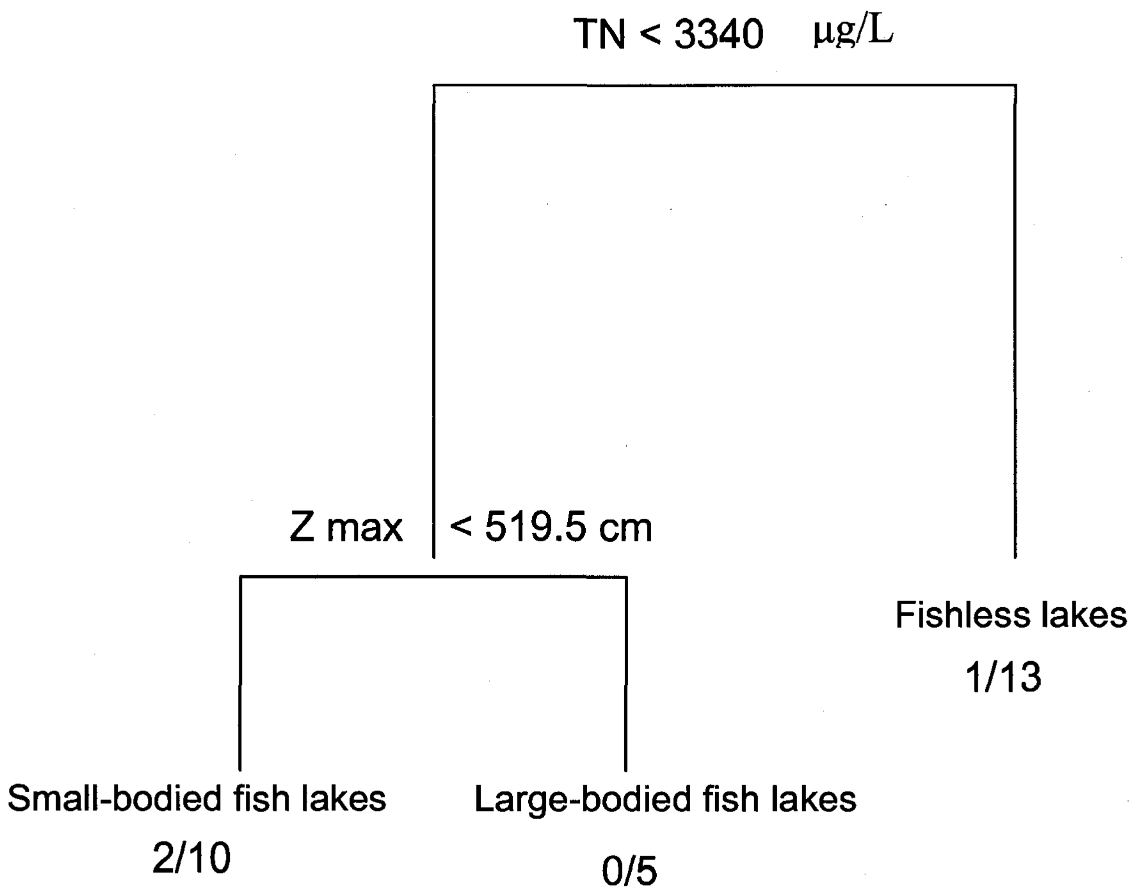

Figure 2.7 Pruned CART Model showing August environmental parameters that best discriminate lakes according to their fish assemblages. Misclassification rates shown below fish assemblage type.

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Chapter 3

Influence of fish assemblages on waterfowl communities of shallow lakes in the southern Boreal Plains Ecozone in Alberta

3.1 Introduction:

Wetland loss and associated waterfowl population declines across North America are major conservation concerns. These declines have led to the establishment of continental waterfowl population goals under the North American Waterfowl Management Plan (Ducks Unlimited Canada (DUC) 2004) and a wide range of local and regional conservation plans and research initiatives that focus on identifying essential habitat for waterfowl (e.g. Melinchuk 1995, Williams et al. 1999, Fleskes et al. 2007). A number of studies also suggest that waterfowl conservation strategies should consider the influence of biotic interactions on waterfowl, especially those associated with fish (Giles 1994, Hanson and Butler 1994, Bouffard and Hanson 1997, McParland and Paszkowski 2006, Norris 2006). In particular, some fish can negatively influence waterfowl by reducing macroinvertebrate food resources (Hanson and Butler 1994, McParland and Paszkowski 2006) and by increasing lake turbidity and phytoplankton abundance through trophic cascades (Hanson and Butler 1994, Carpenter et al. 1985).

Abundance of macroinvertebrate prey is an important factor determining waterfowl diversity, population density and reproductive success (Elmberg et al. 1993, 2000, Murkin and Kadlec 1986, Cox et al. 1998, Gunnarson et al. 2004). Macroinvertebrates are also important prey for many species of fish and competition between fish and waterfowl for invertebrate food resources has been documented in a variety of aquatic systems (Eadie and Keast 1982, DesGranges and Rodrigue 1986, Giles 1994, Santoul and Mastrorillo 2003). In oligotrophic lakes, competition with large-bodied fish such as perch (*Perca* spp.) has been linked to decreased reproductive effort by Common Goldeneye (*Bucephala clangula*) (Mallory et al. 1994a), changes in duckling diet (DesGranges and Gagnon 1994, Bendell and McNicol 1995), and decreased duckling growth and survival (DesGranges and Rodrigue 1986, Cox et al. 1998). Recent studies also reveal that small-bodied fish such as fathead minnow (*Pimephales promelas*) and brook stickleback (*Culea inconstans*) can also significantly reduce important macroinvertebrate food resources consumed by waterfowl in eutrophic prairie lakes of western North America (Zimmer et al. 2002, Hornung and Foote, 2006) and can alter foraging patterns in Blue-winged Teal (*Anas discors*) (MacParland and Paszkowski, 2006). Removal of planktivorous or benthivorous fish from lakes during biomanipulation experiments increased waterfowl use of the lakes (Giles 1994, Hanson and Butler 1994) and macroinvertebrate food resources within those lakes (Giles 1994). In some cases, establishment of piscivorous fish populations after biomanipulation experiments was necessary for maintenance of a clear, macrophyte-dominated state and associated improved waterfowl habitat conditions (Hanson and Butler 1994), indicating that the fish species composition of a lake can influence fish-waterfowl interactions.

Few studies have examined general patterns between fish and waterfowl community composition, species richness and overall abundance. The concept of community concordance refers to the degree that two different groups vary in a similar and ordered way along an environmental gradient (Jackson and Harvey 1993). Community concordance is a useful approach to detect general patterns in ecosystems and can be an important starting point to identify the mechanisms that structure ecological communities (Paszkowski and Tonn 2000). Examining community concordance between two or more taxonomic groups has been used for a variety of purposes: to evaluate the use of one taxon as a surrogate for many taxa in biological monitoring programs (Bilton et al. 2006, Paavola et al. 2006, Bini et al. 2007), to examine the relative importance of regional and local environmental parameters to two or more taxonomic groups (Allen et al. 1999, Heino 2001), and to examine whether two different communities respond in a similar way to the same set of abiotic factors (Jackson and Harvey 1993, Paszkowski and Tonn 2000). Given the influence that fish can have on waterfowl, community-level relationships between fish and waterfowl should be evaluated to incorporate biotic factors into models of waterfowl productivity and habitat use.

The southern portion of the Boreal Plains Ecozone, more commonly referred to as the Boreal Transition Zone (BTZ), is characterized by mixedwood forests, shrub and grassland habitats, shallow lakes and wetland complexes (DUC, 2004). Shallow lakes in the BTZ are naturally productive systems that provide important breeding and moulting habitat for waterfowl. Waterfowl surveys conducted in the BTZ from 2003-2005 revealed breeding pair densities often exceeding 39 pairs per km^2 of lake area (J. Thompson, DUC, personal communication). The BTZ region is, however, experiencing rapid increases in agricultural, industrial and residential development, and conversion rates of native upland habitats to other land uses often ranges from 0.8 % to 1.8 % of the remaining area per year (DUC 2004). Because of the region's importance to waterfowl and its rapid rate of development, DUC has identified the BTZ as a priority area for waterfowl conservation initiatives. The objective of this study was to examine the relationship between waterfowl and fish communities in shallow lakes of Alberta's BTZ and to evaluate the importance of fish to waterfowl density, species richness, and community composition. The findings will contribute to current DUC wetland-waterfowl modeling initiatives and will help target important guide priority habitat for waterfowl conservation in the BTZ.

In chapter 2, I found that shallow lakes in the BTZ region can be classified into 3 groups based on fish species composition including 1) fishless lakes; 2) small-bodied fish lakes, characterized by the presence of brook stickleback and occasionally fathead minnow; and 3) large-bodied fish systems characterized by the presence of northern pike (*Esox lucius)* or rainbow trout (*Oncorhynchus mykiss),* together with a variety of other fish species. Fishless lakes were most shallow and were especially high in phosphorus, nitrogen, and dissolved organic carbon. Large-bodied fish lakes were deeper and less nutrient rich. Small-bodied fish lakes were intermediate in depth and nutrient concentration.

I surveyed 30 lakes in the BTZ of Alberta in 2006 and examined the relationship between fish assemblage and waterfowl density, species richness and community composition. I hypothesized that waterfowl density and species richness would be greatest in fishless lakes and lowest in small-bodied fish lakes because small-bodied fish can reduce important macroinvertebrate prey resources for waterfowl (Cox et al. 1998, Zimmer et al. 2000, 2002, Hornung and Foote 2006) and change foraging patterns (MacParland and Paszkowski 2006). Because large-bodied piscivorous fish, such as pike, can reduce small-bodied fish populations (Robinson and Tonn 1989) and presumably affect macroinvertebrate populations, I hypothesized that waterfowl density and diversity would be intermediate where those fish dominate. Furthermore, I hypothesized that the relationship between fish and waterfowl communities would be strongest during the breeding season in May when protein-rich macroinvertebrates are especially important to waterfowl (Poysa et al. 2000) and most highly correlated with waterfowl density (Murkin and Kadlec 1986). I also hypothesized that waterfowl and fish communities in the BTZ would demonstrate concordance: similar patterns in community structure along an environmental gradient because both fish and waterfowl rely on depth, area, nutrient concentrations and submerged aquatic vegetation for habitat and food resources (Paszkowski and Tonn 2000).

3.2 Methods:

3.2.1 Description of study sites:

The study lakes were located in the BTZ in central Alberta, Canada (53°5'N, 112°4'W to 56°7'N, 119°7'W) and distributed among 4 different sub-regions near the communities of Grande Prairie (11 lakes), Grimshaw (4 lakes), Barrhead (11 lakes) and Athabasca (4 lakes) (Figure 3.1). The surrounding landscape is a mosaic of mixedwood forest and agricultural lands used for pasture and hay production. The study lakes, ranging in size from 11 to 498 hectares, are shallow, alkaline, and naturally eutrophic with median total phosphorus concentrations of 247.64 μg/L (Table 3.1). The study lakes have abundant submerged aquatic vegetation and many are surrounded by a fringe of marsh vegetation. Typical for the region, the study lakes have few if any permanent inlet and outlet streams and connectivity to the regional drainage system is low. Annual precipitation in 2006 ranged from 414.8 mm (Grande Prairie weather station) to 482.3 mm (Athabasca weather station) in the region, with most of it falling between May and August (Environment Canada 2007). The study lakes were selected from a cohort of 125 lakes sampled in 2005 by Dr. S. Bayley (University of Alberta) and Dr. J. Thompson (Ducks Unlimited Canada), who in a related project, are examining the relationship between waterfowl, lake, and landscape characteristics. The study lakes were selected to establish gradients in waterfowl density, lake depth, lake area, and agricultural development surrounding the lake.

3.2.2 Sampling methods:

Fish

The fish communities in 28 study lakes were sampled from May - August 2006. Fish communities were sampled using a combination of minnow traps, gill nets and fyke nets. Fish sampling was based on the protocol described by Tonn et al. (2003), an Alberta based modification of the Nordic survey protocol (Nyberg and Degerman 1988). Unbaited Gee minnow traps (36 trap nights) were set overnight (14-20 hours) at random locations on all lakes to establish fish presence and to sample small-bodied fish communities. Lakes with small-bodied fish were sampled further with either fyke or gill nets to assess presence and identify large-bodied fish. Lakes where no fish were caught in minnow traps were considered fishless and were not sampled further. Even though northern pike can survive in lakes without forage fishes (Venturelli and Tonn 2006), the maximum depth in all fishless lakes sampled was under 6 m, the depth determined by

Conlon (2002) as the minimum maximum depth necessary to support northern pike in the boreal regions of Alberta. Therefore I considered it reasonable to deem shallow lakes without any small-bodied species as being fishless. All fish caught were identified and enumerated. Fork length, total length, and fish mass were measured in a subset of 150 (length) and 50 (mass) fish for each lake. Length distribution, combined with length–mass regression were used to determine the mass of the remaining fish. Data on the presence-absence of fish species for two additional lakes were obtained from Earle (2007) (lake 448) and McGregor (2003) fish surveys (lake 43), bringing the total number of study shallow lakes to 30. Lake 448 was surveyed again during the summer 2007 and the fish species present in 2007 were in agreement with Mitchell and Prepas (1990) and Earle (2007).

Waterfowl

Three rounds of aerial, basin-specific waterfowl surveys were conducted by Ducks Unlimited Canada, as part of a larger waterfowl survey program in the BTZ, during each of the 2006 waterfowl breeding (May, sampled by helicopter) and moulting (July-August, sampled by fixed-wing aircraft) seasons. Indicated Breeding Pairs (IBP) of each species were calculated from May survey data and reported as IBP/ km^2 of open water. Breeding survey counts were corrected using a visibility correction factor (United States Fish and Wildlife Service and Canadian Wildlife Service 1987) calculated from ground based waterfowl surveys on 10 % of the surveyed lakes. Moulting season waterfowl counts were reported as individuals/ km^2 of open water. For each species, the maximum count or IBP value across the three rounds was used to account for temporal variation in peak abundance of species. Because Lesser and Greater Scaup (*Aythya* *affinis* and *A. marila*, respectively) could not be distinguished by aerial surveys, counts of these species were grouped together under the heading "Scaup". However, during the breeding and moulting periods in the BTZ of Alberta, *A. affinis* is much more common than *A. marila* and would represent the majority of scaup observed during the breeding and moulting periods.

Dytiscidae

I counted adult invertebrates of the family Dytiscidae that were trapped in the 36 unbaited minnow traps to get a proxy of macroinvertebrate abundance in the study lakes. Dytiscids were selected because they are easily caught in minnow traps and are consumed by waterfowl (Elmberg 2000, Hornung 2006) in the boreal region. Minnow traps were the same as ones used to sample fish; adult beetles are too large to be consumed by fathead minnows or brook stickleback. Dytiscids were counted in a subset of 22 lakes, as this count was begun part way through summer 2006. Of these 22 lakes, 11 were fishless, 8 contained small-bodied fish assemblages, and 3 contained large-bodied fish assemblages. The average Dytiscidae count per trap per hour was calculated for each lake.

