RESPONSES OF FISH AND ZOOPLANKTON TO CLIMATE VARIATION ON THE PRAIRIES, AND THEIR SENSITIVITY TO CLIMATE CHANGE

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Elizabeth Raye Starks, candidate for the degree of Master of Science in Biology, has presented a thesis titled, *Responses of Fish and Zooplankton to Climate Variation on the Prairies, and Their Sensitivity to Climate Change*, in an oral examination held on December 14, 2012. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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ABSTRACT

Climate change is anticipated to significantly increase temperatures and alter current rainfall patterns, which will have important ramifications for aquatic habitats and their biological communities. Current observations indicate that climate effects will vary depending on region and lake type, and some lacustrine areas, such as the Great Plains, are particularly sensitive to these effects. Variations in local climate and lake morphometry create different habitats, which each have unique environmental controls.

The anticipated impacts of climate change on aquatic biota can be difficult to evaluate because of potentially contrasting effects of temperature and hydrology on lake ecosystems, particularly in closed-basin lakes within semi-arid regions.

To address these challenges, I quantified decade-scale changes in chemical and biological properties of 20 endorheic lakes in central North America in response to a pronounced transition from a drought to a pluvial period during the early 21st century. Lakes exhibited marked changes in chemical characteristics and formed two discrete clusters corresponding to periods of substantially differing effective moisture (as per Palmer Drought Severity Index, PDSI). Discriminant function analysis (DFA) explained 90% of variability in fish assemblage composition and showed that fish communities were predicted best by environmental conditions during the arid interval (PDSI < -2). DFA also predicted that lakes could support more fish species during pluvial periods, but their realized occurrences may be limited by periodic stress due to recurrent droughts and physical barriers to colonization. Zooplankton taxonomic compositions in fishless lakes were resilient to short-term changes in meteorological conditions, and did not vary between drought and deluge periods. Conversely, zooplankton taxa that were exposed to
fish decreased substantially in biomass during the wet interval, likely due to increased zooplanktivory by fish.

Based on my results, climate change is expected to alter fish species distributions, but it is less clear to what extent non-lethal environmental effects will influence physical health of populations in fish-habitable lakes. To address this question, I investigated the environmental controls of body condition and parasite load in walleye (*Sander vitreus*), northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*) in seven lakes from the prior study. Over a two-year observation period (2009 vs. 2010), I observed large differences in the number of days within the favorable temperature range for ambient fish species. Surprisingly, environmental variables such as lake morphometry and nutrient levels had little relevance, despite their importance in previous studies conducted in boreal lakes. Instead, temperature and salinity were important correlates of fish health.

In regard to species-specific effects, walleye was most sensitive to interannual temperature differences, as well as salinity, while yellow perch and northern pike exhibited temperature sensitivity to a lesser degree. Apparently, temperature increases are of particular concern in prairie lakes, as their polymictic nature deprives fishes of a hypolimnetic thermal refuge.

Together these findings suggest that semi-arid lakes provide a useful model system for anticipating the effects of global climate change on aquatic communities in closed-basin lakes of semi-arid regions. The particular importance of temperature and salinity indicates that the interaction of global climate change and local hydrology may have particularly detrimental effects not only on the health but also the survival of established fish populations of the Great Plains.
ACKNOWLEDGMENTS

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1. INTRODUCTION

1.1. Climate Effects On Lakes

The IPCC has stated that climate change effects on freshwater resources are a critical concern (Bates et al. 2008). Changes in climate are expected to include regional shifts in temperature, precipitation and frequency of extreme weather events, such as drought or flooding, all of which have ramifications for sustainability of freshwater resources (Gleick 1989, Millet et al. 2009). Climate change research on lake ecosystems is broad in scope, including assessments of hydrology (Gleick 1989), water chemistry (Hammer 1990, Jeppesen et al. 2009), and biota (Chu et al. 2005, O’Reilly et al. 2003, Winder and Schindler 2004).

Climate impacts on lake ecosystems occur primarily by changing inputs of solar energy and mass (water and dissolved/particulate substances) (Leavitt et al. 2009). Solar energy enhances regional evapotranspiration rates, not only reducing water volume but also concentrating solutes. Mass inputs are usually more localized and can come from tributaries, surface runoff, seasonal meltwater and groundwater, at rates which are determined by precipitation, seasonal thermal variation and local hydrology.

While most lacustrine regions are expected to experience warming and reduced precipitation (Adrian et al. 2009, Bates et al. 2008), research indicates that climate responses will differ depending on ecoregion and lake type (Williamson et al. 2009). As a consequence, small boreal lakes are expected to stratify earlier in the season and with greater intensity (De Stasio et al. 1996), while lakes in areas with substantial groundwater contributions might show asynchronous responses (Webster et al. 2000), and saline lakes could be at risk of complete desiccation (Williams 2002). Of all lake types, endorheic
Prairie lakes are considered among the most vulnerable to climate change due to their closed hydrology and high dependency on winter precipitation (Hammer 1990).

1.2. Prairie Lake Climate Response

The regional climate of the northern Great Plains is extremely seasonal, experiencing a thermal range of up to 85˚C throughout the year, ranging from -45˚C to 40˚C (Hammer et al. 1978). Lakes are frozen for approximately 155 days per year due to long and extreme winters (Buffalo Pound Water Treatment Plant report). The grassland region of southern Saskatchewan is classified as sub-humid to semi-arid, based on precipitation deficits. Yet, precipitation rates are highly variable in time and space and can result in a range from dry to humid conditions (Sauchyn et al. 2002).

For endorheic lakes, seasonal meltwater and groundwater are key contributors to lake water budgets. Nevertheless, seasonal meltwater contributions vary substantially from year to year depending on winter snowfall, and a year with low winter precipitation can result in drought-like conditions for lakes during the subsequent summer (McGowan et al. 2005). Groundwater structure on the prairies is complex and spatially variable, and depending on climate and the state of the aquifer, direction of groundwater flow shift between sink and source in respect to lake water budgets (Winter and Rosenberry 1998).

Concentrations of dissolved substances in lake waters are closely linked to climate either through evaporative concentration in arid periods, or dilution in periods of high precipitation. As a consequence of evaporative deficits and abundance of closed-basin lakes in this region, many lakes have elevated salinities and nutrient concentrations, which could be intensified by saline groundwater contributions (Last and Ginn 2005). Additionally, the naturally high concentrations of phosphorus and nitrogen in the region
are augmented by fertilizer run-off, such that most lakes are classified as eutrophic or hypereutrophic (Biehuizen and Prepas 1985). However, saline lake nutrients are often less bioavailable (Waier and Robarts 1995).

1.3. Prior Research On Prairie Biota

Aquatic communities in prairie lakes are diverse in species richness and trophic complexity, supporting between two and four trophic levels and ranging from simple invertebrate communities to diverse communities of fishes, zooplankton and benthic invertebrates (Cooper and Wissel 2012b, Hammer 1978). Although trophic state and salinity levels are higher in southern Saskatchewan lakes than many other lake ecoregions, Saskatchewan has historically supported a variety of fish populations, with 26 species identified in a 1944 survey (Rawson and Moore 1944).

In respect to environmental controls of community structure, salinity has been identified as a master variable in prairie lakes, reducing species richness and preferentially selecting halophiles (Hammer 1978, Rawson and Moore 1944). Among major taxonomic groups, fishes were identified as most sensitive to salinity, followed by zooplankton and finally benthic invertebrates (Hammer 1978). Surprisingly, recent studies showed that most fishes are now eliminated from lakes at salinities well below their physiological thresholds, indicating that controls other than salinity may be important for structuring these lake communities (Cooper and Wissel 2012b). Seasonal or spatial oxygen depletion is commonly responsible for loss of fishes and other sensitive organisms, and is likely an important community structuring mechanism in these lakes (Robarts et al. 2005). Due to the polymictic nature of many prairie lakes, summer hypoxia is usually not a major concern except in meromictic lakes. In contrast, oxygen
depletion in winter could pose a serious threat to established fish populations on the prairies as low water depth and high eutrophic state can significantly deplete oxygen reserves under ice during the prolonged winter (Robarts et al. 2005). Climate change scenarios predict a reduction in winter hypoxia as winter temperatures rise, although summer temperatures may rise beyond comfortable limits for fishes in some regions, leaving the net effect of a temperature increase somewhat ambiguous (Fang et al. 2004).

Such lethal effects clearly determine the presence and absence of species in particular ecosystems. Nevertheless, environmental parameters can also impact aquatic species at a sub-lethal level. For example, lake depth is often positively associated with body condition for larger fishes (Cena et al. 2006), and a high rate of primary productivity reduces foraging efficiency of visual predators (Craig and Babaluk 1989), while optimal temperature ranges are associated with better growth rates (Quist et al. 2002). Additionally, environmental stressors can reduce body condition and increase parasite load by weakening the immune system (Bly et al. 1997, Lewis et al. 2003).

1.4. Research Needs

Climate and other environmental conditions in prairie lakes are distinct from better studied boreal lakes. So far, very few studies have tested the impacts of climate and water quality on fish populations in northern polymictic lakes. Effects of temperature and water chemistry on these populations are as yet not fully characterized. Shallow temperate reservoirs are the nearest analogue for temperature effects, with studies showing a large effect of temperature changes on fishes in these systems due to the lack of thermal stratification (Quist et al. 2002). It is currently assumed that high temperatures do not exceed critical thresholds for northern fish populations, but based on projected
temperature increases, this may no longer be the case in the future (Sharma et al. 2007). Fish populations in these lakes currently experience water chemistry that is unusual (high nutrient content and high levels of uncommon ions such as Mg+ and SO4-) relative to other regions (Rawson and Moore 1944), and yet the sub-lethal effects of the unique chemical properties have not been fully characterized (Pollock et al. 2010).

Climate change scenarios for moderate climates often predict increases in seasonal variability, as well as increases in ice-free time (Bates et al. 2008). In contrast, the climate in central Canada is already considered extreme, with very pronounced seasonal shifts in temperature, a brief growing season and high interannual variation in precipitation (Hammer et al. 1978). This area also experiences cyclical drought and deluge events that may further construct species assemblages (Michels et al. 2007). Due to the extreme variability in short-term (seasonal, annual) and long-term (decadal, centennial) weather this region experiences, it is highly suited for climate research, and the periodic droughts and deluges experienced by Saskatchewan could serve well as a proxy for climate change conditions.

Few studies have had the ability to evaluate environmental and community effects simultaneously in order to get a more comprehensive view of the biological response to climate change. Studies of stratified lakes imply that zooplankton sensitivity to environmental change, particularly shifts in thermal stratification and timing of seasonal events, could reduce their overlap with predators (Hampton et al. 2006, Winder and Schindler 2004). However, in the polymictic lakes of Saskatchewan such habitat overlap effects would not occur, so it is less clear how predator/prey interactions would be altered in a climate-change scenario. Due to polymixis, it is possible that community outcomes
and any resulting shifts in relative abundance will be dependent on the abilities of each species to thrive under future conditions.

1.5. Objectives and Relevance

The primary goal of the second chapter of this study was to determine how climate variability, particularly during a transition between deluge and drought, structures aquatic communities in prairie lakes. Because climate may also have indirect effects through altering species interactions, environmental and community effects were evaluated simultaneously using zooplankton species abundances and fish habitat suitability models. These interactions were evaluated within the context of environmental parameters of known relevance to aquatic species composition, such as lake morphometry and nutrient loads.

The third chapter addressed non-lethal environmental effects on game fish. Non-lethal effects of environment and climate on fish are of importance due to their relevance to total fisheries yields and long-term population sustainability, and are therefore an important consideration beyond habitability. Because Saskatchewan lakes have such variable water chemistry, I compared the importance of inter-lake chemical variation versus a two-year difference in seasonal temperature that was similar across the study lakes. All parameters identified as important to species composition were evaluated as potential sublethal stressors in order to determine whether these parameters were relevant to physical health, and could have detrimental effects increasing with the degree of environmental change.

Finally, I evaluated potential global climate change effects on local biota using what was learned from chapters 2 and 3. Projected reductions in winter precipitation and
increasing temperatures could induce conditions similar to regional droughts, with extreme drought conditions acting as a habitat filter (Chase 2007), while anticipated lake surface-temperature increases would surpass thermal thresholds for many cool- and cold-water fishes (Sharma et al. 2007). This study therefore demonstrates that the inherent climate variability of this region makes it a useful model system for climate change projections.
2. EFFECTS OF DROUGHT AND PLUVIAL PERIODS ON FISH AND
ZOoplankTON COMMUNiTYs IN PRAirIE LAKes: DETErMINiSTiC VS.
STOCHASTiC RESPONSES

2.1. iNTRODUCtiON

The Intergovernmental Panel on Climate Change (IPCC) has identified arid regions and endorheic basins as particularly vulnerable to climate change effects due to low water availability and high temporal variation in precipitation and evaporation (Bates et al. 2008). Lakes in these areas do not receive continuous inputs through streams or rivers and frequently lack surface outlets. Across the northern Great Plains, endorheic lakes are sustained by spring snow melt, while evaporation during summer represents the predominant loss of water from lakes (McGowan et al. 2005, Pham et al. 2008). Consequently, these lakes are susceptible to partial or total desiccation during droughts, particularly those lasting multiple years. Conversely, the low relief of the landscape can result in significant flooding during spring snow melt or intense summer deluges (Winter and Rosenberry 1998), resulting in dilution of dissolved substances (e.g., major ions, nutrients, dissolved carbon). These strong effects of hydrologic variability on limnological conditions is further intensified as many lakes in central North America are shallow, exhibit high surface to depth ratios, and are often polymictic. In particular, the lack of continuous thermal stratification during summer can increase vulnerability of the biota to rising water temperatures as cool hypolimnetic refuges are absent. Ultimately, changes in hydrology and the associated changes in nutrient concentrations and salinity have the potential to strongly alter biological diversity, taxonomic composition and
trophic interactions within aquatic food webs (Cooper and Wissel 2012a, Hammer 1990, Wissel et al. 2011).

Endorheic lakes on the semi-arid Great Plains represent an important model to study the long-term effects of climate on lake ecosystems (Pham et al 2008, 2009, Wissel et al. 2011). At present, global circulation models predict a uniform increase of about 4 °C in all seasons of 2050 across the Canadian prairies (Barrow 2009), further raising the probability of drought conditions due to intensified evaporation. In conjunction, extreme precipitation events are expected to become more common as elevated atmospheric energy in summer favors increased evapotranspiration rates and atmospheric vapor content (Bates et al. 2008), while warmer winters may reduce snowpack and subsequent runoff during spring melt periods. In both cases, the sustainability of prairie lakes may be compromised by rapid changes in lake level during severe summer droughts (Van der Kamp et al. 2008) or pluvial intervals (Winter and Rosenberry 1998). Furthermore future climate change may exhibit high geographic variability, with increased precipitation in the southeastern prairie of Minnesota and the Dakotas, and increased temperature combined with static or declining precipitation in the northwestern prairies including southern Alberta and Saskatchewan (Millet et al. 2009). If such trends continue, the prairie region could diverge into two distinct ecozones, with central regions in Canada experiencing a more arid climate. Such changes may have profound socio-economic implications for central North America, a region which encompassed a high proportion of continental cropland (e.g., 40% of arable farmland in Canada).

During drought periods when energy inputs (radiation) dominate, a higher synchrony of water chemistry is expected across lakes, while wet periods with high mass
inputs (hydrological flux) result in asynchrony of lake parameters (Leavitt et al. 2009, Pham et al. 2009). A synchronous response of water chemistry during drought could shift environmental parameters in a common direction that restricts the diversity of species assemblages. In instances where species composition is controlled primarily through deterministic mechanisms (environmental filters), community similarity should increase during droughts, as inferred from analysis of zooplankton communities in experimental ponds (Chase 2007), and plankton in hydrologically connected prairie lakes (Vogt et al. 2011). Conversely, if water chemistry responds asynchronously to a prolonged deluge, increased differences in water chemistry reduce the effect of environmental filters and favor elevated biological diversity. Unfortunately, the lack of long-term monitoring of endorheic lakes combined with limited ranges of observed meteorological conditions has often prevented explicit tests of these hypotheses.

In this paper, I describe a recent decade-scale shift from drought conditions to an above-average pluvial interval that provided a unique opportunity to study the effects of extreme climate on water chemistry and biota of this vulnerable prairie region. During 2000-2003, central Canada experienced a severe multi-year drought (Sauchyn et al. 2005) which was followed immediately by several years of unusually high rain fall in 2005-2010 (Van der Kamp et al. 2008). Effects of these hydrological extremes on lake ecosystems were evaluated by comparing lake properties and biological communities monitored during 2002-2005 with those recorded during 2007-2010.