Environmental parameters

I measured or calculated 35 environmental parameters for all study lakes. Water samples were collected from study lakes in both May and August and analysed in the University of Alberta Biogeochemistry lab using techniques described in Bayley and Prather (2003) to determine 23 water quality parameters; dissolved oxygen [DO], turbidity, total phosphorus [TP], total dissolved phosphorus [TDP], soluble reactive phosphorus [SRP], total nitrogen [TN], ammonium nitrogen [$NH4^+$], total dissolved nitrogen [TDN], nitrite +nitrate [NO_2^- +NO_3^-], sodium [Na^+], chloride [Cl^-], sulphate [SO_4^-], dissolved organic carbon (DOC), magnesium [Mg^{2+}], silicon [Si], potassium [K^+], calcium [Ca^{2+}], carbonate, bicarbonate, alkalinity, chlorophyll *a*, color, and total dissolved solids (TDS). Specific conductivity and pH and were measured in the field using a Hydrolab MiniSonde 5. Estimated cover and density of submersed aquatic vegetation (SAV) were determined based on Bayley and Prather (2003). Visual assesment (Bayley et al. 2007) was used to designate each lake as either "clear" or "turbid". Maximum depth for each lake was estimated from a minimum of 25 depth soundings along 2-5 transects measured with a calibrated weighted rope at the time of fish sampling. Secchi depth was measured in the field at the time of water chemistry sampling. Area and perimeter were calculated by DUC using digital versions of the National Topographic Survey Maps (NTS) (1:50 000 scale) and DUC's Landsat-based habitat inventory for sites that did not appear on the NTS maps. The percentage of agricultural development within a 1.6 km radius surrounding each lake was calculated using The Prairie Farm Rehabilitation Administration (PFRA) data (Agriculture and Agri-food Canada 1995). These data were cross referenced and updated to current climatic and surrounding land use conditions based on aerial photos of the study lakes taken during the 2006 and 2007 waterfowl surveys.

Two landscape level metrics of surface water connections, lake isolation and connectivity as defined by Conlon (2002), were evaluated from aerial photos (1:20,000 or 1:30,000) and verified using maps (1:70,0000-1:100,000) and field notes. I created a third metric, modified lake connectivity, an extension of Conlon's 2002 connectivity metric. Lakes were assigned to 4 categories based on their connectivity to the regional drainage system: those with permanent inlets and outlets, those with intermittent connections, those connected to isolated wetland complexes, those with neither inlets nor outlets.

3.2.3 Statistical analyses:

General approach

To examine how waterfowl species richness and overall waterfowl density varied between fishless, small-bodied fish and large-bodied fish lakes, I used univariate statistical techniques. To examine patterns in waterfowl species composition and how waterfowl composition related to fish and to environmental parameters, I used a series of multivariate techniques.

The relationships of waterfowl species richness and density to fish assemblage

I used a Kruskal -Wallis test to evaluate whether waterfowl species richness differed in relation to fish assemblage type (SPSS v. 14) for breeding and moulting survey periods. This non-parametric test was used because waterfowl species richness data did not meet assumptions of normality and homogeneity of variance, even after transformations.

Preliminary analyses revealed that waterfowl density differed in lakes with different fish communities (ANOVA ($F_{2,25} = 15.20$), $p<.0005$, SPSS v 14). However, because waterfowl density is known to vary with area (Leschisin et al. 1992, Svingen and Anderson 1998), Analysis of Covariance (ANCOVA, SPSS v 14) was used to determine whether breeding and moulting waterfowl densities differed among the different fish communities after adjusting for lake area. Both graphical analysis and ANCOVA were used to examine the assumption of homogeneous slopes across fish communities.

Waterfowl breeding and moulting density values were $\log_{10}(x+1)$ transformed to meet the assumptions of normality and homogeneous distribution, which were verified with the Kolmogorov-Smirnov and Levene tests, respectively (SPSS v 14).

A Kruskal-Wallis test was used to evaluate whether Dytiscidae counts differed in fishless and fish lakes (SPSS v. 14). This non-parametric test was used because Dytiscidae counts did not meet assumptions of normality and homogeneity of variance even after transformations.

The relationship between waterfowl communities and fish assemblage

Preliminary Detrended Correspondance Analyses revealed that the waterfowl community gradient lengths were well under 4 standard deviation units (1.3 SD for breeding waterfowl IBP density and 2.1 for moulting bird density). Ordination methods based on linear response models, such as PCA and RDA, were therefore considered appropriate for this dataset (Jongman 1987). In all multivariate analyses, breeding and moulting waterfowl density values were $\log_{10}(x+1)$ transformed and waterfowl species that occurred on less than two study lakes were removed from the analyses. Because the density of each waterfowl species was included in the multivariate matrix, all multivariate analyses examined both waterfowl density and species composition. Hence, waterfowl community composition refers to both the combination of species present and the densities of those species. As a result, seventeen waterfowl species were included in the breeding data set and fifteen waterfowl species were included in the moulting data set. I included 29 lakes in all breeding waterfowl analyses. Lake 15 was removed from both breeding and moulting data sets because it was a multivariate outlier (Outlier Analysis, PC-ORD v 5.0) and univariate outlier for total waterfowl breeding density and total waterfowl moulting density (boxplots, SPSS v 14). All analyses using moulting waterfowl density data included 27 shallow lakes, because two shallow lakes dried up in August and most environmental parameters could not be measured.

Principle Components Analysis (PCA, PC-ORD v 5.0) was used to examine patterns in waterfowl community composition and seasonal variation in waterfowl communities between breeding and moulting seasons. Relationships between waterfowl community composition and environmental variables were examined using graphical joint plots, overlays, and correlations with PC scores. All quantitative environmental variables except pH were $\log_{10}(x+1)$ transformed.

The Mantel Test, a non-parametric test that assesses the correlation between two distance matrices of the same entities (McCune and Grace, 2002), was used to test the null hypothesis of no relationship between waterfowl and fish communities. In this case, one distance matrix consisted of the pairwise differences in waterfowl communities among shallow lakes and the other distance matrix comprised the difference in fish communities among the same shallow lakes. Both breeding and moulting waterfowl density datasets were compared to the (same) fish assemblage data on the presence/absence of 5 fish species. Fish species that only occurred in one lake were removed from the analysis. A Sorenson (Bray-Curtis) distance measure was used. Monte Carlo randomizations were used to assess the significance of the correlation between the two matrices. Similarly, the Mantel Test was also used to test the null hypothesis of no relationship between waterfowl communities and the environmental parameters for both May (breeding) and August (moulting) data sets.

Multi-Response Permutation Procedures (MRPP, PC-ORD v 5.0), a non-parametric multivariate procedure for testing differences between groups, was used to determine if the waterfowl community structure was different in lakes with different fish assemblages. MRPP was performed using Euclidean distance because the waterfowl data sets demonstrated a linear response based on earlier Detrended Correspondence Analyses. The Benjamini-Hochberg method for controlling False Discovery Rate was used to account for multiple comparisons (Roback and Askins 2004, Waite and Campbell 2006).

To better understand whether specific waterfowl species were associated with a particular fish assemblage, Indicator Species Analysis (ISA, PC-ORD v 5.0) was used on both waterfowl density and waterfowl species presence datasets. ISA identifies species that are concentrated in one lake type. ISA values for each waterfowl species were calculated based on Dufrene and Legendre (1997). Statistical significance of Indicator Values for each species in each group were evaluated by a Monte Carlo method.

The relative importance of fish and environment to waterfowl density and community composition

Variance partitioning, outlined by Borcard et al. (1992), was used to determine the relative contribution of fish and environmental characteristics of the lakes to patterns in the waterfowl community. This method used two Redundancy Analyses (RDA, CANOCO 4), each ordination constrained by one of the sets of explanatory variables (fish or environment) and two partial Redundancy Analyses (RDA, CANOCO 4), each ordination constrained by one explanatory variable with the other explanatory variable acting as a covariable. Forward selection was used to identify the environmental variables and fish species most correlated to the breeding and moulting waterfowl density data sets. All quantitative environmental variables except pH were $\log_{10}(x+1)$

transformed prior to analyses. Using the May data set, forward selection identified 4 significant ($p<0.05$) environmental variables, water color, submerged aquatic vegetation (SAV), K^+, and lake area that were most related to waterfowl community composition and were used in all subsequent RDA and partial RDA analyses. Using the August data set, forward selection identified total phosphorus, lake area, maximum depth, and dissolved organic carbon as the most important ($p<0.05$) environmental variables. I also used forward selection to identify the fish species whose presence was most related to the waterfowl community data sets. Brook stickleback, rainbow trout, and northern pike were chosen for both breeding and moulting analyses. Because variance partitioning is sensitive to either many variables or highly unbalanced numbers of variables in the two explanatory variable sets (Peres-Neto et al. 2006), environmental variables were limited to the top 4 significant variables, and the 3 selected fish species were significant at the $p<0.15$ level.

3.3 Results

Eighteen waterfowl species were observed on the study lakes in 2006 (Table 3.2). During the breeding season 17 waterfowl species were counted with a mean (±SD) of 11.7 ±3.0 species per lake, while during the moulting period 16 species were observed (8.7 ± 3.9 species per lake). Hooded Merganser (*Lophodytes cucullatus*) was identified on only one lake during the moulting season and was removed from all analyses. Nine fish species were present in the study lakes (Table 3.3). Three different lake types were identified, based on their fish assemblages: fishless lakes, small-bodied fish lakes, and large-bodied fish lakes (Epners Chapter 2). Fifteen lakes were fishless (i.e., no fish were caught after 36 minnow trap nights). Ten lakes contained small-bodied fish; either brook stickleback alone or both fathead minnow and brook stickleback. Five lakes were classified as large-bodied fish lakes and contained, along with various small-bodied fish, a combination of species including northern pike, rainbow trout, cisco (*Coregonus artedi*), yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*). However, four species, cisco, walleye, spottail shiner (*Notropis hudsonius*) and iowa darter (*Etheostoma exile*), occurred in only one study lake each and these species were removed from all analyses.

3.3.1 The relationships of waterfowl species richness and density to fish assemblage

Waterfowl species richness was greater in fishless lakes and small-bodied fish lakes than in large-bodied fish lakes during the breeding season and moulting season (Figures 3.2 a and b). Waterfowl species richness differed significantly with lake fish status during the breeding season (Kruskal-Wallis test $p=0.033$). Large-bodied fish lakes had fewer waterfowl species (mean 6.5) than in fishless lakes (mean 10.7) or small-bodied fish lakes (mean 10.7). Waterfowl species richness also differed during the moulting season (Kruskal-Wallis test $p=0.004$) when large-bodied fish lakes had only one third the waterfowl species as fishless lakes (3.2 waterfowl species/lake compared to 9.7 waterfowl species/lake). Notably, Blue-winged Teal, Northern Shoveler, Northern Pintail, Redhead, Canvasback and White-winged Scoter were almost totally absent from large-bodied fish lakes during both breeding and moulting seasons. Similarly, neither breeding Cinnamon Teal nor moulting Bufflehead and Gadwall were observed on large-bodied fish lakes.

Breeding waterfowl densities were two times greater on fishless lakes than fish-bearing lakes after lake area had been accounted for (ANCOVA $F_{(2,25)}=15.25$, $p<0.01$;

Figure 3.3). Pairwise comparisons revealed that breeding waterfowl densities were significantly greater in fishless lakes than in small-bodied fish lakes (ANCOVA $p<0.01$) or large-bodied fish lakes (ANCOVA $p< 0.01$) but that there were no differences in breeding waterfowl density between small-bodied fish lakes and large-bodied fish lakes ($p=0.78$).

A similar trend was observed using total waterfowl counts/lake, with area acting as a covariable. Because the equal variance between group assumption was not met for the latter assessment, however, direct hypothesis testing was not carried out. Moulting waterfowl density and count data also demonstrated high variance and both the assumptions of homogeneity of variance and homogeneity of slope were violated.

As an index of food resources for waterfowl in fishless lakes and lakes with fish, the median number of dytiscid beetles was greater in fishless lakes (0.07/trap/hour) than in lakes with fish (0.01/trap/hour) ($p=0.05$, Mann-Whitney test; Figure 3.4). This trend is noteworthy since low sample size ($n=22$) and the use of a non-parametric test lowered statistical power.

3.3.2 The relationship between waterfowl communities and fish assemblage

The PCA of waterfowl assemblages based on breeding waterfowl density illustrated some basic patterns in waterfowl communities in my study lakes. The first two axes of the PCA for the breeding season were significant and together explained 44.7% of the variation in the waterfowl community composition, with eigenvalues $\lambda_1=5.11$ (30.1 % variation) and $\lambda_2=2.49$ (14.6 % variation) (Figures 3.5). Axis 1 separated lakes with high breeding waterfowl density (low axis 1 scores) from lakes with relatively low breeding waterfowl density (high axis 1 scores). Accordingly, the most abundant species on BTZ wetlands; scaup, was highly correlated (negatively) with PC1. Gadwall, Northern Shoveler, Redhead, Canvasback and Ruddy Duck were also highly correlated with PC1 ($r < -0.70$). Axis 2 separated lakes with high breeding densities of dabbling ducks, especially Mallard, Blue-winged Teal and Green-winged Teal, (high axis 2 scores) from lakes with high breeding densities of diving ducks, particularly those with higher densities of Common Goldeneye, Surf Scoter and Bufflehead. Total phosphorus, water color, area, maximum depth and SO_4^- were all significantly correlated with the first two PCA axes, $r^2 > 0.30$ (figure 3.5). Graphical overlays showed that waterfowl communities were also correlated with fish presence. No discernable trends between waterfowl communities and other categorical variables (e.g. region, SAV, isolation) were observed in graphical overlays of the PCA.

Patterns in moulting waterfowl communities were very similar to those observed for the breeding period. The first two axes of the PCA were significant, together accounting for 50.90% of the variation in the waterfowl community structure, with eigenvalues of $\lambda_1=5.31$ (35.40 % variation) and $\lambda_2=2.33$ (15.52 % variation) (Figure 3.6). Axis 1 separated lakes along a high to low moulting waterfowl density gradient and axis 2 separated lakes with high densities of moulting dabbling duck from those with high densities of moulting diving ducks. Maximum depth, color, secchi depth, total phosphorus, total dissolved phosphorus, soluble reactive phosphorus, ammonium NH_4^+, total dissolved nitrogen (TDN), and total nitrogen (TN) were all significantly correlated with the PCA axes, $r^2 > 0.30$. During the moulting period, measures of nitrogen (NH_4^+, TDN, TN) were more correlated with waterfowl community structure than during the breeding period. Moulting waterfowl communities were correlated with fish presence, though not as clearly as during the breeding period (Figure 3.6).

Fish communities were concordant with both breeding and moulting waterfowl communities, indicating that patterns in waterfowl communities varied in a similar and ordered way compared to patterns in fish species assemblage (breeding period: Mantel Test, $r=0.39$, $p<0.01$, 9999 randomization runs, Bray-Curtis distance measure; moulting Period: Mantel Test, $r=0.23$, $p<0.01$, 9999 randomization runs, Bray-Curtis distance measure). Breeding and moulting waterfowl communities were also concordant with their respective environmental parameters (breeding period: Mantel Test, $r=0.28$, $p<0.01$, 9999 randomization runs, Bray-Curtis distance measure; moulting period: Mantel Test, $r=0.43$, $p<0.01$, 9999 randomization runs, Bray-Curtis distance measure).

MRPP analyses demonstrated that waterfowl community composition differed among lakes with different fish assemblages during both the breeding and moulting periods. Analyses were run for both periods using both waterfowl presence/absence and waterfowl density data to examine how both waterfowl species presence and waterfowl density differed among fish assemblages. Waterfowl species presence/absence differed significantly during the breeding period ($p = 0.02$, MRPP test statistic; $T= -2.5$, chance corrected within - group agreement; $A = 0.03$) and the moulting period ($p <0.01$ $T = -3.66$, $A =.03$). Similarly waterfowl species densities differed significantly during the breeding period ($p <0.01$, $T = -4.08$, $A =0.05$) and the moulting period ($p<0.01$, $T = -3.1$, $A = 0.04$).

Pairwise MRPP comparisons of waterfowl community composition between lakes with different fish assemblages using waterfowl presence/absence were generally consistent with results from species richness analyses for both the breeding and moulting periods. Both breeding and moulting waterfowl community composition in fishless lakes differed significantly from that in large-bodied fish lakes (breeding season: $p < 0.01$ moulting season: $p < 0.01$) (Table 3.4). Other comparisons of breeding and moulting waterfowl community composition were non significant.

Using density values in the MRPP analyses, both breeding and moulting waterfowl community composition in fishless lakes differed significantly from that in large-bodied fish lakes (breeding season: $p < 0.01$ moulting season: $p < 0.01$) (Table 3.5). When density values were used, the p-values for comparisons between fishless and small-bodied fish lakes dropped from 0.34 to 0.07 (breeding season, Table 3.4) and from 0.08 to 0.03 (moulting season, Table 3.5), indicating that the differences in waterfowl community composition between the two assemblages increased when waterfowl density was considered.

3.3.3 Waterfowl species linked to fish assemblage

To evaluate the extent to which each waterfowl species was associated with fish assemblage, Indicator Species Analysis was used on both presence absence data and waterfowl density data. Significant association between waterfowl species and fish assemblage was indicated by p-values less than .05 and ISA values greater than .25, the criteria set for a significant indicator species (McCune and Grace 2002). Northern Shoveler presence was associated with fishless lakes (Table 3.6). Using density data, Blue-winged Teal, Mallard, Gadwall, American Wigeon and Scaup were also associated with fishless lakes, as these species were more abundant on fishless lakes (Table 3.6). Conversely, during the breeding period, Common Goldeneye density was greatest in large-bodied fish lakes (Table 3.6). During the moulting period, Blue-winged Teal, Mallard, Gadwall, American Wigeon presence were associated with fishless lakes (Table 3.5a). Canvasback presence alone and Ringnecked Duck density were associated with small-bodied fish lakes during the moulting period (Table 3.6).

3.3.4 The relative importance of fish and environment to waterfowl composition:

Variance partitioning using RDA analysis explained 51.5 % of the total variation in the breeding waterfowl assemblage (Figure 3.7). The variation in breeding waterfowl density community composition due to environment, 24.3%, was 2 times greater than the variation attributed to fish alone, 13.4 %, and the overlap between fish and environment; 13.8 %. All RDA were significant ($p < 0.05$). Variance partitioning using RDA analysis explained 55.5 % of the variation in the moulting waterfowl community. Environment alone explained 21.7 % of the variation in waterfowl communities (Figure 3.7). The percentage of variation in moulting waterfowl density and composition that could be attributed to the overlap of fish and environment (25.7 %) was greater than environment alone. Fish alone explained a small (8.1%) and statistically non significant amount of variation in the moulting waterfowl community. All RDA were significant at $p < .05$, except the partial RDA constrained by fish with environment as a covariable.

3.4 Discussion

As predicted, shallow fishless lakes supported the greatest density of breeding waterfowl. Fishless lakes and small-bodied fish lakes supported similar numbers of waterfowl species and large-bodied fish lakes supported the lowest waterfowl species richness. In addition, waterfowl and fish communities were concordant, indicating that patterns in waterfowl assemblages varied in ways similar to the patterns in fish species assemblages. These results were consistent with a number of studies that report decreased waterfowl use of lakes with fish (Eadie and Keast 1982, Hanson and Butler 1994, Giles 1994, Norris 2006). However, my results suggested that the environmental characteristics of my study lakes were more important determinants of breeding waterfowl density and composition; i.e., waterfowl responded most to the environmental characteristics that distinguished the fish assemblages. Fish species assemblage contributed to a small but significant proportion (8.8%) of the variation in breeding waterfowl density and composition, suggesting that biotic interactions such as competition likely influenced breeding waterfowl density and composition to some extent. The importance of environmental determinants to BTZ waterfowl communities is consistent with Paszkowski and Tonn (2000) who found that concordance between waterbirds and fish in boreal Alberta was the result of the two taxonomic groups largely responding to the same environmental variables. The lake environment and the interaction between fish and the shallow lake environment, contributed similar proportions to the variation in moulting waterfowl density and composition. The interaction term, indicating high correlation between fish and environmental variables during the moulting period, explained slightly more. Fish alone did not contribute significantly to the variation in moulting waterfowl density and composition. The large degree of interaction between the fish and environment variables is consistent with Jackson and Harvey (1993) who found complex interactions between abiotic and biotic factors in community-environment relationships. The interaction term indicates that there is much overlap in fish and environmental variables important to waterfowl particularly during the moulting season between July and August, which makes it difficult to distinguish between the effects of fish or environment on moulting waterfowl. However, environment alone contributed more to the variation in the moulting waterfowl than did fish alone, and environmental determinants are more important than fish to waterfowl in both the breeding and moulting seasons.

3.4.1 Highly productive, shallow fishless lakes supported the most waterfowl.

Waterfowl density and species richness were greatest in shallow, nutrient-rich lakes. These same characteristics also distinguished fishless lakes from those that contained fish (Epners Chapter 2). Waterfowl community composition also varied with nutrient richness, which is identified with lake productivity in the shallow lake and wetland litereature and throughout this discussion. This finding is consistent with other studies that found that abundant SAV (Milberg 2002), nutrient load and trophic conditions (Fernandez 2005) influenced waterfowl community composition. Increased waterfowl density along a productivity gradient has been well documented in studies that consider lakes ranging from oligotrophic to hypereutrophic (Nilsson and Nilsson 1978, Eriksson 1985, Elmberg et al. 1993, Hoyer and Canfield 1994, Longcore et al. 2006). My results indicate that this relationship also holds in a set of lakes ranging from eutrophic to hypereutrophic. This finding contrasts with several studies (Hanson and Butler 1994, Hargeby et al. 1994) where increased nutrient concentrations in eutrophic lakes were associated with decreased waterfowl density, decreased submerged aquatic vegetation abundance and increased phytoplankton and turbidity. SAV, which provides important food resources for waterfowl (Hornung and Foote 2006) and habitat for macroinvertebrate prey of waterfowl (Hanson 1990, McAbendroth et al. 2005, Hornung and Foote 2006, Longcore et al. 2006), is typically less abundant in turbid and eutrophic lakes according to clear /turbid alternate stable state theory (Scheffer et al. 1993, 2001). In contrast, highly productive lakes in the BTZ, which were mostly fishless, also supported denser quantities of SAV. Fishless lakes were richer in nutrients (TN, TP) than fish-bearing lakes but there was no difference in turbidity between fish-bearing and fishless lakes (Epners Ch. 2). It is possible that fish presence or absence influenced the relationship between SAV, productivity and turbidity. High productivity (TN, TP) may have led to increased anoxic conditions and winterkill frequency and contributed to fish absence. The absence of fish, in turn, may have promoted conditions that lead to abundant SAV conditions because fish presence can increase predation pressure on invertebrate grazers that control phytoplankton (Zimmer et al. 2000, 2002) and indirectly influence SAV density (Hanson and Butler 1994) . The ability of fish to influence the environmental characteristics of shallow lakes may have contributed to the high degree of interaction between fish and environment that was important to moulting waterfowl. In the BTZ, fish may have an indirect influence on waterfowl through their influence on environment.

Invertebrate abundance is an important determinant of waterfowl density and species richness (Nudds 1983, Svingen and Anderson 1998, Elmberg et al. 1993). Predation by fish can reduce invertebrate abundance, diversity, and composition (Zimmer et al. 2002, Hornung and Foote 2006). In the BTZ, fishless lakes were most productive and based on the abundance of dytiscids, likely contained more abundant macroinvertebrate food resources. If this is true, then breeding waterfowl density and species richness were greatest in shallow lakes with the most invertebrate food resources and my results are consistent with the aforementioned studies.

Waterfowl density and species richness often increases with lake area and shoreline development (Leschisin et al. 1992, Stevens et al. 2003). Large lakes have a greater potential to have irregular shorelines and greater habitat diversity which are important for waterfowl (Svingen and Anderson 1998) and therefore large shallow lakes often show greatest species diversity (Paszkowski and Tonn 2000). In contrast, small shallow lakes in the BTZ supported the highest waterfowl densities. In my study lakes, lake size was highly correlated with lake depth, with larger lakes typically being deeper. Large deep lakes tend to have a larger proportion of pelagic area with less SAV and may therefore contain considerable areas of poor foraging habitat for waterfowl. Greater species richness in fishless lakes and small-bodied fish lakes compared to large-bodied fish lakes was mostly due to the presence of Canvasback, Redheads, Northern Shoveler, Northern Pintail, and Blue-winged teal. These species tend to prefer marshy habitats that are less likely to be available in deeper lakes. Interestingly, lake depth best distinguished large bodied fish lakes from fishless and small bodied fish lakes (Epners Chapter 2). Small shallow lakes can result in low winter oxygen levels, an important filter that limits the presence of northern pike and other large bodied fish (Tonn and Magnuson 1982). Thus lake depth appears to be an important morphometric trait in the BTZ with shallow lakes supporting the greatest waterfowl species density and species richness. Both waterfowl and fish responded strongly to shallow lake depth but in opposite ways.

Water transparency can increase prey detectability for diving ducks (Eriksson 1985), and can positively influence waterbird density and species richness (Svingen and

Anderson 1998, Paszkowski and Tonn 2006). In the BTZ however, darker water colour was associated with higher waterfowl density and species richness during the breeding season. Water colour was positively associated with total phosphorus and turbidity and thus in the BTZ is acting as a surrogate variable for lake productivity. Similarly DOC which was associated with higher moulting waterfowl density and species richness was also highly correlated with TN, TP, and SRP. Interestingly DOC was also highly correlated with region, being lowest in the Lakeland and Barrhead regions and greater in the Grande Prairie and Grimshaw regions. The latter regions also tended to have shallower lakes than the first two regions, so high DOC likely reflected shallow lake depth. K^+ , which was highly correlated with waterfowl density and composition in the BTZ was also associated with increased scaup brood use of wetlands in the Northwest Territories (Walsh et al. 2006). However, in the Northwest Territories, scaup use of wetlands was attributed to high amphibod invertebrate densities rather than water chemistry and amphipod density has also been linked to scaup density in a number of other studies (Austin et al. 1998, Lindeman and Clark 1999, Anteau et al. 2008, Strand et al. 2008).

3.4.2 Fish more important to waterfowl during the breeding season

Despite the importance of environmental characteristics for waterfowl density and species richness, waterfowl responded to fish, independent of environment, more strongly during the breeding season than during the moult. In the BTZ, fish assemblage variables explained 13.4% of the total variation in breeding waterfowl composition and density but only 8.1% during the moulting season. Furthermore, breeding waterfowl density was greater in fishless lakes than lakes with fish but the relationship between fish assemblages and moulting waterfowl remained unclear. Because the daily energy demands for egg production in waterfowl are at their highest during the breeding season compared to other times of year (Thompson and Ankney 2002), the potential for competition for food resources between fish and waterfowl is also highest during the breeding season. Invertebrate food resources are important to female ducks during egg laying, to their ducklings and to fish (Swanson et al. 1985, Krapu and Reinecke 1992, Hornung and Foote 2006). Fishless lakes were richest in nutrients, and based on the abundance of Dytiscid beetles, likely contained the most aquatic invertebrate food resources. The importance of fish may therefore vary with invertebrate abundance. This is the only study I know of that compares the relationship between fish and waterfowl in different seasons.

My results indicated that environmental characteristics are more strongly related to waterfowl density, species richness and community composition than are interactions with fish. It is possible, however, that the latter can impact waterfowl behaviour and reproductive vital rates (e.g., nest success or duckling survival) that this study did not measure. Fish presence increased Blue- winged Teal foraging effort in wetlands of the Aspen Parkland region of Alberta (McParland 2006). Fish presence can also reduced clutch size (Mallory et al 1994a) and duckling survival (Giles 1994) of diving ducks in acidic and oligotrophic systems. It would be worthwhile to examine the impact of fish on these aspects of waterfowl ecology in the BTZ.

3.4.3 Waterfowl species linked to fish assemblage:

In contrast to many studies that document decreased Common Goldeneye abundance in lakes with fish, specifically perch, (e.g. Eadie and Keast 1982; Desgranges and Rodrigue 1986; Mallory et al. 1994a), Common Goldeneye densities in the BTZ region were greater in large-bodied fish lakes (almost all of which contain perch) than in either fishless or small-bodied fish lakes. Similarly, in the boreal region of Alberta, Common Goldeneye were also distinctly associated with large fish assemblages (Paszowski and Tonn, 2000). It is possible that there are sufficient food resources for waterfowl in the more productive lakes of the BTZ and that little competition between Common Goldeneye and fish is occurring in the region. This contrasts with oligotrophic lakes of eastern North America and Northern Europe where competition for limited food resources has been linked to decreased Common Goldeneye abundance in fish lakes (Eadie and Keast 1982, Desgranges and Rodrigue 1986, Mallory et al.1994a). In the BTZ and western boreal regions, the Common Goldeneye preference for large bodied fish lakes may be a response to the environmental characteristics of the large bodied fish lakes, including water clarity, surrounding forest age and availability of suitable tree cavities, which are important to Goldeneye nest selection (Eadie et al. 1995).

Declining Lesser Scaup abundance across North America in recent decades is a pressing waterfowl conservation concern (Austin et al. 2000, Afton and Anderson 2001, Anteau and Afton 2004, Walsh et al. 2006, Strand et al. 2008). In the BTZ of Alberta, scaup populations have declined approximately 30% from their abundance in the 1970's (DUC 2004). In the BTZ, breeding scaup species densities were greatest in fishless lakes to the extent that high abundance of scaup was linked with fishless lakes. Continental declines in scaup abundance have been linked to fish presence, changing wetland condition, and decreased amphipod abundance (Lindeman and Clark 1999, Austin et al. 2000, Kahara 2007, Strand et al. 2008). The spring condition hypothesis states that female Lesser Scaup are arriving at breeding areas in poorer body condition than they did historically, leading to decreases in reproductive success and subsequent population decline (Anteau and Afton 2004). Decreased food availability for spring migrating scaup has been linked to loss of wetland habitat, low wetland quality and increased fish presence in wetlands along the migration corrider (Anteau and Afton 2004, 2008). Preferred use of BTZ fishless lakes by scaup may be related to greater food resources because of higher productivity and because selective predation by fish can reduce amphipod availability for scaup in fish-bearing lakes (Strand et al. 2008). Scaup were also the most abundant species in the BTZ lakes, accounting for approximately 20% of the total waterfowl abundance. As a result, their association with fishless lakes had a large influence on the relationships between total breeding and moulting waterfowl densities and fish assemblage.

Several other waterfowl species were also linked to fish assemblage. Northern Shoveler nests in shallow-water wetlands with adjacent grass or rangelands in the prairie or Aspen Parkland regions of the Prairie Pothole region (Dubowy 1996). Its ties with fishless lakes reflects its preference for small and shallow lakes and grassy upland habitat. Ring-necked Duck associated with fishless lakes in the boreal (Paszkowski and Tonn, 2000) was linked to small-bodied fish lakes in the BTZ. Canvasback prefers small lakes or deep-water marshes surrounded with dense emergent vegetation (Mowbray 2002), characteristics of small-bodied fish lakes in the BTZ with which it was associated. Correlation between fish presence and invertebrate density may allow fish to act as cues for waterfowl (Mallory et al. 1994b). Furthermore, correlation between specific waterfowl species and fish assemblage can also serve as cues for wildlife managers interested in conservation of specific species, regardless of whether waterfowl are responding to interactions with fish or to environmental characteristics of a lake. These relationships should be verified regionally, however, because of the different patterns that have been observed in the Canadian Shield and Boreal Plains regions.