Previously, it has been shown that landscape differences in taxonomic compositions in endorheic lakes are regulated by pronounced spatial variation in water chemistry and lake morphology, whereas short-term meteorological variability (2-3 yrs.)
had little significant effects on food-web composition (Cooper and Wissel 2012a, Wissel et al. 2011). Here I take advantage of the wide range of chemical and morphological conditions associated with decadal scale shifts in effective moisture to quantify the effects of climate change on fish and zooplankton communities within endorheic lakes and to evaluate if the observed community changes are associated with deterministic mechanisms or are stochastic. The results of this study are important not only to better understand the responses of prairie lake communities to climate change, but should also be applicable to lakes in other arid regions world-wide (Hughes 2003).

2.2. METHODS

2.2.1. Study Area

Meteorological conditions in southern Saskatchewan are extremely variable. Annual temperatures vary between extremes of -40 °C and +30 °C, and precipitation averages 350 mm year^{-1} (Saskatoon) but ranges from < 250 to > 600 mm year^{-1}. Relative humidity rarely exceeds 50% during the growing season, which together with the high number of sunshine hours (> 2000) and low precipitation, results in evaporative deficits in most years (Last and Ginn 2005). Sensitivity to evaporative deficits is commonly expressed as Palmer Drought Severity Index (PDSI), accounting for precipitation and temperature to determine effective precipitation. PDSI values are centered on 0 under conditions of normal effective precipitation, while negative or positive values represent dry or wet periods, respectively. PDSI values below -2 are considered droughts.

To evaluate the impacts of climate on lake ecosystems, 20 study lakes were sampled over a nine-year observation period (Table 2.1). The study lakes were located in the prairie ecozone of southern Saskatchewan in central Canada (Fig. 2.1), and were sampled
Table 2.1. Characteristics of the 20 study lakes utilized for the survey from 2002 to 2010. Ecoregions are abbreviated as MG (mixed grassland), AP (aspen parkland) and MMG (moist mixed grassland). Fish communities are abbreviated as Fishl. (fishless), Plankt. (planktivorous) and Pisc. (piscivorous). Zooplankton species clusters are identified as 1 through 4 (see Figure 2.4 for details). Maximum lake depth (m), salinity (g L\(^{-1}\)), DOC (mg L\(^{-1}\)) and TKN (µg L\(^{-1}\)) are calculated averages across the 9-year study period by lake.

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<td>Fishl.</td>
<td>3</td>
</tr>
<tr>
<td>Rabbit</td>
<td>AP</td>
<td>5</td>
<td>2174</td>
<td>4</td>
<td>32</td>
<td>Fishl.</td>
<td>3</td>
</tr>
<tr>
<td>Snakehole</td>
<td>MG</td>
<td>64</td>
<td>11357</td>
<td>3</td>
<td>372</td>
<td>Fishl.</td>
<td>4</td>
</tr>
<tr>
<td>Middle</td>
<td>AP</td>
<td>23</td>
<td>6182</td>
<td>5</td>
<td>79</td>
<td>Fishl./Plankt</td>
<td>4</td>
</tr>
<tr>
<td>Edouard</td>
<td>AP</td>
<td>0.3</td>
<td>1511</td>
<td>6</td>
<td>21</td>
<td>Plankt.</td>
<td>2</td>
</tr>
<tr>
<td>Deadmoose</td>
<td>AP</td>
<td>2.0</td>
<td>1199</td>
<td>13</td>
<td>31</td>
<td>Plankt.</td>
<td>3</td>
</tr>
<tr>
<td>Redberry</td>
<td>AP</td>
<td>11</td>
<td>2081</td>
<td>13</td>
<td>39</td>
<td>Plankt.</td>
<td>3</td>
</tr>
<tr>
<td>Waldsea</td>
<td>AP</td>
<td>16</td>
<td>1688</td>
<td>12</td>
<td>61</td>
<td>Plankt.</td>
<td>3</td>
</tr>
<tr>
<td>Clair</td>
<td>AP</td>
<td>1.4</td>
<td>1481</td>
<td>4</td>
<td>29</td>
<td>Plankt.</td>
<td>2</td>
</tr>
<tr>
<td>Pelletier</td>
<td>MG</td>
<td>0.4</td>
<td>713</td>
<td>9</td>
<td>16</td>
<td>Pisc.</td>
<td>1</td>
</tr>
<tr>
<td>Wakaw</td>
<td>AP</td>
<td>1.9</td>
<td>1023</td>
<td>9</td>
<td>18</td>
<td>Pisc.</td>
<td>1</td>
</tr>
<tr>
<td>Shannon</td>
<td>AP</td>
<td>2.6</td>
<td>1582</td>
<td>8</td>
<td>21</td>
<td>Pisc.</td>
<td>1</td>
</tr>
<tr>
<td>Humboldt</td>
<td>AP</td>
<td>1.3</td>
<td>1875</td>
<td>7</td>
<td>29</td>
<td>Pisc.</td>
<td>1</td>
</tr>
<tr>
<td>Kipabiskau</td>
<td>AP</td>
<td>0.4</td>
<td>1167</td>
<td>8</td>
<td>31</td>
<td>Pisc.</td>
<td>1</td>
</tr>
<tr>
<td>Fishing</td>
<td>AP</td>
<td>2.0</td>
<td>1199</td>
<td>13</td>
<td>31</td>
<td>Pisc.</td>
<td>1</td>
</tr>
<tr>
<td>Lenore</td>
<td>AP</td>
<td>1.3</td>
<td>870</td>
<td>9</td>
<td>33</td>
<td>Pisc.</td>
<td>1</td>
</tr>
</tbody>
</table>
**Fig. 2.1:** Locations of the 20 study lakes in southern Saskatchewan, Canada in the northern Great Plains. Sampling sites are coded by fish community type (*piscivorous*=black, *planktivorous*=gray, *fishless*=white). Dashed lines represent annual precipitation deficits. The solid line represents the transition from southern grassland to northern forest.
over a nine-year observation period (Table 2.1). Four lakes were situated in the semi-arid southwestern mixed grasslands ecoregion and the remaining sixteen existed in the sub-humid mixed grasslands/aspen parkland ecoregions of central Saskatchewan. The lakes have long retention times, exceeding ten years when known (Pham et al. 2009), and most lakes are classified as endorheic. Salinity (as total dissolved solids, TDS) ranged from fresh to hypersaline, maximum lake depth was between 3 m and 30 m, and trophic status covered mesotrophic to hypereutrophic conditions (Wissel et al. 2011). Of the 20 lakes, seven had piscivorous, planktivorous and benthivorous fishes (hereafter referred to as *piscivorous*), six had only planktivorous and benthivorous fishes (*planktivorous*), and seven were fishless (*fishless*). Further analyses of the lakes were based on these three fish community classes.

### 2.2.2. Lake Sampling

The 20 lakes were sampled at central locations over their maximum depth in May, July and September of 2002 to 2005, and in June and August of 2007 to 2010. Lakes were not sampled in 2006. I relied on annual averages for all subsequent analyses, as monthly sampling of a sub-set of eight lakes (between May and September from 2008 to 2010) identified no significant differences between the two sampling periods (analysis not shown).

Vertical profiles of temperature, oxygen and salinity were recorded with a YSI model 556 probe at 1 meter depth intervals. Changes in lake depth were recorded at established GPS coordinates with an electronic depth finder (model), and water clarity was measured using a 20 cm diameter Secchi disk. Small and large pelagic zooplankton were collected using 30 cm and 50 cm diameter plankton nets with mesh sizes of 80 µm
and 500 µm, respectively, towed vertically to the surface from 0.5 m above the sediment or above the anoxic monimolimnion in meromictic lakes. Zooplankton samples were stored in 50% ethanol sucrose, identified to species (Hanley et al. 2010, Hudson and Lesko 2003) and enumerated using a dissecting microscope. Pelagic fish were collected using overnight sets of multi-panel 1.5x30 meter gillnets with 55 mm mesh size. Littoral fishes were caught during daylight using a beach seine (2 m x 30 m, 10 mm mesh) from shore to a depth of two meters (Cooper and Wissel 2012a). All fish were identified to species (Scott and Crossman 1973) and preserved frozen for further analysis.

2.2.3. Laboratory Analysis

Nutrient analyses were conducted on integrated water samples taken with a 5 cm diameter tygon tubing sampler deployed from the surface to the bottom in shallow polymictic lakes, from 0 to 6 meters in deeper polymictic lakes, or to the depth of the monimolimnion in meromictic lakes. Water samples were prescreened in 80-µm mesh then filtered through sterile 0.45 µm glass fiber filters and analyzed for total dissolved phosphorus (TDP), total Kjeldahl nitrogen (TKN), nitrate (NO₃), nitrite (NO₂), ammonium (NH₄), dissolved organic carbon (DOC) dissolved inorganic carbon (DIC) and chlorophyll a (Chl a) using standard methods described by Cooper and Wissel (2012a). Nutrient analyses were conducted at the University of Alberta water chemistry laboratory following the procedures of Stainton et al. (1977). DOC and DIC were quantified using a Shimadzu TOC5000 analyzer at the Environmental Quality Analysis Laboratory (EQAL) at the University of Regina. To estimate algal biomass (Chl a), an aliquot of 1 liter was filtered onto GF/C filters and stored at -10 °C until extraction with
acetone:methanol:water (80:15:5), and analyzed with a spectrophotometer (Hewlett-Packard model 84452A) (Wetzel and Likens 1991).

2.2.4. Statistical Analyses

To test if the chemical characterization of lakes by year would be associated with drought and pluvial-influenced periods I used a Multi-Response Permutation Procedure (MRPP, PC-ORD version 5.0) (McCune and Mefford 1999). MRPP tests for clustering of group members by comparing intragroup average distances with the average distances of all possible data permutations into groups. Included parameters (NH$_4$, TKN, TDP, salinity, and maximum lake depth ($Z_{max}$)) were selected based on prior analysis of the lakes (Cooper and Wissel 2012a, Wissel et al. 2011). All data were z-transformed around a common origin of zero and a standard deviation of one in order to standardize water chemistry among lakes and isolate temporal differences. Because the transformed dataset contained negative values, relative Euclidean distance was used as distance measure, and the distance matrix was weight-transformed due to the high heterogeneity of the data.

Subsequently, I conducted a Principal Components Analysis (PCA) to evaluate the differences in water chemistry between drought and pluvial periods using averaged log$_{10}$-transformed water chemistry data from the two periods. The polar coordinates of drought and deluge water chemistry data for each lake were exported to Oriana (version 2, 2003) and converted to vectors for a quantitative characterization of the strength and direction of change in water-chemistry between the two time periods. Oriana calculates directional statistics by quantifying the distance ($r$) and direction ($\mu$) that data points shift from a common origin, testing for a significant directional trend.
Previous zooplankton cluster analysis results (Wissel et al. 2011) showed that zooplankton taxa fall into four different groups that were largely defined by the impacts of salinity, fish assemblage and lake depth. Subsequently, PCA was used to generate coordinates for each taxon during drought- and deluge-influenced periods. Environmental parameters used for the PCA were identical to those used for the MRPP, and log$_{10}$-transformed abundance data were used to ordinate the zooplankton taxa in environmental space. The coordinates of the zooplankton taxa during drought and deluge periods were used as inputs for Oriana to analyze the strength and directionality of changes in the zooplankton communities between these two periods (see above). The four identified zooplankton clusters were tested independently for significant directional change in Oriana.

Fish assemblage data were only collected during the deluge-influenced time period (2007-2010). Therefore, climate effects on fish assemblages were evaluated indirectly using discriminant functions based on water chemistry variables. Discriminant functions were developed for both drought and deluge water chemistry data in order to determine which climate period best predicted the complexity of fish community as indicated by the three classes: *fishless*, *planktivorous* or *piscivorous*. Predictive abilities of averaged water chemistry during drought and deluge periods were quantified using Discriminant Function Analysis (DFA, PASW Version 18.0). DFA develops a predictive function for a categorical variable (fish trophic class) using one or more continuous independent variables (water chemistry). The input variables for DFA (TDP, salinity, lake depth and DOC) were selected based on ecological relevance and statistical performance, with variables selected to minimize covariance and maximize effect size.
Due to eutrophic conditions in combination with shallow water depth, prairie lakes are often prone to winterkill (Barica and Mathias 1979), and the susceptibility of individual lakes to winterkill can be altered by climatic conditions (Robarts et al. 2005). To investigate the potential impacts of drought vs. deluge conditions on the occurrence of winterkill I applied the model of Barica and Mathias (1979) to the 20 study lakes. This model was developed particularly for eutrophic prairie lakes, and incorporates initial oxygen storage, stratification, lake depth and eutrophic status to estimate lake oxygen depletion for up to 100 days of ice cover. Model outcomes are categorical and lakes are classified as low, moderate or high risk. Subsequently, I conducted two PCAs using average water chemistry data for either drought or wet periods. The results of the winterkill models were then superimposed onto the PCAs of water chemistry during drought and deluge, respectively, to evaluate the potential role of additional environmental parameters not included in the model.

2.3. RESULTS

2.3.1. Climate

The most intense drought conditions across southern Saskatchewan were reported to occur during 2001, a year prior to the study, however, extremely arid conditions extended until 2003 (Bonsal and Wheaton 2005, Marchildon et al. 2007). The Palmer Drought Severity Index (PDSI) exceeded -5 in Saskatoon during 2001, and surpassed the limit for drought in both 2002 and 2003 before rising to neutral values in 2004 (Bonsal et al. 2011) (Fig. 2.2). Pluvial conditions (PDSI ≥ 3) were recorded in 4 of 6 years thereafter, and flooding occurred in many lakes starting in 2007 (Saskatchewan Watershed Authority 2007 runoff report).
Fig. 2.2: Palmer Drought Severity Index (PDSI) for Saskatoon in August of 2000-2010.

Negative values indicate effective precipitation deficit, while positive values indicate excess.
Table 2.2. Comparison of average water chemistry parameters for *fishless*, *planktivorous* and *piscivorous* lake communities. Lake characteristic records shown here include maximum lake depth ($Z_{\text{max}}$, m), salinity (g L$^{-1}$), TKN (µg L$^{-1}$), TDP (µg L$^{-1}$) and DOC (mg L$^{-1}$). For each community type, means are reported for the drought and fluvial periods and mid-range values are reported for the drought-based DFA model.

<table>
<thead>
<tr>
<th>Community</th>
<th>Fishless</th>
<th>Planktivorous</th>
<th>Piscivorous</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
<td>Drought</td>
<td>Deluge</td>
<td>Model</td>
</tr>
<tr>
<td>$Z_{\text{max}}$</td>
<td>5.5</td>
<td>7.0</td>
<td>3.0</td>
</tr>
<tr>
<td>Salinity</td>
<td>24.5</td>
<td>22.0</td>
<td>26.0</td>
</tr>
<tr>
<td>TKN</td>
<td>4752</td>
<td>4549</td>
<td>4927</td>
</tr>
<tr>
<td>TDP</td>
<td>240</td>
<td>216</td>
<td>612</td>
</tr>
<tr>
<td>DOC</td>
<td>80</td>
<td>111</td>
<td>165</td>
</tr>
</tbody>
</table>
The effects of drought and deluge periods were clearly reflected in the changes in water chemistry (Table 2.2). Hierarchical cluster analysis revealed two primary temporal groups based on lake water chemistry, one ranging from 2002-2005 (drought-influenced) and the other from 2007-2010 (deluge-influenced). A Principal Components Analysis explained 62.5% of total variation on axis one and two, and showed good separation between climatic groups along PCA axis 2, mainly reflecting differences of lake depth and salinity. PCA axis 1 largely separated lakes on the basis of nutrient concentrations, which differed to a lesser degree between time periods. The MRPP test of these two groups across all lakes generated a within-group agreement of $A = 0.14$, with values above 0.1 in ecological data suggesting a strong separation between groups (McCune et al. 2002). All further analyses were conducted on the mean values for drought- and pluvial-influenced temporal groups (2002-2005 and 2007-2010, respectively).