3.4.4 Management Implications and Conclusions:

My analysis suggested that environmental characteristics of a lake contributed more to variation in breeding and moulting waterfowl density and community composition than did interactions between fish and waterfowl. Breeding and moulting waterfowl density increased with shallow lake productivity. Selection of priority waterfowl habitat for conservation should therefore focus on basin productivity based on parameters such as TP, SAV, and depth. However, my results also indicated that interactions with fish contributed to a small but significant portion of variation in the breeding waterfowl communities. The greater importance of fish presence to waterfowl during the breeding season and the lower densities of Dytiscidae in fish lakes, suggest that competition with fish may be a minor force structuring breeding waterfowl density and community composition. Further investigation of the impact of fish presence and fish assemblages on waterfowl reproductive vital rates and foraging behaviour during the breeding season is necessary to fully understand the interactions between fish and waterfowl in the BTZ. That certain waterfowl species are linked to the fish assemblage of a lake in BTZ is of particular note for wildlife managers interested in targeted delivery of conservation programs.

Table 3.1 Environmental characteristics of 30 study lakes in 2006.

Environmental Variable	Mean	Median	Max	Min
Total phosphorus (µg/L)	306.91	247.64	986.61	12.63
Total nitrogen (µg/L)	3735.29	3240.00	8030.00	923.00
Soluble reactive phoshorus (µg/L)	125.28	38.51	775.00	1.00
Chlorophyll a (µg/L)	65.45	30.92	633.97	1.87
Maximum depth (cm)	426.07	229.00	1880.00	44.00
Secchi depth (cm)	40.49	39.59	232.32	14.00
Turbidity (NTU)	18.58	12.05	82.60	0
Submerged Aquatic Vegetation *	4.15	4.00	5	1
DOC (mg/L)	68.70	64.04	108.60	0.10

*Submerged Aquatic Vegetation abundance described by 1-5 scale defined in (Bayley and Prather 2003)

Table 3.2 Waterfowl species present in my study lakes in 2006.

Common Name	Species Code	Scientific Name
Dabbling Ducks		
American Wigeon	AMWI	*Anas Americana*
Blue-winged teal	BWTE	*Anas discors*
Cinnamon Teal	CITE	*Anas cyanoptera*
Gadwall	GADW	*Anas strepera*
Green-winged Teal	AGWT	*Anas crecca*
Mallard	MALL	*Anas platyrhynchos*
Northern Pintail	NOPI	*Anas acuta*
Northern Shoveler	NOSH	*Anas clypeata*
Diving Ducks		
Bufflehead	BUFF	*Bucephala albeola*
Canvasback	CANV	*Aythya valisineria*
Common Goldeneye	COGO	*Bucephala clangula*
Hooded Merganser	HOME	*Lophodytes cucullatus*
Redhead	REDH	*Aythya Americana*
Ring-necked Duck	RNDU	*Aythya collaris*
Ruddy Duck	RUDU	*Oxyura jamaicensis*
Scaup (Lesser and Greater)	SCAU	*Aythya (affinis and marila)*
Surf Scoter	SUSC	*Melanitta perspicillata*
White-winged Scoter	WWSC	*Melanitta fusca*

Table 3.3 Fish species present in my study lakes in 2006.

Common Name	Species Code	Scientific Name
Small- bodied fish		
Fathead minnows	FTMN	*Pimephales promelas*
Brook stickleback	BRST	*Culea inconstans*
Spottail shiners	SPSH	*Notropis hudsonius*
Iowa darter	IWDA	*Etheostoma exile*
Large- bodied fish		
Northern pike	NRPK	*Esox lucius*
Cisco	CISC	*Coregonus artedi*
Rainbow trout	RNTR	*Oncorhynchus mykiss*
Yellow perch	YLPR	*Perca flavescens*
Walleye	WALL	*Sander vitreus*

Table 3.4 MRPP pairwise comparisons of breeding waterfowl community composition based on A. waterfowl species presence-absence and B. waterfowl density. Bolded p-values indicate significance using the Benjamini-Hochberg method to control the False Discovery Rate.

A.

	Small-bodied fish lakes	Large-bodied fish lakes
Fishless lakes	.34	**.007***
Small-bodied fish lakes	--	.07

B.

	Small-bodied fish lakes	Large-bodied fish lakes
Fishless lakes	.07	**.0009***
Small-bodied fish Lakes	--	.038

Table 3.5 MRPP pairwise comparisons of moulting waterfowl community composition based on A. waterfowl species presence-absence and B. waterfowl density. Bolded p-values indicate significance using the Benjamini-Hochberg method to control the False Discovery Rate.

A.

	Small-bodied fish lakes	Large-bodied fish lakes
Fishless lakes	.081	**.002***
Small-bodied fish lakes	--	.022

B.

	Small-bodied fish lakes	Large-bodied fish lakes
Fishless lakes	.025	**.007***
Small-bodied fish lakes	--	.12

Table 3.6 Breeding and moulting waterfowl species linked by indicator species analysis to fish assemblage based on A. species presence-absence data and B. waterfowl density data.

A.

	Fishless lakes	Small-bodied fish lakes	Large-bodied fish lakes
Breeding period	Northern Shoveler	None	None
Moulting period	Mallard Gadwall American Wigeon Blue-winged Teal	Canvasback	None

B.

	Fishless lakes	Small-bodied fish lakes	Large-bodied fish Lakes
Breeding period	Blue-winged Teal Northern Shoveler Mallard Gadwall American Wigeon Scaup	None	Common Goldeneye
Moulting period	Blue-winged Teal Mallard Gadwall American Wigeon	Canvasback Ringnecked duck	None

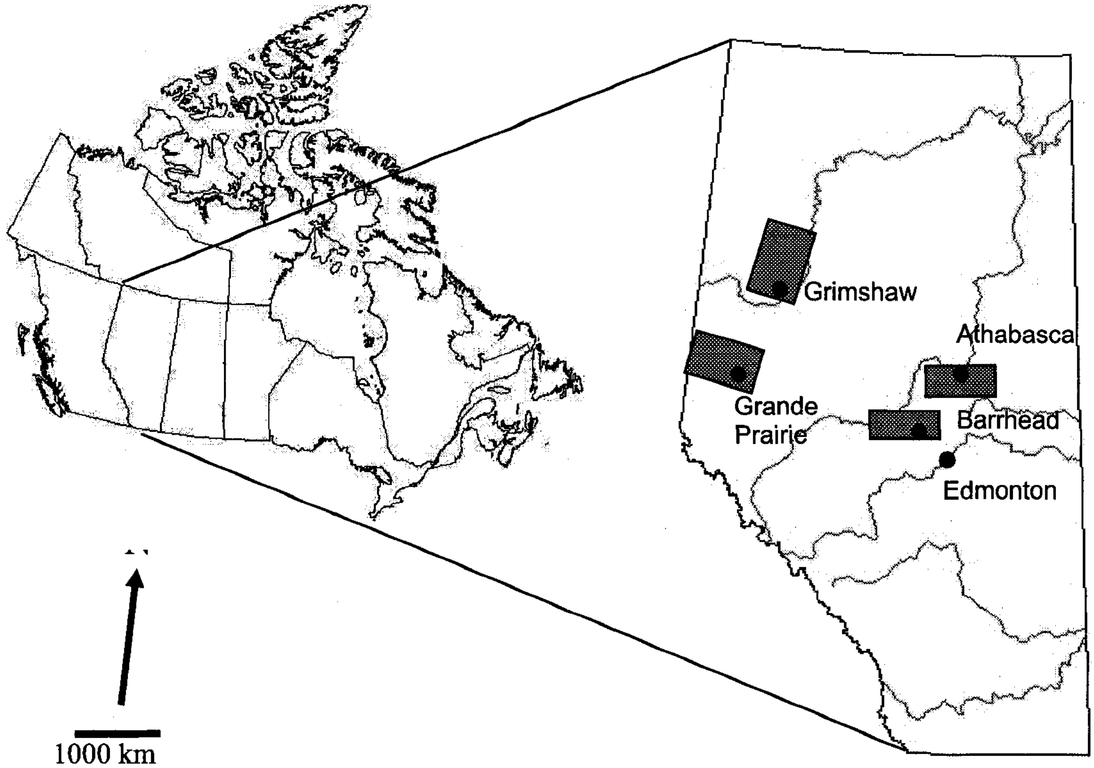
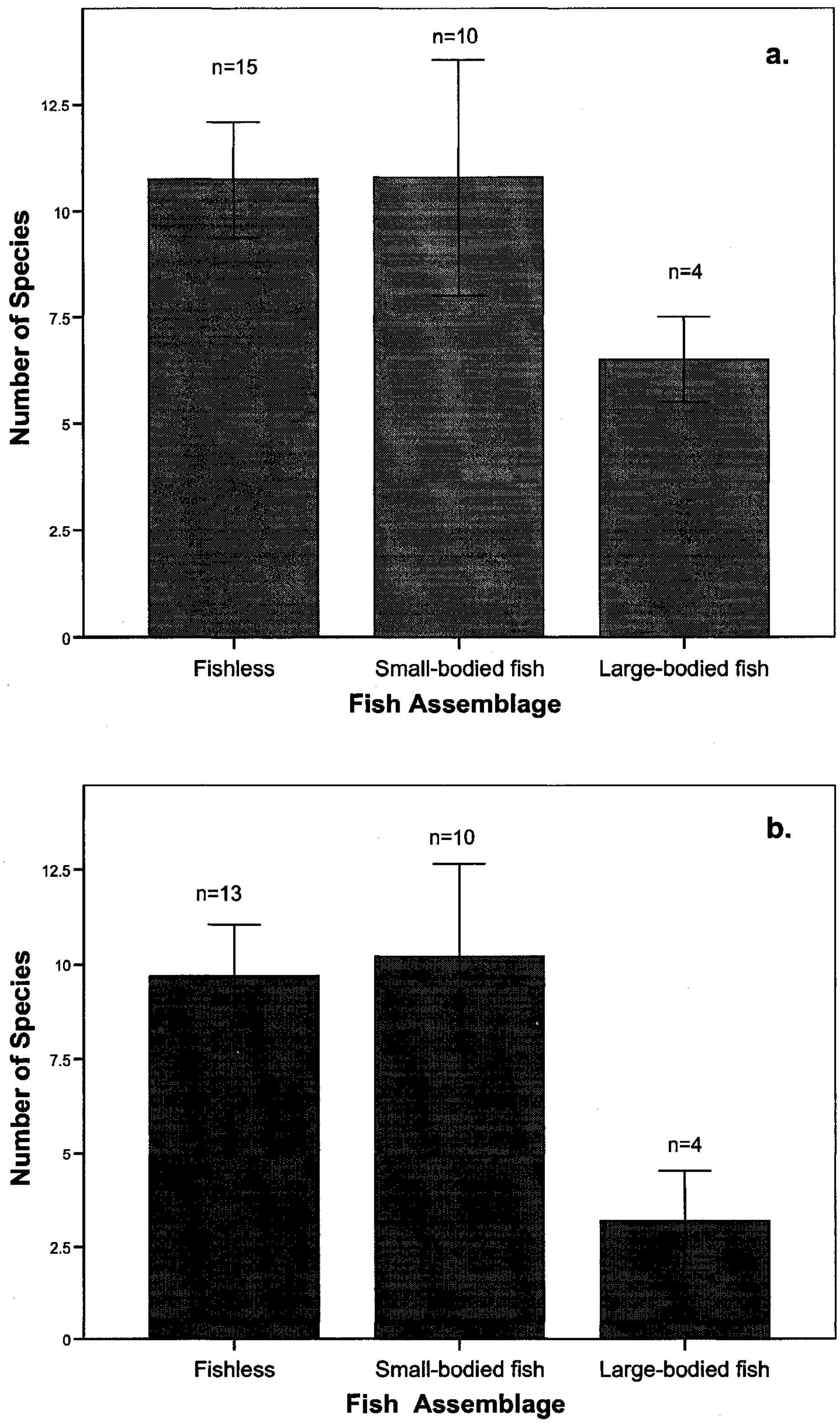


Figure 3.1 Location of four Boreal Transition Zone sub-regions in Alberta, Canada. Study lakes are located within the shaded areas. Black dots are nearby communities.



Figures 3.2 a. Breeding waterfowl species richness in BTZ lakes grouped according to fish assemblage and b. Moulting waterfowl species richness by fish assemblage.

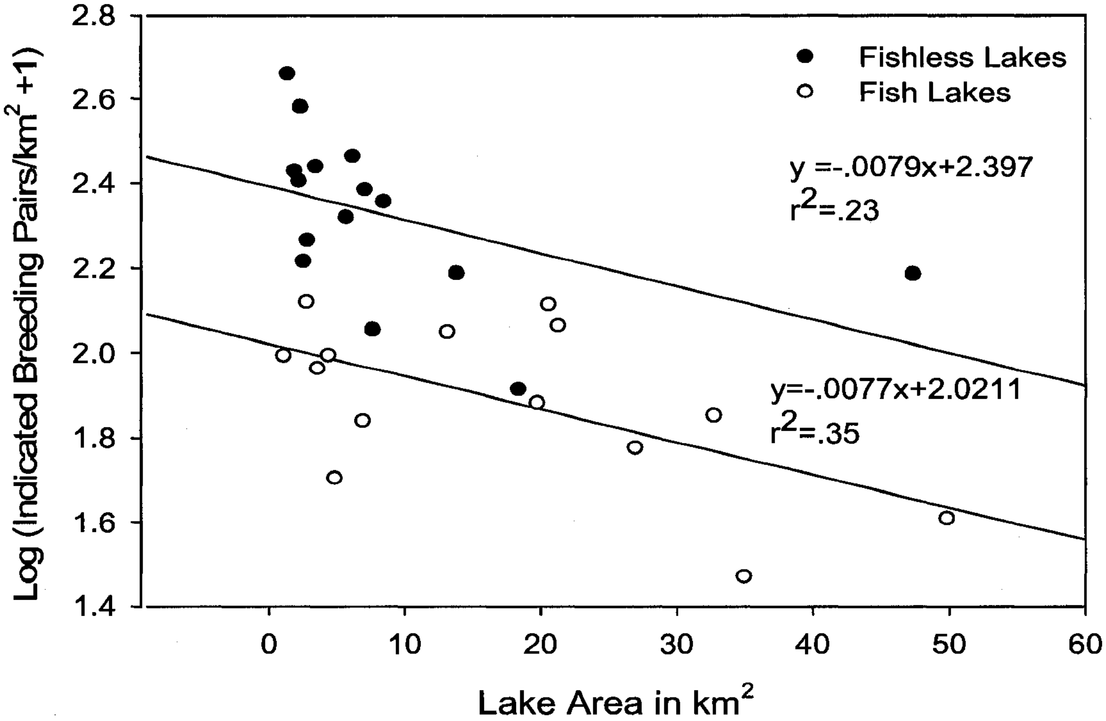


Figure 3.3 Breeding waterfowl density in fishless and fish-bearing lakes regressed against lake area. The difference in intercept values is the difference in the waterfowl density of the two groups after accounting for area.

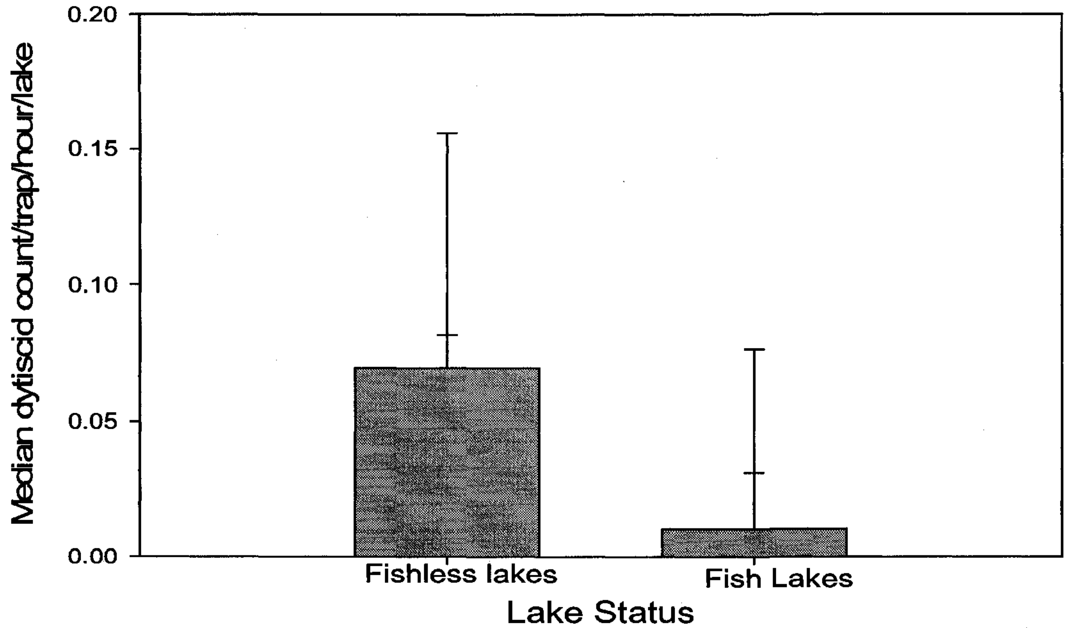


Figure 3.4 Median abundance of dytiscid beetles per trap per hour per lake in fishless and fish-bearing lakes. Horizontal bars are upper and lower standard error limits.

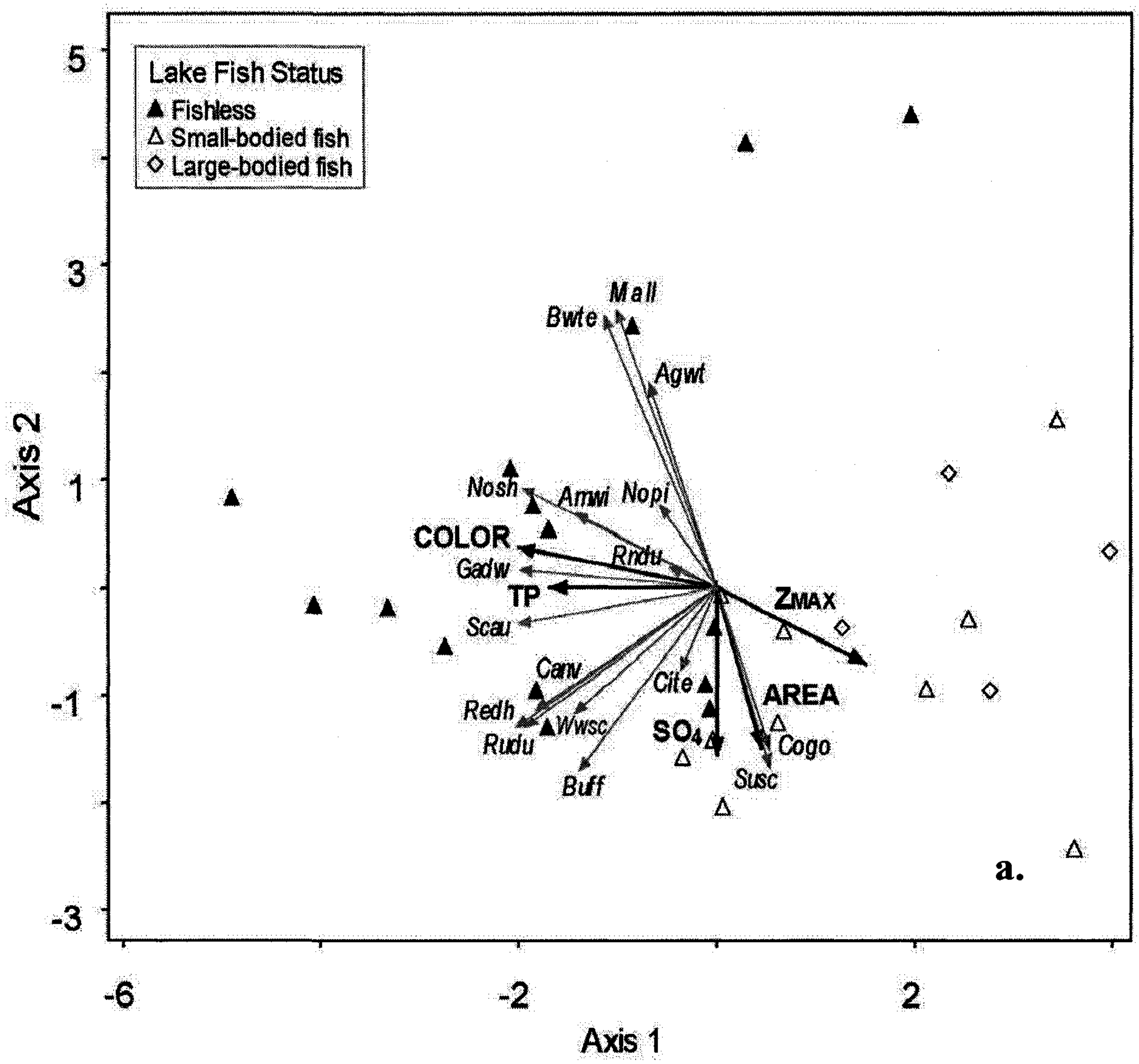


Figure 3.5 Principle Components Analysis joint plot of breeding waterfowl density in 27 lakes in the BTZ. Triangles and diamonds represent lakes (categorized by their fish assemblages) plotted in waterfowl species space. Lines are joint plot vectors, the angles and lengths of which represent the directions and strengths of the species (grey) or environmental variables (black) to the ordination axes. R^2 cutoff = 0.35 for environmental variables. Waterfowl species codes (Table 3.2) are plotted at end points of species vectors.

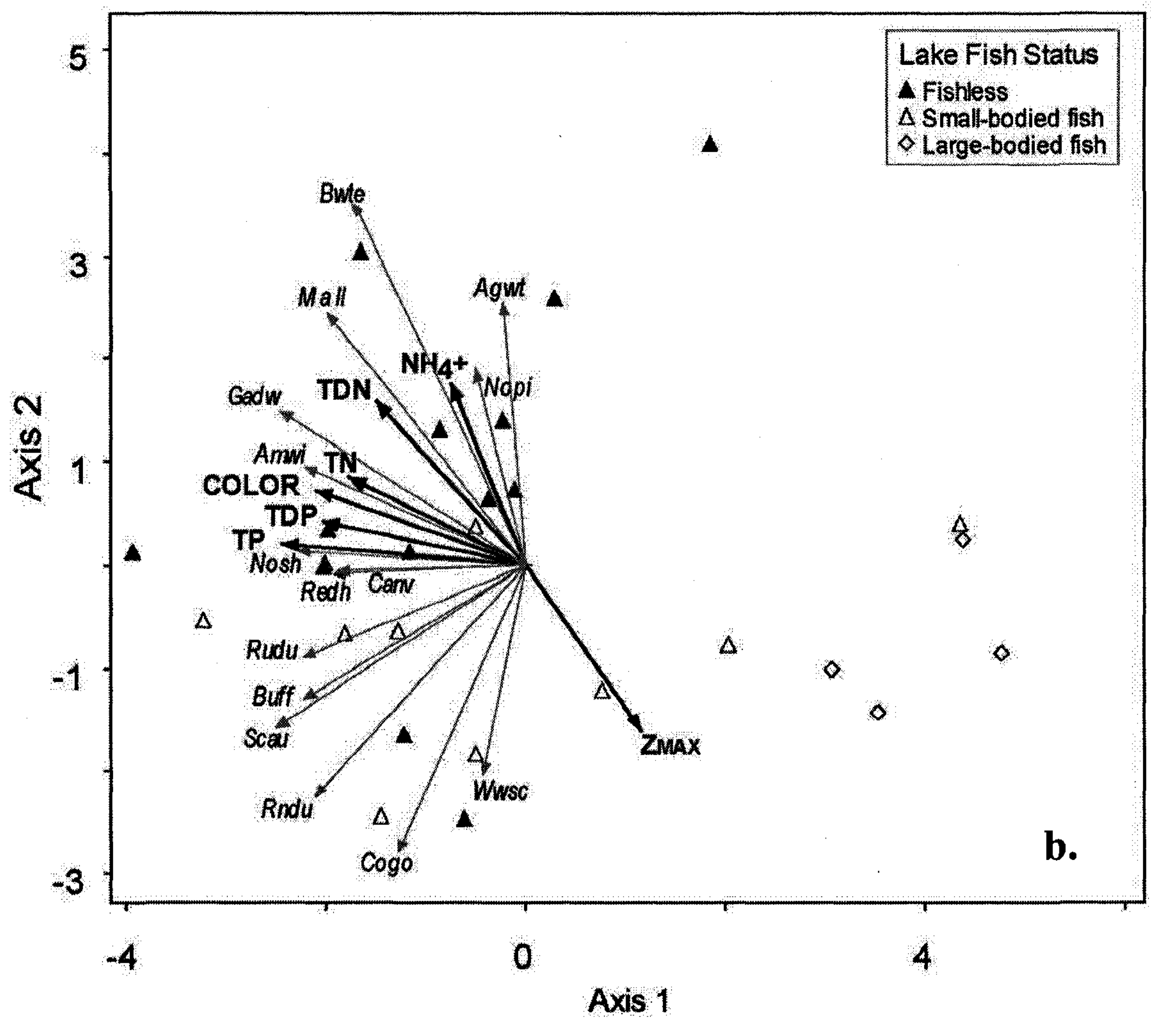


Figure 3.6 Principle Components Analysis joint plot of moulting waterfowl density in 27 lakes in the BTZ. Triangles and diamonds represent lakes (categorized by their fish assemblages) plotted in waterfowl species space. Lines are joint plot vectors, the angles and lengths of which represent the directions and strengths of the species (grey) or environmental variables (black) to the ordination axes. R^2 cutoff = 0.35 for environmental variables. Waterfowl species codes (Table 3.2) are plotted at end points of species vectors.

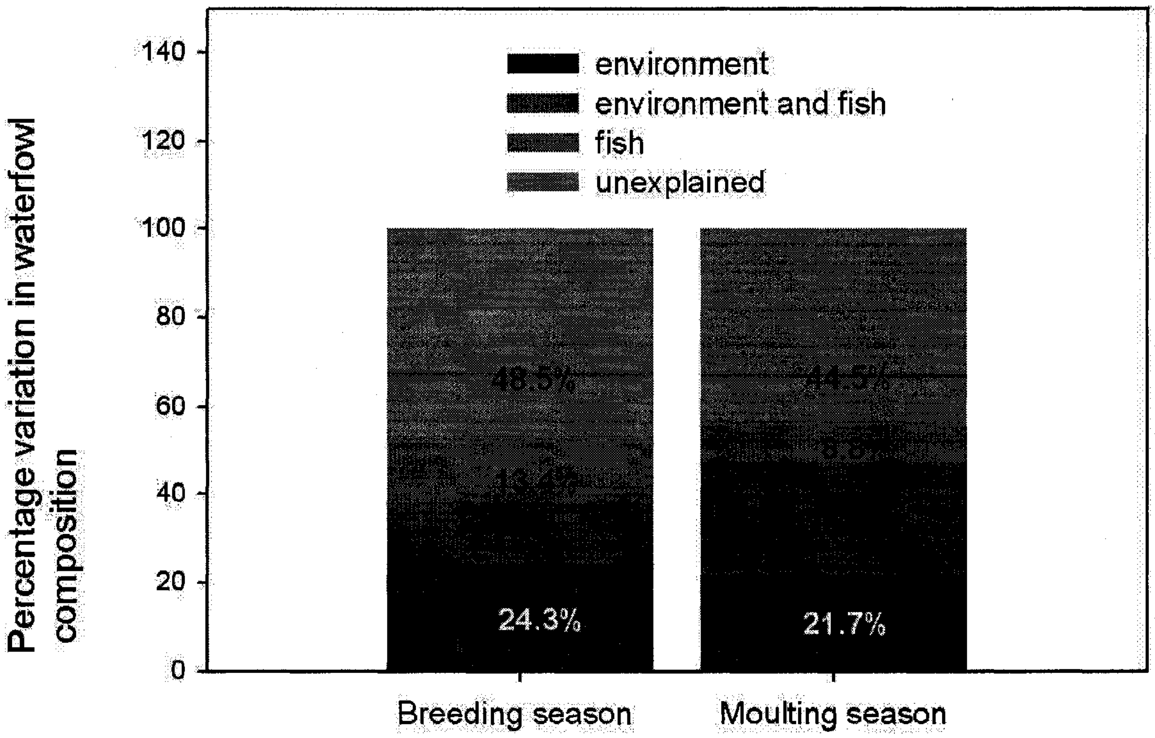


Figure 3.7 The relative contributions of fish and environment to variation in waterfowl communities (density of all waterfowl species present) in BTZ study lakes, as determined through variance partitioning based on RDA. The percentage variation in waterfowl community structure for which each explanatory data set can account is shown for both breeding and moulting waterfowl data. During the breeding season, environment was summarized by color, SAV, K^+, and area. During the moulting season, environment was summarized by TP, maximum depth, DOC, and lake area.

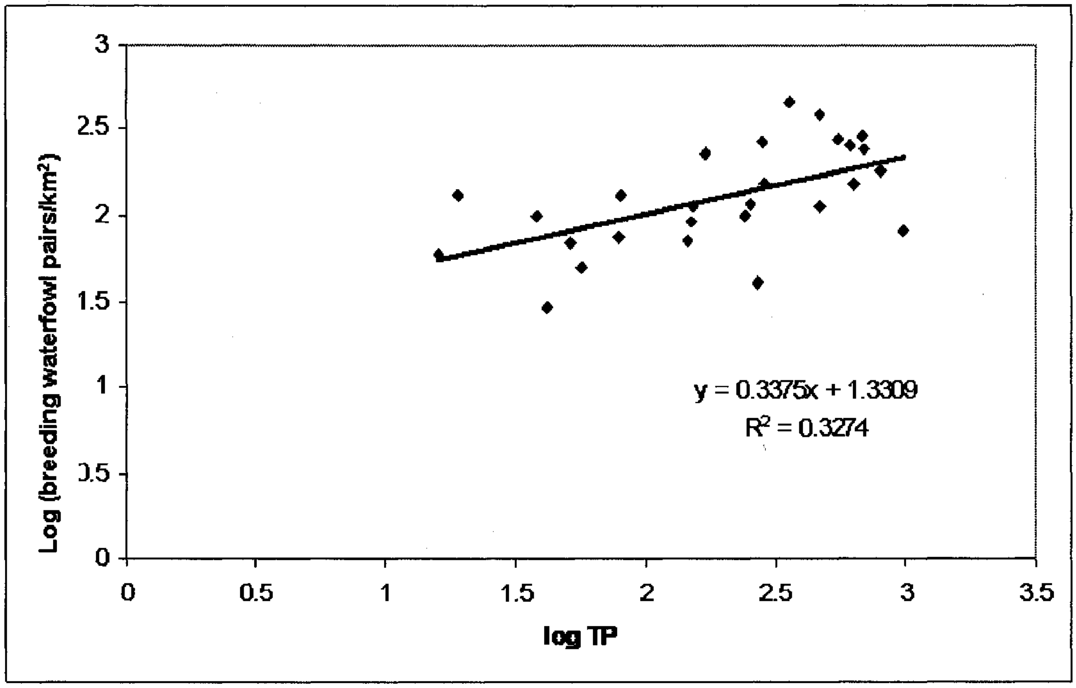


Figure 3.8 Breeding waterfowl density as a function of total phosphorus. Values on both axes are log (x+1) transformed.