Analysis of survey data with circular statistics revealed that lake depth increased during the deluge period, while salinity and nutrient concentrations decreased (Fig. 2.3). This pattern was further supported by the significant differences in mean water chemistry and morphometric values for the 20 lakes between the two time periods (Table 2.2). Average lake deepening was at least 1 m for lakes of all fish community types. Total dissolved solids decreased by 1 g L$^{-1}$ on average in piscivorous lakes, and by 6 g L$^{-1}$ in planktivorous lakes. Reductions in TKN and TDP also occurred in fishless and planktivorous lakes but were not substantial enough to change the trophic classifications of individual basins. Fishless lake water chemistry changed less over the observation period than in the other lake types.
Fig. 2.3: (a) PCA of water chemistry in the 20 study lakes. Labeled gray arrows represent water chemistry variables used to generate the ordination space (TDS, TDP, TKN, DOC, Z_max, Secchi depth). Each black arrow represents an individual lake, originating at environmental conditions of this lake during the drought and extending to conditions during the deluge. Generally, directional changes trend toward increased depth and water clarity and reduced nutrient load.

(b) Circular plot identifying directional changes in water chemistry from drought to deluge. Labeled arrows represent the superimposed PCA water chemistry variables. Each unlabeled arrow represents the direction and magnitude of change in water chemistry for one of the 20 study lakes. With some exceptions, most lakes increased in depth and water clarity and decreased in nutrient load and temperature. The directional change was statistically significant (p<0.05).
Synchronous regional changes in water chemistry resulted in an increase in lake similarity, forming a tighter cluster when ordinated on environmental axes during periods of high inputs of water. In contrast similarity of lake chemistry was reduced during periods of higher solar energy input.

2.3.2. Zooplankton

Four zooplankton taxonomic groups were identified using PCA, explaining 42% of the total variability on axis 1 and 2 (Fig. 2.4). The four separate groups coincided with piscivorous communities, planktivorous communities, mesosaline fishless communities and hypersaline fishless communities, respectively (Table 2.1, see Wissel et al. 2011 for more detailed taxonomic resolution). Overall, the freshwater piscivorous component was composed mainly of small daphnids, non-daphnid cladocerans and cyclopoid copepods, whereas the planktivorous group contained amphipods, calanoid copepods and daphnids. Large daphnids and calanoid copepods characterized mesosaline fishless zooplankton, while hypersaline fishless communities contained Artemia franciscana and harpacticoid copepods. Based on analysis with circular statistics, of the four zooplankton clusters, only the freshwater piscivore-influenced cluster showed a significant shift in community composition and species abundances during the transition from drought to deluge (p < 0.05). The remaining three communities showed a stochastic response as they shifted unpredictably in composition and abundance without significant directional trends.

2.3.3. Fishes

The fish communities in prairie lakes were relatively simple, not exceeding ten species per lake (Cooper and Wissel 2012b). The most common piscivorous fishes were walleye (Sander vitreus), northern pike (Esox lucius) and yellow perch (Perca flavescens).
Fig. 2.4 Principal Components Analysis of zooplankton taxonomic composition during drought- and deluge-influenced periods. Labeled lines represent taxa used to generate the ordination space. Vectors of individual lakes within taxonomic space are plotted between drought and deluge periods, with arrows terminating in the deluge period. Of the four zooplankton assemblages, the most change occurred in the piscivores group with small cladocerans in the lower right segment (Ceriodaphnia, Simocephalus, Diaphanosoma).
Common benthivorous species included white suckers and lake whitefish. Species with mixed planktivorous / benthivorous preference included spottail shiner and brook stickleback, as well as juvenile piscivores and a few less prevalent species. Fish assemblages were most effectively predicted by a discriminant function model that was based on water chemistry data during drought conditions (Fig. 2.5). The drought-based model showed 90% classification success relative to the 60% success of the model that was based on water chemistry during the deluge. Of the included variables, TKN was most important, and differed notably between the three lake types during this time period (Table 2.2). In addition to TKN, salinity, DOC and lake depth also distinguished between fish-habitable and fishless lakes on axis 1.

During the pluvial interval, total nitrogen levels were lower and more similar across lakes (Table 2.2), and salinity replaced total nitrogen as the most influential variable separating communities along axis 1. When the drought-based model was applied to water chemistry values during the deluge period, many formerly fishless, borderline fresh and mesosaline lakes were identified as fish-habitable. In the case of Middle Lake, water chemistry values shifted from fishless to planktivorous classification, consistent with the appearance of planktivore/benthivore communities during the 2007 to 2010 observation period. While the DFA classified two other historically fishless lakes as fish-supporting during the wet interval, no other fishless lakes were colonized by fish over the study period.

The risk of winterkill in prairie lakes may have been alleviated during the deluge due to changes in water chemistry associated with increased precipitation. Based on the model of Barica and Mathias (1979), nine lakes were at risk of winterkill during the
Fig. 2.5: Discriminant Function Analysis of the 20 study lakes using drought-influenced water chemistry data (a) and deluge-influenced chemistry data (b). The discriminant function classified lakes as *fishless* (white), *planktivorous* (gray) or *piscivorous* (black) using conductivity, dissolved organic carbon (DOC), depth ($Z_{\text{max}}$) and nutrient load (TDP and TKN) as variables. The components of the discriminant functions are listed on each axis in order of contribution. During the drought and deluge, nitrogen and conductivity were the most important factors on axis 1. Axis 2 was not significant for either scenario. Classifications based on the drought model were 90% accurate, with a high level of distinction between all community types. Deluge-based classifications were only 60% accurate, with most misclassifications arising due to overlap in the chemistry of *planktivorous* and *piscivorous* lakes.
Fig. 2.6: Principal Components Analysis of the 20 study lakes during the drought- and deluge-influenced periods (a and b, respectively), coded by level of winterkill risk (Barica and Mathias 1979). White indicates low risk, gray indicates moderate risk and dark gray indicates high risk. Moderate to high winterkill risk was predicted for 9 lakes during the drought period, which was reduced to 4 lakes during the deluge. Risk is negatively associated with depth and positively associated with nutrient load.
drought, seven of which were fishless. Only four of these nine at-risk lakes retained moderate or high risk during the deluge (Fig. 2.6). No lakes exhibited an increase in risk of winterkill during the pluvial period, but six decreased in risk ranking. At-risk lakes shared morphological and chemical properties that formed a cluster in the PCAs. In particular, shallow lake depth and high nitrogen and phosphorus concentrations were strongly associated with elevated risk of winterkill. Similarly parameters included in the Barica and Mathias (1979) model (lake depth and primary productivity (Chl α)), were prominent factors in the PCA. However, nutrient concentration was also a critical and non-redundant covariate in the PCAs.

2.4 DISCUSSION

2.4.1. Climate

In 2001, Saskatchewan experienced one of the driest years recorded in a century, followed by a persistent period of above-average effective precipitation from 2005 to 2010. This climate variation occurred over a relatively brief period of time, yet comparable drought and fluvial periods have been encountered repeatedly over the last several centuries (Michels et al. 2007). Longer and sometimes more extreme droughts and pluvial periods have been occurring on millennial scales in the past, but projections imply that climate extremes could occur over shorter periods in the future (Michels et al. 2007). Consequently, the observation period may provide a glimpse of processes representing the future "climate-normal" as a consequence of climate change.

2.4.2. Water Chemistry

The extreme weather shift demonstrably impacted the water chemistry of lakes, but with a short temporal delay. This delay may reflect the relatively slow flow of
groundwater into and out of lakes. The groundwater acting as a capacitor could have mitigated the initial effects of drought by supplying groundwater to the lakes, and storing excess water during the deluge that was then slowly released into the lakes (Bredehoeft and Durbin 2009, Webster et al. 2000).

During the observation period, lake water chemistries were more disparate during the drought interval, but became more similar during the pluvial period, possibly because the increasing addition of precipitation resulted in an asymptotic approach toward a freshwater, oligotrophic endpoint. In particular, inputs of water to parkland lakes during the wet interval had a homogenizing effect compared to the drought period, in contrast to prior observations that mass inputs tend to reduce intra-annual synchrony of lake ecosystems (Pham et al. 2008, Vogt et al. 2011). However, both studies evaluated synchrony rather than homogeneity or directionality of change as performed here, making the discrepancy less surprising. These apparently contrasting observations may also be reflected by the sampling frequency, as Pham et al. (2008) and considered intra-annual changes in synchrony whereas my study focused on a pronounced step change in effective moisture resulting from the end of a multi-year drought and influx of above average precipitation (Fig. 2.2). In particular buffering effects of groundwater may mute the effects of short-term changes in precipitation, yet may increase ecosystem coherence over decadal time scales. Webster et al. (2000) determined that lakes within geographic regions with simple surface runoff hydrology responded synchronously to precipitation changes, whereas groundwater and lake-specific factors resulted in an unstructured response to short-term changes in water flux. Consistent with this hypothesis, once the
systems became overwhelmed with mass influx toward later years of the deluge, lakes increased in similarity, possibly because groundwater ceased to regulate mass flux.