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Chapter 4

Conclusions

This thesis represents a significant contribution towards understanding fish assemblages and their influence on waterfowl density, species richness, and community composition in shallow lakes of the Boreal Transition Zone (BTZ) of Alberta and the broader Boreal Plains Ecozone. In Chapter 2, I demonstrated that lakes in the BTZ can be classified into 3 groups based on fish assemblage; fishless lakes, lakes with only small-bodied fish and lakes with large-bodied fish. These groups were consistent with findings from other studies in Alberta (Robinson and Tonn 1989, Paszkowski and Tonn 2000, Tonn et al. 2003) providing further support that lakes contain a limited number of fish assemblages rather than random sets of regional species.

Chapter 2 also identified the importance of environmental factors that influence hypoxic conditions and associated fish kills to fish assemblage structure in the BTZ. Landscape disturbances that increase the likelihood of hypoxic conditions therefore have the greatest potential to influence fish assemblages in the BTZ. Because high lake productivity (TP or chlorophyll *a*) increases winter oxygen depletion rates (Babin and Prepas 1985), increased agricultural or other developments that increase nutrient loads would likely impact fish assemblages and could increase the number of small-fish and fishless lakes, but do not appear to be doing so at present in my study lakes. I found that maximum depth was also an important determinant of fish assemblage, as depth can influence oxygen depletion and associated fish kills (Welch et al. 1976, Barica and

Mathias 1979). Because lake depth may be affected by changing hydrologic regimes, climate change will likely influence fish assemblage structure in the BTZ.

In contrast to studies that show increases in turbidity with fish additions (Hanson and Butler 1994, Hanson et al. 2005, Norris 2006), I found that fishless lakes in the BTZ were not clearer than fish-bearing lakes. I suggested that high TP and TN concentrations overshadowed any contribution of fish to increased frequency of turbid lakes. Thus, increased nutrient loads would likely influence clear-turbid state dynamics in BTZ shallow lake systems. Naturally eutrophic - hypereutrophic Alberta lakes may demonstrate different clear-turbid state dynamics than oligotrophic-eutrophic systems in eastern North America.

In Chapter 3, I found that highly productive, fishless systems were the most important type of shallow lake to breeding and moulting waterfowl. This result is consistent with other studies that report a positive relationship between waterfowl and productivity (Nilsson and Nilsson 1978, Eriksson 1985, Elmberg et al. 1993, Hoyer and Canfield 1994, Longcore et al. 2006) and indicates that the relationship holds in a set of eutrophic to hypereutrophic lakes. Indeed, I found that environmental characteristics of shallow lakes were more important determinants of waterfowl density and composition than were fish. This is an important scientific contribution to understanding fish-waterfowl interactions because many studies have examined indirect interactions between fish and waterfowl (i.e. impacts of fish on macroinvertebrates; Giles 1994, Hanson and Butler 1994, Mallory et al. 1994 or diet overlap between fish and waterfowl; Eadie and Keast 1982) but few have compared the relative contributions of both environment and fish to waterfowl. My results suggested that fish and waterfowl in the BTZ responded to many of the same environmental factors. This may be true in many other regions as well. Close examination of negative associations between fish and waterfowl is therefore important before concluding that fish negatively affect waterfowl.

The smaller but significant contribution of fish to variation in breeding waterfowl density and composition and the link between fish assemblage and certain waterfowl species (e.g. scaup) indicates that the influence of fish on waterfowl should also not be ignored. Management of waterfowl species that are linked to fish assemblage in the BTZ, particularly Lesser scaup (*Aythya affinis*) a species of concern in the region, should consider this relationship in targeted conservation program delivery. Fish stocking or accidental fish introductions to important waterfowl habitat should not be encouraged because of the negative relationship between fish and waterfowl during the breeding season. Waterfowl conservation initiatives would further benefit from future research initiatives focused on the effect of fish on waterfowl reproductive vital rates. Given continued waterfowl habitat loss and increasing competing demands for remaining wetlands and lakes (Norris 2006), consideration of the interactions between fish and waterfowl is important to shallow lake conservation and management.

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Appendix 1: Breeding waterfowl survey visibility correction factor amendment

After completion of this thesis, Ducks Unlimited Canada amended their visibility correction factor for breeding waterfowl. This amendment slightly altered the Indicated Breeding Pair (IBP) values of certain species in the waterfowl data set. To evaluate how the amended data set compared with the original data set, I used a Mantel Test for concordance between the two waterfowl data sets. The original and the amended waterfowl data sets were highly concordant (Mantel Test, r=0.999, p=0.0001, 9999 randomization runs, Bray-Curtis distance measure). I also ran a Principal Components Analysis (PCA) of the amended waterfowl data set. The PCA of the amended waterfowl dataset was nearly identical to the original PCA. Overlays of the fish assemblage classification and a joint plot of the environmental parameters most associated with the PCA showed nearly identical relationships between waterfowl, fish and environmental parameters as the original data set. Because amended data was only provided for 27 of the original 30 lakes, comparisons have been made between the original and amended data sets in these 27 lakes and between the amended data set for these 27 lakes and the 29 lakes original data set presented in Chapter 3.

I concluded that the amendment did not alter the differences in waterfowl densities between individual lakes or lake types, presumably because the amendment resulted in systematic changes in IBP values of certain waterfowl species across all lakes and lake types. Thus, despite the amendments to the waterfowl data set, I believe that the analyses, discussions and conclusions presented in this thesis remain valid and complete.

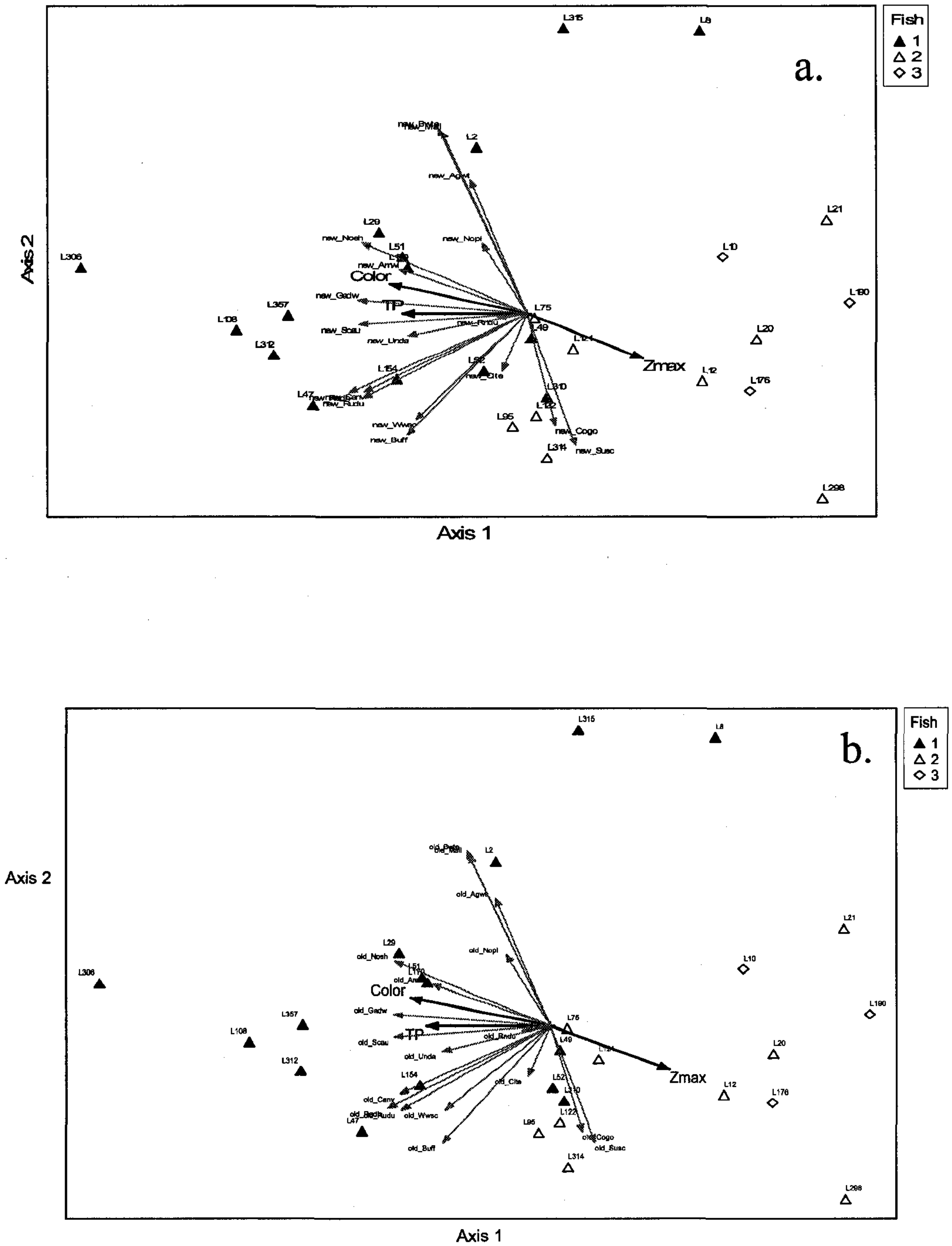

Figure A1. Principal Components Analysis joint plot of a. breeding waterfowl from the amended data set and b. breeding waterfowl from the original data set. See table 3.2 for species codes. Environmental variables with a $r^2 > 0.35$ are plotted as black vectors.

Appendix 2: Data Tables

Table A1: May environmental characteristics of 30 lakes surveyed in 2006

Fish Site	TDN (µg/L)	TDP (µg/L)	DOC (mg/L)	Cl (mg/L)	SO4 (mg/L)	Na (mg/L)	K (mg/L)	Ca (mg/L)	Mg (mg/L)	Si (mg/L)	Alkalinity (mg/L)	Bicarbonate (mg/L)
L10	1870.00	21.52	21.98	5.45	14.47	28.24	31.99	15.75	71.07	0.30	400.95	433.05
L108	1840.00	32.53	36.03	2.54	19.11	2.85	14.14	22.77	8.68	6.23	78.27	95.44
L12	2010.00	361.51	27.57	3.49	5.37	4.67	10.65	35.56	8.54	0.30	124.62	131.13
L121	1230.00	15.40	24.04	7.28	11.10	15.00	4.40	25.24	7.79	0.30	100.71	122.79
L122	1610.00	37.90	27.64	3.95	3.38	13.52	4.30	23.37	7.33	0.30	106.23	129.53
L15	787.00	8.10	12.99	1.31	53.65	7.09	5.99	35.62	22.25	0.30	142.97	165.94
L154	2540.00	62.76	43.77	1.32	4.06	10.91	15.79	28.14	9.98	0.30	131.39	160.19
L170	2620.00	60.82	31.75	7.17	566.45	92.89	32.39	137.58	46.52	0.30	155.05	189.05
L176	1820.00	41.30	15.38	2.88	6.88	3.60	10.65	29.47	10.21	1.06	120.88	147.39
L190	965.00	9.28	15.76	1.49	1.21	9.77	9.44	21.85	26.62	0.30	186.29	212.74
L2	3510.00	55.33	48.02	6.13	1.72	39.34	32.19	25.53	48.17	2.94	370.00	395.91
L20	1720.00	14.47	25.28	2.61	0.83	20.31	14.24	29.57	19.83	0.30	203.90	241.27
L21	1650.00	18.49	25.98	1.34	2.74	25.07	6.30	27.29	10.30	1.23	159.92	194.99
L29	2540.00	42.80	34.25	4.29	1.12	14.64	20.64	33.71	19.98	1.67	207.43	242.77
L298	1580.00	14.90	26.53	1.23	198.55	24.55	17.12	31.49	41.20	0.30	95.46	83.59
L306	1660.50	56.93	22.66	10.26	2.25	23.05	23.16	29.81	11.13	0.30	172.94	192.52
L310	2630.00	809.30	38.27	18.07	4.38	89.24	55.42	28.61	29.48	0.30	407.80	445.41
L312	2980.00	191.88	36.39	17.05	1.74	48.26	35.08	31.09	21.48	0.30	273.70	328.21
L314	1690.00	59.50	27.23	3.80	23.62	32.10	8.25	35.32	10.47	1.07	173.63	202.98
L315	2110.00	205.68	31.63	45.51	0.05	41.11	53.63	30.58	14.98	0.56	213.93	260.84
L357	2550.00	1070.32	34.71	3.73	8.58	8.57	32.59	45.52	17.55	7.30	217.74	216.07
L43	1590.00	31.70	20.09	7.77	53.86	8.56	24.01	30.13	26.27	0.30	156.21	151.41
L448	1890.00	72.26	19.10	12.49	102.98	20.84	25.11	36.28	30.74	0.59	169.49	198.61
L47	1420.00	394.62	16.71	1.40	10.25	6.47	9.65	25.92	7.45	1.28	105.52	39.85
L49	3170.00	81.50	40.05	9.30	1.02	32.29	17.54	22.47	10.36	0.30	173.35	160.09
L51	2610.00	56.10	37.96	6.45	0.84	33.33	14.54	11.72	3.42	0.30	123.50	150.58
L52	2960.00	63.30	32.75	5.92	1.05	34.85	13.94	16.39	5.34	0.30	150.11	183.02
L75	2470.00	24.40	36.19	11.32	311.21	162.34	19.37	33.06	35.07	0.73	272.78	307.48
L8	4840.00	47.00	57.08	4.63	0.08	13.42	19.69	66.60	26.80	5.19	313.58	380.24
L95	1370.00	24.07	26.26	1.05	1.69	4.19	5.95	41.40	13.89	2.29	163.47	193.59

Fish Site ID	DO (mg/L)	Specific Conductivity (µS/cm)	pH	Secchi Depth (cm)	Turbidity Reading (NTU) 1	SAV rating	Turbid Clear or Mixed	TP (µg/L)	NH4+ (µg/L)	NO2+NO3 (µg/L)	TN (µg/L)	SRP (µg/L)
L10	9.65	718.93	8.27	321.33	0.30	1.00	T	42.75	27.63	5.55	1790.00	4.54
L108				57.00		2.00	C	193.10	4.61	2.93	2305.00	2.98
L12	10.27	260.30	8.43	90.00	3.10	2.00	M	435.14	41.93	5.21	2170.00	297.92
L121	0.00	242.80	7.72	119.00	2.50	4.00	T	47.30	24.80	2.51	1290.00	2.10
L122	0.05	222.50	7.73	75.00	10.80	3.00	C	115.70	36.60	2.44	1970.00	7.00
L15	0.09	370.60	7.36	319.67	0.00	2.00	T	15.10	18.30	2.48	906.00	4.20
L154	0.05	270.60	8.13	80.00	12.00	2.00	C	148.77	46.90	1.97	3000.00	3.48
L170	0.01	1372.33	9.01	49.00	2.20	3.00	T	94.90	307.00	71.40	2680.00	26.56
L176	0.06	256.23	8.14	262.33	0.60	2.00	C	52.00	364.00	256.00	1920.00	16.68
L190	0.06	342.00	8.33	180.00	0.80	3.00	M	24.88	17.20	2.65	1250.00	1.90
L2	9.17	671.03	8.22	31.33	16.00		C	199.84	31.53	6.55	4350.00	6.15
L20	11.55	381.07	7.98	71.67	4.60	2.00	M	44.82	23.53	4.80	1880.00	4.51
L21	10.74	276.00	7.80	90.00	1.80	4.00	T	44.44	35.17	5.13	1560.00	2.69
L29	0.08	400.87	7.91	37.33	12.00	2.00	T	173.70	30.67	2.92	3210.00	2.00
L298	0.07	589.57	9.46	128.67	2.10	3.00	T	36.90	21.90	3.44	1870.00	1.00
L306	0.00	359.20	8.27	80.00	5.20		C	138.11	58.40	3.96	1890.00	12.34
L310				53.00		3.00	M	917.84	1.00	3.21	3060.00	722.04
L312	0.00	558.30	7.80	74.00	8.00	2.00	C	286.56	105.00	6.30	3260.00	137.30
L314	0.00	379.10	8.40	30.00	35.00		C	336.30	10.30	4.69	2750.00	7.40
L315	0.08	583.70	7.62	35.00	6.60	4.00	M	301.46	110.00	4.33	2310.00	142.60
L357	0.06	423.60	8.55	37.00	14.50	2.00	C	1169.26	32.60	4.51	3150.00	889.53
L43	0.07	409.83	7.92	53.67	17.30		C	126.30	16.90	2.19	2240.00	7.70
L448	0.08	562.57	9.18	71.33	12.10	2.00	C	169.07	226.00	2.95	2710.00	16.70
L47	12.26	218.30	9.53	50.67	3.50	3.00	M	491.26	64.57	4.03	1490.00	320.95
L49	12.18	297.40	8.73	27.67	31.80	2.00	C	390.78	161.67	9.47	4140.00	5.73
L51	10.46	240.90	7.89	29.33	7.00		M	291.50	58.23	5.87	3790.00	3.57
L52	9.66	304.77	7.83	48.00	29.00		C	188.90	70.03	7.54	3040.00	5.79
L75	0.09	1150.00	7.80	85.33	8.50		C	75.80	62.50	2.80	2700.00	1.00
L8	0.05	573.10	7.80	10.00		4.00	T	158.70	65.13	4.70	5420.00	9.70
L95				62.00			C	141.76	2.92	3.31	1930.00	1.88

Fish Site ID	Carbonate (mg/L)	Color (mg/L Pt)	TDS (mg/L)	Chl-a (µg/L)	%ag	Zmax (in cm)	Isolation Metric	Connectivity Metric	Modified connectivity	Area (ha)	Region
L10	27.45	19.60	509.00	0.91	50.00	937.00	1.00	1.00	1.00	28.17	Barrhead
L108	0.00	100.00	240.00	11.29	60.20	135.00	1.00	0.00	0.00	23.58	County W
L12	10.23	50.50	217.00	17.79	75.57	400.00	0.00	2.00	3.00	498.62	Barrhead
L121	0.00	39.90	195.00	9.43	18.06	208.00	0.00	2.00	3.00	327.91	County W
L122	0.00	73.70	192.00	4.61	16.46	184.00	0.00	2.00	3.00	213.30	County W
L15	4.12	9.60	261.00	2.54	36.06	1880.00	0.00	2.00	3.00	240.03	Lakeland
L154	0.00	104.10	233.00	40.58	38.49	95.00	1.00	0.00	0.00	138.70	County W
L170	0.00	76.90	1098.00	2.34	71.53	69.00	1.00	0.00	1.00	85.05	Grimshaw
L176	0.00	27.80	255.00	3.20	21.27	639.00	1.00	0.00	1.00	36.28	Grimshaw
L190	7.08	12.10	238.00	2.65	7.62	1412.00	1.00	0.00	1.00	269.81	Lakeland
L2	27.15	70.00	497.00	54.39	67.97	146.00	1.00	0.00	1.00	57.16	Barrhead
L20	3.61	33.00	318.00	16.03	45.38	220.00	1.00	0.00	0.00	49.00	Barrhead
L21	0.00	44.90	237.00	6.84	29.86	186.00	1.00	0.00	0.00	11.13	Barrhead
L29	4.99	67.00	307.00	52.61	39.65	328.00	1.00	0.00	1.00	19.35	Barrhead
L298	16.13	17.20	462.00	6.17	0.44	333.00	1.00	0.00	1.00	349.86	Grimshaw
L306	9.02	66.90	265.00	17.86	82.93	75.00	1.00	0.00	1.00	13.81	County W
L310	25.48	47.40	606.00	27.08	92.84	588.00	1.00	0.00	0.00	184.13	County W
L312	2.71	66.50	412.00	22.95	86.67	113.00	1.00	0.00	0.00	61.81	County W
L314	4.28	100.70	324.00	74.07	80.37	121.00	1.00	0.00	1.00	131.64	County W
L315	0.00	102.80	378.00	6.23	82.39	54.00	1.00	0.00	0.00	28.53	County W
L357	24.30	85.80	382.00	39.38	69.51	115.00	1.00	0.00	0.00	35.00	Grimshaw
L43	19.20	28.60	294.00	55.99	54.91	668.00	0.00	2.00	3.00	69.00	Lakeland
L448	3.96	45.90	387.00	28.16	40.90	850.00	0.00	1.00	1.00	341.00	Lakeland
L47	43.67	63.70	218.00	17.90	49.14	72.00	1.00	0.00	0.00	22.58	Barrhead
L49	25.21	83.60	300.00	108.61	40.89	247.00	1.00	0.00	0.00	474.34	Barrhead
L51	0.00	87.30	222.00	66.68	60.00	122.00	1.00	0.00	0.00	71.31	Barrhead
L52	0.00	69.00	234.00	51.49	53.00	246.00	1.00	0.00	0.00	76.86	Barrhead
L75	12.35	54.60	845.61	12.42	53.18	398.00	0.00	2.00	3.00	197.84	Barrhead
L8	1.03	84.70	458.00	80.66	43.22	44.00	1.00	0.00	0.00	25.80	Barrhead
L95	2.82	56.70	248.00	19.56	0.00	229.00	1.00	0.00	1.00	206.15	County W

Table A2: August environmental characteristics of 30 lakes surveyed in 2006

Fish Site ID	Region	DO (mg/L)	Specific Conductivity (µS/cm)	pH	Secchi Depth (cm)	Turbidity (NTU)	SAV rating	Clear, Turbid or Mixed	TP (µg/L)	NH4+ (µg/L)	NO2+NO3 (µg/L)	TN (µg/L)
L10	Barrhead	10.59	715.87	10.11	166.33	1.60		T	19.11	5.67	2.14	1,590.00
L108	County W	7.34	219.50	8.05	22.00	21.30	2.00	T	465.50	19.30	1.17	4,380.00
L12	Barrhead	9.67	257.03	9.09	47.00	9.50	4.00	T	271.17	37.60	1.45	3,260.00
L121	County W	10.17	241.10	10.69	70.00	5.10	5.00	T	145.19	52.10	1.00	2,620.00
L122	County Wt	9.31	222.40	10.61	75.00	3.00	4.00	T	254.17	49.80	3.93	2,620.00
L15	Lakeland	8.55	367.50	7.97	232.33	0.00	2.00	C	12.63	4.45	1.00	945.00
L154	County W	8.78	273.20	11.00	50.00	4.40	5.00	T	289.07	112.00	1.00	5,670.00
L170	Grimshaw	17.32	1714.00	8.56	39.33	0.00	3.00	T	170.95	76.30	1.55	3,720.00
L176	Grimshaw	12.23	225.07	9.16	116.00	7.90	2.00	T	149.81	15.30	2.71	2,200.00
L190	Lakeland	9.20	344.30	10.03	230.00	0.00	2.00	C	16.10	20.40	1.22	923.00
L20	Barrhead	11.95	319.13	7.85	52.33	1.80	4.00	C	57.02	22.90	1.47	2,330.00
L21	Barrhead	11.71	247.87	8.05	90.67	0.00	5.00	C	38.05	23.60	2.56	2,940.00
L29	Barrhead	10.67	342.20	9.63	36.67	39.40	3.00	T	282.20	35.40	1.21	4,330.00
L298	Grimshaw	11.22	672.33	10.05	72.33	4.50	4.00	T	42.25	24.60	2.52	2,250.00
L306	County W	7.83	430.30	8.46	43.00	2.40	5.00	C	358.00	81.30	3.21	4,760.00
L310	County W	12.99	889.20	9.49	50.00	24.30	5.00	T	985.61	51.50	3.66	4,080.00
L312	County W	8.16	602.90	9.42	68.00	2.60	4.00	T	682.80	89.80	3.22	6,855.00
L314	County W	7.37	379.10	8.63	14.00	50.20	5.00	T	467.40	27.40	4.57	5,900.00
L315	County W	6.64	951.60	7.38	15.00	2.50	5.00	C	799.00	92.10	3.45	6,660.00
L357	Grimshaw	13.14	387.30	12.67	32.33	23.70	4.00	T	547.65	25.50	2.44	5,475.00
L43	Lakeland	8.25	396.70	8.54	58.00	10.90	2.00	T	51.20	51.80	4.31	2,530.00
L448	Lakeland	6.22	582.03	8.36	33.33	56.10	1.00	T	241.10	11.10	1.69	2,970.00
L47	Barrhead	11.56	391.77	8.67	45.67		5.00	T	611.74	45.40	1.00	3,140.00
L49	Barrhead	15.99	385.43	8.24	22.00	82.60	5.00	T	628.88	86.40	4.45	8,030.00
L51	Barrhead	20.23	342.10	10.10	28.00	19.70	4.00	M	694.88	50.90	2.64	6,170.00
L52	Barrhead	12.94	350.00	10.72	74.33	0.00	4.00	T	153.53	43.10	1.00	3,420.00
L75	Barrhead	7.28	125.63	10.68	70.00	10.40	3.00	T	78.46	89.40	2.68	3,220.00
L95	County W	9.37	288.00	6.26	90.00	5.80	3.00	T	80.00	5.31	1.28	1,600.00

Fish Site ID	SRP (µg/L)	TDN (µg/L)	TDP (µg/L)	DOC (mg/L)	Cl (mg/L)	SO4 (mg/L)	Na (mg/L)	K (mg/L)	Ca (mg/L)	Mg (mg/L)	Si (mg/L)	Alkalinity (mg/L)
L10	5.02	1,620.00	16.38	0.10	4.69	13.25	33.29	32.08	9.78	74.45	0.82	402.05
L108	442.44	2,730.00	550.90	111.50	1.86	9.63	4.35	15.79	25.75	9.52	7.52	95.92
L12	89.29	2,380.00	177.82	0.10	3.48	4.41	6.37	9.44	34.44	9.02	1.32	122.55
L121	8.92	2,110.00	56.06	31.69	9.88	6.14	18.62	4.36	20.10	7.60	0.40	51.61
L122	81.96	1,976.00	175.01	33.35	4.56	2.31	17.48	3.37	20.28	7.25	0.79	50.94
L15	1.50	797.00	5.01	14.61	1.29	54.92	7.69	6.06	32.66	22.37	0.31	137.18
L154	61.61	4,590.00	199.31	64.14	1.23	4.53	16.76	18.79	24.56	11.12	1.73	64.19
L170	55.99	3,370.00	103.43	44.59	10.43	143.85	149.38	32.48	129.68	62.50	0.30	104.98
L176	8.53	1,210.00	31.38	17.16	3.08	4.24	3.54	11.12	23.14	10.47	1.32	109.89
L190	2.90	897.00	8.10	16.36	1.58	1.36	10.19	9.24	20.43	27.44	0.82	185.64
L20	1.00	1,810.00	17.02	0.10	1.51	0.53	25.72	14.05	13.41	19.78	0.36	171.86
L21	1.48	2,040.00	19.46	0.10	0.58	0.89	22.50	4.12	16.74	10.32	1.28	126.23
L29	21.03	2,060.00	90.57	0.10	3.40	0.57	18.67	20.26	19.23	19.99	1.86	178.73
L298	5.40	1,830.00	15.01	31.83	2.35	250.71	28.15	18.97	35.87	46.50	0.71	99.94
L306	115.73	4,060.00	265.40	74.98	17.70	0.10	44.00	39.08	18.33	12.20	0.30	194.13
L310	775.33	3,090.00	874.24	40.52	18.91	4.25	106.90	62.45	32.27	31.70	0.30	233.37
L312	406.92	5,360.00	545.75	63.99	23.03	0.60	72.32	42.61	23.47	21.19	0.30	300.71
L314	66.40	3,550.00	194.90	53.97	3.52	35.46	48.50	9.39	24.23	10.20	4.61	160.56
L315	525.79	6,160.00	686.00	108.60	136.04	0.11	104.85	99.05	24.14	12.10	0.31	233.30
L357	160.27	3,620.00	246.89	41.29	3.73	12.53	10.35	38.14	33.06	18.50	0.92	190.60
L43	3.75	1,660.00	18.90	22.97	7.97	55.43	9.11	24.04	22.06	25.98	0.30	138.17
L448	6.60	1,570.00	38.00	20.70	13.71	111.52	22.16	25.58	37.65	32.38	5.26	169.45
L47	344.35	2,980.00	504.06	0.10	2.29	9.42	21.33	14.65	42.96	14.26	12.60	195.31
L49	103.03	4,080.00	226.34	0.10	9.72	1.66	43.55	17.53	22.06	11.43	5.14	178.59
L51	187.03	4,120.00	391.88	0.10	6.15	0.12	54.17	15.10	11.35	3.61	2.16	145.18
L52	14.64	3,280.00	123.74	0.10	4.52	1.30	53.40	11.02	12.52	4.92	1.03	145.90
L75	9.28	2,820.00	46.12	0.10	11.89	374.51	189.90	19.72	32.01	39.18	3.63	265.70
L95	1.55	1,400.00	25.70	53.97	0.77	1.92	5.03	6.41	35.74	14.50	0.57	152.64

Fish Site ID	Bicarbonate (mg/L)	Carbonate (mg/L)	Color (mg/L Pt)	TDS (mg/L)	Chl-a (µg/L)	%ag	Maximum Depth (in cm)	Isolation Metric	Connectivity Metric	Modified connectivity	Area (ha)
L10	375.69	56.31	23.70	455.00	8.67	50.00	937.00	1.00	1.00	1.00	28.17
L108	73.36	21.43	155.90	334.00	104.67	60.20	135.00	1.00	0.00	0.00	23.58
L12	53.93	46.96	57.80	196.00	76.73	75.57	400.00	0.00	2.00	3.00	498.62
L121	27.27	17.54	75.30	201.00	48.12	18.06	208.00	0.00	2.00	3.00	327.91
L122	27.84	16.86	88.90	173.00	24.76	16.46	184.00	0.00	2.00	3.00	213.30
L15	158.94	4.09	9.60	249.00	3.71	36.06	1,880.00	0.00	2.00	3.00	240.03
L154	53.85	12.01	149.80	293.00	61.20	38.49	95.00	1.00	0.00	0.00	138.70
L170	67.04	29.97	76.30	1,405.00	21.00	71.53	69.00	1.00	0.00	1.00	85.05
L176	114.10	9.78	36.60	177.00	72.58	21.27	639.00	1.00	0.00	1.00	36.28
L190	204.95	10.52	10.40	319.00	2.97	7.62	1,412.00	1.00	0.00	1.00	269.81
L20	152.50	28.05	42.40	250.00	14.37	45.38	220.00	1.00	0.00	0.00	49.00
L21	153.91	0.00	51.50	201.00	4.62	29.86	186.00	1.00	0.00	0.00	11.13
L29	175.29	20.97	72.00	274.00	97.22	39.65	328.00	1.00	0.00	1.00	19.35
L298	80.13	20.52	22.50	526.00	11.55	0.44	333.00	1.00	0.00	1.00	349.86
L306	110.30	62.15	133.30	357.00	19.50	82.93	75.00	1.00	0.00	1.00	13.81
L310	197.93	42.59	95.30	593.00	38.15	92.84	588.00	1.00	0.00	0.00	184.13
L312	179.39	92.08	143.80	522.00	70.90	86.67	113.00	1.00	0.00	0.00	61.81
L314	70.95	61.38	189.20	353.00	87.90	80.37	121.00	1.00	0.00	1.00	131.64
L315	175.14	53.76	220.50	699.00	5.50	82.39	54.00	1.00	0.00	0.00	28.53
L357	68.50	80.59	76.00	356.00	75.46	69.51	115.00	1.00	0.00	0.00	35.00
L43	127.90	19.95	24.80	278.00	37.07	54.91	668.00	0.00	2.00	3.00	69.00
L448	206.61	0.00	24.60	428.00	128.43	40.90	850.00	0.00	1.00	1.00	341.00
L47	78.61	78.45	141.10	338.00	1.87	49.14	72.00	1.00	0.00	0.00	22.58
L49	145.00	35.77	124.10	307.00	633.98	40.89	247.00	1.00	0.00	0.00	474.34
L51	101.51	37.13	160.30	341.00	154.82	60.00	122.00	1.00	0.00	0.00	71.31
L52	60.91	57.53	95.70	251.00	3.22	53.00	246.00	1.00	0.00	0.00	76.86
L75	294.68	14.40	71.20	865.00	6.93	53.18	398.00	0.00	2.00	3.00	197.84
L95	171.82	7.02	55.30	221.00	16.74	0.00	229.00	1.00	0.00	1.00	206.15