2.4.3. Zooplankton

Zooplankton species compositions are known to vary in response to strong differences in environmental conditions across the northern Great Plains. Previous studies by Wissel et al. (2011) and Cooper and Wissel (2012b) show that zooplankton communities in prairie lakes can be classified into four main functional groups based on water chemistry and predatory effects of fishes. Governing variables identified here were similar to prior studies, as zooplankton composition was controlled primarily by salinity, total nitrogen, lake depth and fish assemblage. While some differences in taxonomic composition occurred across the studies, the four groups were functionally similar with substantial taxonomic overlap.

Zooplankton assemblages were more differentiated among lakes in drought years than in pluvial periods, as indicated by a higher taxonomic diversity among lakes (β-diversity). These findings contrast with those of Chase (2007), who found that β-diversity of zooplankton decreased during drought years in fishless ephemeral ponds. This comparison suggests that size and permanence of a water body, as well as trophic complexity, are important factors to consider before generalizations can be made across ecosystems. Nevertheless, increased β-diversity likely occurs in lakes of the northern Great Plains due to the highly variable hydrology of endorheic basins, resulting in diverse responses to a uniform climate influence (Last and Ginn 2005). In contrast, prolonged high precipitation would partially negate differences in local hydrology and create more uniform (dilute) water chemistry across ecosystems.
Zooplankton communities in *piscivorous* freshwater lakes increased in similarity and declined in population density during the pluvial interval. Potentially, these changes may reflect a greater sensitivity of freshwater species to changes in environmental conditions; however, I discount this explanation because absolute changes in water chemistry were small relative to documented tolerances of most species (Table 2.2). Similarly, dilution did not reduce Chl α, as nutrients likely did not dilute sufficiently to limit algal growth, and in fact, mesotrophic lakes exhibited elevated Chl α content during the wet interval, while Chl α decreased in historically eutrophic and hypereutrophic systems. Instead I hypothesize that changes in abundances of freshwater zooplankton taxa were due to increased young-of-the-year recruitment and planktivory during the deluge when fishes encountered more suitable environmental conditions. Fish communities are key regulators of overall lake communities, and their loss or reintroduction has drastic impacts on zooplankton composition (Srinivasan et al. 2007). In contrast, zooplankton communities in *fishless* mesohaline and hypersaline lake seemed robust to changes, and exhibited little response to climate-related water chemistry changes over the study period.

### 2.4.4. Fishes

Discriminant function analysis suggested that the level of habitability for a complex fish community depended on a functional interaction of nitrogen, phosphorus, lake depth, salinity and DOC. Although abundances of fish populations could not be quantified, past studies have observed strong associations between fish recruitment and climate-related environmental variables. Fry recruitment can vary considerably between years due to changes in lake depth and water chemistry (Zalewski 1990), with late-
summer water temperature and disease prevalence being particularly good predictors of recruitment of some species (Paxton et al. 2004).

The long-term habitability of lakes for gamefish appeared to be defined best by conditions associated with drought intervals, in particular osmotic stress (salinity) and winterkill risk. The factors influencing winterkill risk also appeared to be interactive because multiple variables contribute to the rate of under-ice oxygen depletion. Risk of winterkill coincided with community classifications based on DFA, as moderate to high risk lakes only occurred in the fishless and planktivorous lakes, while all piscivorous lakes were classified as low risk. Piscivorous communities only existed in lakes with salinities below 2 g L\(^{-1}\), despite being documented in lakes with salinity up to 7 g L\(^{-1}\) in recent history (Bayly 1972, Burnham and Peterka 1975, Rawson and Moore 1944). Consistent with these observations, the DFA identified a conductivity threshold of < 8 mS m\(^{-1}\) for piscivorous communities (approximately equivalent to 5 g L\(^{-1}\)). The interactive effects of depth, nutrient levels and primary productivity (leading to winterkill) seemed, however, to limit fish populations in several of the 20 study lakes before conductivity thresholds were reached. The importance of DOC as a predictive variable is likely associated with in situ DOC production due to high primary productivity (Baines and Pace 1991), rather than its effects on visual and thermal lake properties (Williamson et al. 1999), as in these systems DOC is colorless and has no associations with light, temperature or oxygen profiles (Cooper and Wissel 2012a). It is also correlated with Chl-\(\alpha\), yet more coherent between measurements and therefore a more reliable indicator for this sampling regime.

2.4.5. Ecosystem responses
The decadal transition from drought to deluge intervals was accompanied by pronounced changes in water chemistry in prairie lakes, with lake-depth increases and reduced concentrations of nutrients and major ions (Fig. 2.3). Concomitantly, fish communities were largely determined by lake habitability due to changes in water chemistry during droughts. In contrast zooplankton showed a predominantly asystematic response to meteorological variability during the study period, as most taxa were resilient to short-term drought impacts, the notable exception being piscivore lakes where declines in abundances during the deluge appeared to reflect more planktivory by fish. It is probable that zooplanktivore lakes did not experience a similar increase in recruitment and planktivory due to their differing habitat requirements from piscivore larvae.

In the future the northern Great Plains could experience substantial fragmentation and differentiation to ultimately have a wider diversity of community types, but may support fewer gamefish species and have fewer lakes containing piscivorous fish. Endorheic basins are particularly sensitive to climate-change impacts, as they respond rapidly to drought events due to their shallow morphology and long retention times. Direct and indirect effects of drought and warming, such as reduced lake depth and increased productivity, can increase the risk of winterkill, potentially extirpating fish populations. Yet, if precipitation events were to drastically increase, as envisioned in some climate scenarios (Barrow 2009), saline communities could be lost, resulting in a reduction of landscape diversity and an increase in gamefish-supporting lakes. In such a scenario, the thermal stress of climate change could replace water chemistry as the primary determinant of game fish prevalence.

2.4.6. Conclusions
This and other studies have shown that endorheic lake systems across the northern Great Plains and other semi-arid regions are sensitive to the impacts of increasing temperatures and extreme weather due to future climate change (Adrian et al. 2009, Bates et al. 2008). In general, the impacts of climate change on endorheic systems will appear to be more severe than anticipated for boreal temperate lakes, which are expected to be largely impacted by deepening of epilimnion, stronger stratification and changes in light penetration (De Stasio et al. 1996, Fee et al. 1996, King et al. 1999, Schindler 1998, Williamson et al. 2009). The greater resilience of boreal lakes to climate change is in part due to stronger hydrological connectivity, lower retention times and stability of thermal stratification (Fee et al. 1996, Heitman 1973, Kling 1988, Schindler et al. 1996, Webster et al. 2000). Consequently, endorheic lakes should be considered separately in respect to the impacts of future climate change on lake ecosystems.
3. CONDITION AND PARASITE LOAD OF FISHES IN RESPONSE TO CLIMATE-INDUCED CHANGES IN TEMPERATURE AND SALINITY

3.1 INTRODUCTION

Assemblages of fish communities can be impacted by climate-related changes in environmental conditions, which ultimately determine the presence or absence of individual species (Bond et al. 2008, Magoulick and Kobza 2003). In particular, temperature, salinity, lake depth and nutrient levels define the limits of fish habitability either directly by exceeding physiological limits of fishes (Mehner et al. 2005, Ostrand and Wilde 2001), or indirectly, for example by causing seasonal hypoxia (e.g., winterkill or summer hypoxia) (Robarts et al. 2005).

As environmental parameters vary tremendously among lakes, sub-lethal impacts of these factors should occur within the fish-habitable range, and may manifest as lower relative body mass or impaired immune function. Laboratory studies revealed sensitivity of fishes to varying concentrations of dissolved compounds such as salts and metals (Anderson 1997, Victoria et al. 1992) or varying environmental temperatures (Cherry et al. 1977). Such approaches provide invaluable information on physiological limits of fishes under controlled conditions, but they cannot capture longer-term and interactive impacts under natural conditions. Studies on natural systems have shown negative impacts of extreme climate events, such as droughts on both lotic and lentic systems (Bond et al. 2008), which are usually a consequence of changes in hydrology, water chemistry and temperature.