Table A3. Environmental characteristics of interest for 33 additional lakes. Fishless lakes are identified by fish category 1 and small-bodied fish lakes by fish category 2

Basin ID	**Fish**	State	TP (µg/L)	TN (µg/L)	SRP (µg/L)	Chl-a (µg/L)	% Agriculture	Max depth (cm)
0	1	c	415.30	10300.0	6.21	42.51	20.00	5.00
12	1	t	168.30	5170.00	11.10	101.02	57.80	287.00
17	1	c	81.32	3460.00	2.90	16.94	31.34	85.00
19	1	c	67.42	5730.00	11.60	3.56	27.65	120.00
20	1	t	170.85	6800.00	18.30	92.98	14.21	125.00
22	1	c	50.31	3450.00	3.40	5.17	24.81	100.00
27	1	c	252.96	2930.00	175.00	3.76	78.00	90.00
37	1	c	28.94	2040.00	4.40	1.54	10.00	69.00
42	2	c	1171.20	5140.00	785.00	2.49	53.00	148.00
61	1	m	676.90	10900.0	71.49	59.86	70.56	40.00
144	1	c	61.20	1220.00	29.05	1.64	0.00	147.00
155	1	c	201.16	4410.00	23.90	77.73	81.49	59.00
164	1	c	52.09	5350.00	2.90	0.37	42.03	41.00
174	1	c	50.81	5430.00	8.50	7.02	61.94	7.00
180	1	c	44.72	3310.00	7.90	0.98	67.95	31.00
195	2	t	36.10	1400.00	9.80	8.59	26.20	114.00
203	2	t	251.50	4800.00	12.00	135.49	0.00	125.00
228	1	c	45.93	4100.00	17.50	9.25	39.31	49.00
231	1	t	1240.00	12800.0	602.80	574.37	70.00	124.00
276	1	t	124.33	2260.00	34.40	16.16	41.90	191.00
300	1	t	209.80	3610.00	45.06	20.18	0.00	200.00
320	1	c	52.38	1590.00	8.50	10.17	24.44	114.00
362	1	m	361.19	2950.00	194.90	57.22	22.15	184.00
432	1	t	299.60	4350.00	7.10	122.87	54.26	70.00
441	1	t	54.90	2200.00	2.00	22.10	66.13	654.00

Basin ID	**Fish**	State	TP (µg/L)	TN (µg/L)	SRP (µg/L)	Chl-a (µg/L)	% Agriculture	Max depth (cm)
500	1	c	780.90	2270.00	739.00	1.57	90.00	43.00
502	1	t	3605.00	5870.00	3165.40	7.95	72.00	67.00
2004-06	1	c	111.06	3,270.00	2.49	7.37	66.30	42
2004-07	1	c	218.71	5,380.00	24.03	3.92	75.00	41
2004-19	2	c	75.97	1,230.00	16.16	2.25	75.00	73
2004-36	1	c	238.67	8,280.00	37.22	14.79	70.00	114
2004-39	1	c	233.45	4,180.00	49.54	35.47	57.86	39
2004-70	2	t	237.99	4,410.00	9.45	154.87	79.35	63

A4. Fish counts (fish/trap/hour) in 13 fish-bearing lakes

Fish Site ID	BRST	CISC	FTMN	NRPK	RNTR	YLPR
L10	4.482	0.000	0.000	0.000	0.049	0.022
L12	4.912	0.000	1.838	0.000	0.000	0.000
L121	3.325	0.000	0.000	0.000	0.000	0.000
L122	6.758	0.000	0.000	0.000	0.000	0.000
L15	0.000	0.078	0.000	0.219	0.000	0.051
L176	2.006	0.000	2.803	0.000	0.047	0.000
L190	0.000	0.089	0.000	0.262	0.000	0.081
L20	3.126	0.000	2.120	0.000	0.000	0.000
L21	0.003	0.000	0.824	0.000	0.000	0.000
L298	1.556	0.000	0.000	0.000	0.000	0.000
L314	0.001	0.000	0.000	0.000	0.000	0.000
L75	0.316	0.000	5.462	0.000	0.000	0.000
L95	6.989	0.000	0.000	0.000	0.000	0.000

A5. Dytiscid beetle counts (average beetles/trap/hour) in 22 lakes

Fish Site ID	Avg of count/hour on water	FISH Presence
12	0.009864	fish
15	0	fish
20	0.009948	fish
49	0.045134	no fish
51	0.428912	no fish
52	0.261409	no fish
75	0.001221	fish
95	0.059815	fish
108	0.041254	no fish
121	0.186376	fish
122	0.177196	fish
154	0.092398	no fish
170	0.049585	no fish
176	0	fish
190	0	fish
298	0.010836	fish
306	0.069437	no fish
310	0.056158	no fish
312	0.103586	no fish
314	0.136166	fish
315	0.13899	no fish
357	0.019428	no fish

A6. Waterfowl Indicated breeding pairs/km^2

Basin ID	Mal	Gadw	Amwi	Agwt	Bwte	Cite	Nosh	Nopi	Redh	Canv	Scau	Rndu
L10	11.80	0.00	13.11	3.69	10.29	0.00	0.00	0.00	0.00	0.00	12.89	46.60
L108	17.73	7.85	10.51	13.30	12.37	0.00	11.13	0.00	11.41	5.78	124.01	51.72
L12	1.67	3.88	8.16	0.21	2.04	0.00	0.52	0.00	4.83	0.14	2.92	4.87
L121	9.40	0.84	7.90	1.27	1.77	0.00	0.80	1.18	6.53	0.41	18.87	6.48
L122	7.85	1.30	8.72	0.00	4.10	0.00	3.08	1.82	1.89	1.60	48.58	12.87
L15	4.43	1.13	3.53	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.41
L154	9.05	6.01	14.30	2.26	9.47	0.74	3.79	5.61	2.91	2.46	32.52	7.33
L170	18.74	14.19	8.77	0.00	13.76	0.00	54.19	13.75	3.17	1.61	47.42	11.99
L176	11.55	7.67	6.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.73	11.23
L190	11.21	0.34	3.14	0.38	3.70	0.00	0.00	0.00	0.00	0.00	0.44	2.95
L2	55.28	8.05	8.62	9.09	45.65	0.00	4.57	6.76	2.34	0.00	12.72	12.37
L20	5.09	0.00	0.00	2.12	2.96	0.00	0.00	0.00	2.73	0.00	12.36	14.44
L21	14.98	0.00	0.00	0.00	13.06	0.00	0.00	0.00	0.00	0.00	32.73	36.40
L29	30.27	9.57	32.03	0.00	45.23	0.00	6.79	0.00	13.91	0.00	56.70	21.02
L298	2.64	0.53	2.49	0.30	0.42	0.00	0.38	0.00	0.39	0.20	4.89	1.75
L306	36.34	60.32	26.92	15.14	10.56	0.00	76.05	0.00	48.69	9.88	114.70	7.36
L310	7.72	3.02	3.36	0.00	4.75	0.00	4.99	4.22	4.38	0.37	23.82	5.52
L312	25.71	16.47	10.02	1.69	4.72	0.00	59.47	0.00	19.58	3.31	72.93	3.29
L314	8.90	2.11	7.53	0.00	2.22	0.00	8.98	0.00	5.11	0.00	37.95	3.09
L315	23.46	16.22	17.38	11.00	20.45	0.00	32.22	40.88	0.00	0.00	21.36	0.00
L357	11.97	7.95	10.64	0.00	25.04	0.00	7.52	22.26	23.10	15.62	111.62	11.64
L47	18.35	4.06	5.44	0.00	6.40	0.00	17.28	0.00	35.41	5.99	21.39	26.76
L49	3.69	3.11	4.68	1.76	16.53	0.00	3.86	0.00	2.54	0.57	73.41	1.71
L51	11.69	5.18	8.66	2.92	30.57	0.00	9.18	0.00	22.56	0.00	51.10	24.15
L52	6.51	2.40	6.43	2.71	9.46	0.00	0.00	0.00	12.21	0.88	15.80	2.64
L75	6.84	2.67	2.38	3.52	5.61	0.00	3.79	1.87	3.88	1.64	19.33	3.91
L8	58.12	0.00	9.57	8.07	61.92	0.00	5.07	0.00	0.00	0.00	4.70	15.69
L95	2.84	1.80	9.62	2.03	9.20	0.50	0.00	1.89	4.57	1.65	28.96	22.19
L43	5.86	1.30	0.00	1.46	6.13	0.00	1.84	5.44	3.77	0.96	22.19	1.42
L448	3.81	0.79	1.06	0.60	2.07	0.00	1.49	1.11	7.65	2.52	62.06	2.02

Basin ID	Cogo	Buff	Rudu	Wwsc	Susc
L10	22.13	10.14	0.00	0.00	0.00
L108	0.00	24.39	56.54	32.54	0.00
L12	3.76	0.57	6.08	0.00	0.00
L121	1.90	9.60	1.73	0.62	0.00
L122	2.94	14.16	4.47	0.96	0.48
L15	0.00	1.17	0.00	0.00	0.00
L154	18.10	11.41	24.73	2.21	0.00
L170	7.40	28.83	2.25	0.00	0.00
L176	34.66	11.91	0.00	0.00	0.00
L190	34.09	1.04	1.38	0.00	0.00
L2	10.91	27.51	3.31	0.00	0.00
L20	0.00	5.83	3.87	0.00	0.00
L21	0.00	0.00	0.00	0.00	0.00
L29	0.00	22.30	29.55	0.00	0.00
L298	5.39	5.77	0.00	0.73	1.17
L306	0.00	10.41	27.59	3.70	0.00
L310	0.00	7.81	2.07	8.05	0.56
L312	30.45	20.93	18.49	0.83	0.00
L314	4.77	14.20	13.02	1.94	0.78
L315	0.00	0.00	0.00	0.00	0.00
L357	0.00	4.12	16.36	5.86	0.00
L47	55.07	18.93	33.44	0.00	0.00
L49	23.71	3.32	13.20	0.32	0.00
L51	0.00	22.11	53.26	0.00	0.00
L52	8.14	11.19	32.12	0.66	0.00
L75	6.03	2.76	10.07	0.49	0.00
L8	0.00	0.00	0.00	0.00	0.00
L95	18.26	10.46	12.94	0.99	0.00
L43	8.79	6.04	2.67	0.00	0.00
L448	1.79	4.50	5.96	0.00	0.00

A7. Waterfowl moulting individuals/km^2

Site ID	Mall	Gadw	Amwi	Agwt	Bwte	Nosh	Nopi	Redh	Canv	Scau	Rndu	Cogo
L10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.61	0.00
L108	30.37	4.34	60.73	4.34	0.00	17.35	0.00	0.00	0.00	164.85	86.76	21.69
L12	17.56	68.40	64.72	0.00	2.86	17.36	0.00	69.01	10.82	11.23	15.52	0.20
L121	86.34	13.67	50.62	0.00	4.35	17.70	0.00	0.62	6.21	109.01	93.17	3.73
L122	64.30	7.68	70.54	0.00	2.40	12.48	0.00	4.80	2.40	59.02	167.46	2.88
L15	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	2.08
L154	125.45	11.07	4.43	0.74	11.07	18.45	0.00	0.00	0.00	33.94	5.90	0.00
L170	168.92	12.07	20.51	20.51	66.36	196.67	32.58	0.00	2.41	18.10	30.16	2.41
L176	0.00	0.00	0.00	0.00	0.00	19.78	0.00	0.00	0.00	16.95	0.00	2.83
L190	7.78	0.00	0.00	0.37	0.37	0.00	0.00	0.00	0.00	0.00	0.74	0.00
L20	4.15	0.00	62.27	0.00	0.00	2.08	0.00	0.00	0.00	12.45	4.15	0.00
L21	45.80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
L29	126.94	31.73	105.78	0.00	26.45	21.16	0.00	0.00	0.00	105.78	0.00	0.00
L298	11.43	2.34	8.21	0.00	7.33	0.00	0.00	1.17	0.00	23.74	17.59	38.10
L306	303.70	37.04	148.15	0.00	155.55	0.00	0.00	7.41	0.00	37.04	0.00	0.00
L310	3.89	27.77	11.11	0.00	1.11	24.99	0.00	0.56	0.00	99.98	38.88	33.33
L312	195.28	248.23	52.96	0.00	51.30	122.46	0.00	28.13	1.65	198.59	54.61	3.31
L314	64.51	31.09	24.87	7.77	8.55	27.20	0.00	3.89	12.43	97.92	120.46	26.42
L315	39.45	107.59	35.86	143.45	107.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00
L357	117.14	0.00	38.07	0.00	46.85	43.93	0.00	0.00	0.00	64.43	2.93	0.00
L47	4.49	13.47	273.86	0.00	22.45	8.98	0.00	8.98	0.00	31.43	17.96	0.00
L49	98.57	13.74	3.65	0.00	43.59	19.33	0.21	11.17	5.80	142.80	3.65	1.72
L51	55.77	107.25	61.49	0.00	14.30	25.74	0.00	7.15	0.00	91.52	24.31	2.86
L52	75.63	13.27	11.94	0.00	10.61	65.01	0.00	29.19	1.33	5.31	0.00	0.00
L75	27.05	7.87	12.30	0.98	7.87	11.31	0.00	3.93	2.46	64.43	15.25	0.49
L95	63.52	9.93	42.18	0.00	0.99	5.46	0.00	1.49	0.99	52.11	78.91	4.47
L43	1.43	0.00	7.16	0.00	0.00	0.00	0.00	0.00	0.00	21.49	0.00	1.43
L448	5.24	6.40	3.49	0.00	0.87	0.58	0.00	12.52	1.46	93.44	39.59	6.11

Site ID	Buff	Rudu	Wwsc
L10	0	0	0
L108	34.7048	8.6762	0
L12	4.491909	25.52221	0
L121	9.317115	1.552853	0
L122	0.959672	2.399181	0
L15	0	0	0
L154	22.87583	8.117232	0
L170	4.826188	0	0
L176	0	0	0
L190	0	0	0
L20	6.227419	0	0
L21	0	0	0
L29	5.289041	26.44521	0
L298	6.155106	0	0
L306	0	0	0
L310	2.777132	3.332559	1.110853
L312	36.40757	18.20378	0
L314	7.771768	120.4624	0
L315	0	0	0
L357	5.85686	5.85686	0
L47	4.489535	67.34302	0
L49	5.583204	29.63393	0
L51	2.86	41.47	0
L52	0	17.24845	0
L75	0	11.31248	0
L95	9.92545	5.95527	5.95527
L43	0	4.298453	0
L448	3.493063	32.01974	0