Lakes in endorheic (closed) drainage basins are particularly sensitive to the impacts of climate variability, as salinity, nutrients, temperature and water depth in endorheic
lakes all respond quickly and significantly to altered weather conditions (Adrian et al. 2009, Chapter 2 of manuscript). Hence, lake systems such as prairie lakes in the Canadian Great Plains likely represent very good model systems to study the potential impacts of climate variability on fish communities (Hammer 1990, Williams 2002).

Understanding the relationships between climate variability and fish health and performance is particularly important because the potential impacts of future climate change raise new questions about the sustainability of freshwater fisheries, particularly in drought-prone areas (Ficke et al. 2007). In semi-arid systems, such as the northern Great Plains, lake-specific water chemistry is governed by the relative importance of evaporation, precipitation and groundwater inputs (Last and Ginn 2005). Under a high-precipitation climate-change scenario (Barrow et al. 2009), excess precipitation may compensate for increased evaporation due to elevated temperatures, and may maintain sufficient water quality to sustain suitable lake habitats for fishes. Yet, a warm but relatively dry future climate-change scenario (Barrow et al. 2009) would enhance evaporation and result in increased salinity and dissolved nutrients in lake basins, in combination with lower water depths (Chapter 2 of manuscript). In the latter scenario, water chemistry changes could be a significant threat to fish populations. Negative relationships between body condition of fishes and eutrophic state, stocking density, and salinity are often reported, as well as positive relationships with water level and access to prey (Dicenzo et al. 1996, Fisher et al. 1996, Marwitz and Hubert, 1997).

It is foreseeable that the predicted thermal increases of up to 5 ºC by 2050 (Barrow 2009) may have both positive and negative effects. For species with fairly narrow thermal requirements, preliminary findings suggest a warming climate could
improve body condition in colder areas of the species range, but reduce condition in warmer areas (Drinkwater 2005). A water temperature around 22 ºC appears to be optimal for walleye (Sander vitreus) and yellow perch (Perca flavescens) in captivity as well as in natural systems, while temperatures significantly above or below may result in reduced growth rates (Huh et al. 1976, Quist et al. 2002). Hence, temperature increases may offer a direct benefit of enhanced metabolism and faster weight gain if adequate food is available, and the associated reduction in winter duration could lower the risk of winterkill and extend the growing season (Quist et al. 2002). Yet, excessive temperature increases could be detrimental or lethal once bioenergetic limits are surpassed (Ficke et al. 2007, Quist et al. 2002), especially in isothermal prairie lakes that often lack a cool hypolimnion. The metabolic changes from increased temperatures can reduce maximum consumption rates while increasing metabolic rates, and either increase risk of starvation or increase risk of predation through compensatory feeding activity (Biro et al. 2007). Additionally, long hot summers are often associated with toxic algal blooms and hypoxia, threatening fish condition and survival (Heisler et al. 2008).

For this study I chose fish condition and intestinal parasite load as measures of fish health. Parasite load is a good indicator of immune function and host-pathogen interactions, is associated with water quality (Lewis et al. 2003, Poulin 1992), and can significantly respond to environmental change (Marcogliese et al. 2005). At elevated concentrations, naturally-occurring salts and other inorganic and organic compounds can function as environmental stressors and increase parasite prevalence (Bly et al. 1997). By suppressing immune functions or creating a more favorable environment for the pathogens, water chemistry changes can increase host infection rates (Hauton et al. 2000).
Relative weight ($W_r$) of fishes (or plumpness) is another important metric to express fish performance in a changing environment (Blackwell et al. 2000). This metric utilizes species-specific standard weight equations derived from a regression-line percentile technique using representative population data (Murphy et al. 1990). Low plumpness not only reduces the commercial quality of a fish, but is also a precursor to starvation (Dutil and Lambert 2000). Fish body weight is a commonly-used indicator of the health of a fishery, and plumpness metrics such as relative weight have been used as health indicators, to assess prey availability, to inform adjustment of stocking levels, to make comparisons between fish populations, and as an indicator of habitat quality (Blackwell et al. 2000).

For this study, I selected walleye as the primary focal species. As a common top-predator, it not only regulates many lake functions (Vander Zanden and Vadeboncoeur 2002), but is also a desired species for commercial and recreational fisheries (Fenton et al. 1996). Additionally, many lakes in southern Saskatchewan are supplemented with walleye coming from a single hatchery (Lake Diefenbaker). Hence, walleye populations in this region are genetically uniform across lakes (Starks, unpublished data), allowing for isolation of environmental from genetic effects. Unmanaged co-existing northern pike (Esox lucius) and yellow perch populations were also evaluated to determine if any of the observed environmental effects were species-specific.

To be able to analyze the importance of lake-, climate- and species-specific effects on fish health, I included seven different lakes over a two-year period that was characterized by contrasting climatic conditions. I expected that lake-specific effects
would dominate as the study lakes differed strongly in water chemistry and lake morphometry, followed by species and climate effects.

3.2 METHODS

3.2.1 Study sites and field sampling

All seven study lakes were sampled in June and August of 2009 and 2010 (Table 3.1). Lakes varied in water chemistry and physical characteristics, ranging in salinity from 0.5 to 3 g L$^{-1}$ of total dissolved solids (TDS). Trophic state ranged from mesotrophic to hypereutrophic, with a large variability in both nitrogen and phosphorus concentrations. All lakes were located in the prairie ecoregion of southern Saskatchewan in central Canada (Fig. 3.1). Of these seven lakes, all had walleye populations, and six were inhabited by yellow perch and northern pike.

Pelagic fish were netted overnight using a single multi-panel 1.5 x 30 meter gillnet with 55 mm mesh size, set perpendicular to shore at a starting depth of 3 meters. Littoral fishes were captured with a single 2 x 20 meter beach seine during daytime with 5 mm mesh size from shore to a depth of 2 meters. Fish were identified to species (Scott and Crossman 1973) and frozen prior to further analysis. Standard length and weight were recorded for all fish samples, as well as gonad and liver weights for fishes exceeding a length of 10 cm. Stomach contents were identified to family, and recorded in order of prevalence. Internal parasites were recorded for all three piscivorous fish species (walleye, northern pike and yellow perch) in adults exceeding 10 cm.

Sampling for water chemistry was conducted at the location of maximum depth, which was generally in the central area of each lake. Dissolved oxygen (mg L$^{-1}$), total dissolved solids (g L$^{-1}$), conductivity (mS cm$^{-1}$), water temperature (°C) and pH were
Table 3.1. Environmental characteristics of the seven lakes included in the study from 2009 to 2010. Gamefish recorded include walleye (W), northern pike (N) and yellow perch (Y). Recorded values of max depth in meters, surface area in km$^2$, salinity in g L$^{-1}$ (as total dissolved solids, TDS), Total Kjeldahl Nitrogen in ug L$^{-1}$ (TKN), Total Phosphorous in ug L$^{-1}$ (TDP) and Dissolved Organic Carbon in mg L$^{-1}$ (DOC) are means from June and August of 2009 and 2010.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Max Depth</th>
<th>Surface Area</th>
<th>TDS</th>
<th>TKN</th>
<th>TDP</th>
<th>DOC</th>
<th>Gamefish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humboldt</td>
<td>8.0</td>
<td>19</td>
<td>0.80</td>
<td>2159</td>
<td>249</td>
<td>29.4</td>
<td>WNY</td>
</tr>
<tr>
<td>Fishing</td>
<td>19.5</td>
<td>32</td>
<td>1.58</td>
<td>1194</td>
<td>9.8</td>
<td>32.5</td>
<td>WNY</td>
</tr>
<tr>
<td>Pelletier</td>
<td>10</td>
<td>2</td>
<td>0.41</td>
<td>757</td>
<td>11.7</td>
<td>16.4</td>
<td>WNY</td>
</tr>
<tr>
<td>Kipabiskau</td>
<td>8.5</td>
<td>5</td>
<td>0.44</td>
<td>1413</td>
<td>162</td>
<td>32.5</td>
<td>WNY</td>
</tr>
<tr>
<td>St. Brieux</td>
<td>11</td>
<td>0.5</td>
<td>1.40</td>
<td>1110</td>
<td>22.0</td>
<td>37.5</td>
<td>WNY</td>
</tr>
<tr>
<td>Wakaw</td>
<td>11</td>
<td>11</td>
<td>1.61</td>
<td>990</td>
<td>6.3</td>
<td>18.1</td>
<td>WNY</td>
</tr>
<tr>
<td>Shannon</td>
<td>10</td>
<td>1</td>
<td>1.70</td>
<td>1700</td>
<td>56.0</td>
<td>20.4</td>
<td>W</td>
</tr>
</tbody>
</table>
Fig. 3.1. Location of the seven study lakes (filled circles) in the grassland ecoregion of southern Saskatchewan, Canada. Ice dates were recorded from Buffalo Pound Lake (filled square), and air temperature data were recorded from Saskatoon.
measured throughout the water column during daytime at 1 m intervals using a YSI multi
probe (model 556). Water transparency was measured with a 20 cm black and white
Secchi disk. Using a tube sampler, I collected integrated, prescreened (80-μm mesh)
water samples for water chemistry (total Kjeldahl nitrogen (TKN), nitrate (NO$_3^-$), total
phosphorus (TDP), soluble reactive phosphorus (SRP), ammonium (NH$_4^+$), dissolved
inorganic carbon (DIC), dissolved organic carbon (DOC), calcium (Ca) and chlorophyll
a concentration (Chl a)). The tube sampler was suspended in the water column either
down to 6 m for deeper polymictic lakes, or down to 0.5 m above bottom sediments for
shallower polymictic lakes. Water samples were filtered through sterile 0.45 μm glass
fiber filters and analyses of TDP, TKN, NO$_3^-$, NH$_4^+$, were conducted at the University of
Alberta water chemistry laboratory after Stainton et al. (1977). DOC and DIC were
quantified using a Shimadzu TOC5000 analyzer at the Environmental Quality Analysis
Laboratory (EQAL) at the University of Regina. To estimate algal biomass, (Chl a), an
aliquot of 1 liter was filtered onto GF/C filters and stored in -10 °C until extraction with
acetone:methanol:water (80:15:5) and analyzed using trichromatic methods (Wetzel and

3.2.2 Statistical analysis

Daily air temperatures were obtained from the Environment Canada weather
station in Saskatoon for 2008 through 2010 (Fig. 3.1). The dates of ice-off to ice-on were
recorded for nearby Buffalo Pound Lake, which serves as a drinking water reservoir for
the city of Regina (Fig. 3.1), and used as a proxy for the length of the growing season
across the study area. This was deemed appropriate due to the high coherence of ice
coverage dates between lakes in the region (Vogt et al. 2011).
To evaluate the response of fishes to environmental conditions and community factors, relative weight ($W_r$) indices were calculated for each gamefish species at each lake, and averaged for individual sampling periods (Murphy et al. 1991). $W_r$ scores were calculated with species-specific length-weight functions based on a representative sample of North American fish populations. Species-specific functions were used for walleye, northern pike and yellow perch (Blackwell et al. 2000). Scores between 95 and 105 are considered optimal for the species. Scores near or below 80 imply depleted fat reserves due to thermally-induced weight loss and/or lack of food, while extremely high scores can be indicative of hypertrophy or obesity (Murphy et al. 1991).

To compare growth patterns of fishes over time, linear regressions of weight by cubed length were calculated for each species and sampling period. Because individual lake populations were not significantly different within sampling periods (1-way ANOVA $P>0.05$), length and weight data from all lakes were pooled for each period and species. Regression lines were tested for significant differences in slopes and intercepts between sampling periods. Samples were restricted to similar size ranges (> 100 mm) for each comparison to avoid confounding effects of sub-adult growth patterns.

Due to low parasite densities in yellow perch and northern pike, tapeworm infection levels could only be sufficiently evaluated for walleye. Gut tapeworm parasite loads for walleye were compared between lakes and over time, and used as an indicator of immune performance. Number of tapeworms per host and proportion of lake population infected were recorded for each lake and time interval. These values were tested against other environmental factors such as water chemistry using linear regressions; and the effects of gender, lake, year and season were quantified using t-tests.
or 1-way ANOVAs. Other parasites, such as nematodes and *Ergasilus* sp. were also recorded but did not occur in sufficient abundances to be further analyzed.

### 3.3. RESULTS

#### 3.3.1. Climate

The ice-free season of 2008 was slightly longer than long-term average conditions, and had many days within the optimal thermal range for cool water species, such as walleye (10-22 °C) (Cherry et al. 1977, Huh et al. 1976). 2009 had a short ice-free period and was characterized by many days outside the optimal metabolic range for walleye (Table 3.2). In contrast, the 2010 ice-free season was particularly good for walleye, with the vast majority of days in the optimal thermal range (197 days in 2010, relative to 146 in 2009).

#### 3.3.2. Body condition

Throughout the study period, I analyzed 129, 121, and 36 individuals for walleye, perch and pike, respectively. The range of specimens per sampling date varied from 21 to 36 for walleye, while for pike and perch the range was 0 to 25 and 11 to 48, respectively. Walleye, pike and perch did not differ significantly in weight and size class between lakes due to high intrapopulation variability, and were therefore pooled by species for all subsequent analyses. When averaged across all seven lakes and both years, walleye exhibited an intermediate mean relative weight (107) in comparison to perch (97) and pike (119). Walleye and perch achieved the $W_r$ target proposed by Murphy et al. (1990) (Table 3.3), while northern pike were exceeding the target range, despite performing poorly in some lakes (data not shown).
Table 3.2. Climate conditions from 2008 to 2010. Temperatures are recorded from the Saskatoon weather station and ice cover data were taken from the Buffalo Pound water treatment facility. Ice duration data are recorded for the entire winter leading up to the warm season of the indicated year. Mean highs and lows are recorded for the full ice off period.

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean Low (°C)</th>
<th>Mean High (°C)</th>
<th>Ice Duration (Days)</th>
<th>Ice Free (Days)</th>
<th>Ice Off Date</th>
<th>Days &gt; 22 °C</th>
<th>Days &gt; 27 °C</th>
<th>Days &lt; 10 °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>4.2</td>
<td>18.5</td>
<td>150</td>
<td>214</td>
<td>19 April</td>
<td>87</td>
<td>26</td>
<td>13</td>
</tr>
<tr>
<td>2009</td>
<td>3.6</td>
<td>17.2</td>
<td>163</td>
<td>206</td>
<td>1 May</td>
<td>83</td>
<td>24</td>
<td>36</td>
</tr>
<tr>
<td>2010</td>
<td>4.9</td>
<td>16.5</td>
<td>137</td>
<td>224</td>
<td>9 April</td>
<td>61</td>
<td>9</td>
<td>18</td>
</tr>
<tr>
<td>Norm</td>
<td>3.9</td>
<td>16.8</td>
<td>155</td>
<td>210</td>
<td>18 April</td>
<td>NA</td>
<td>NA</td>
<td>44.7</td>
</tr>
</tbody>
</table>
Table 3.3. $W_r$ for walleye, pike and perch over the full study period from 2009 to 2010.

NA = sample size not adequate for calculating an average.

<table>
<thead>
<tr>
<th>Sampling Period</th>
<th>Walleye</th>
<th>Perch</th>
<th>Pike</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 2009</td>
<td>156 (n=21)</td>
<td>91 (n=48)</td>
<td>157 (n=8)</td>
</tr>
<tr>
<td>Aug 2009</td>
<td>95 (n=49)</td>
<td>92 (n=35)</td>
<td>NA</td>
</tr>
<tr>
<td>June 2010</td>
<td>81 (n=23)</td>
<td>89 (n=27)</td>
<td>84 (n=25)</td>
</tr>
<tr>
<td>Aug 2010</td>
<td>105 (n=36)</td>
<td>123 (n=11)</td>
<td>117 (n=3)</td>
</tr>
<tr>
<td>Grand Mean</td>
<td>107 ± 1.7</td>
<td>97 ± 4.7</td>
<td>119± 3.6</td>
</tr>
</tbody>
</table>
Walleye length-weight regressions performed on pooled monthly data (all lakes combined) were significantly different between June and August of both years, decreasing in intercept in 2009, but increasing in intercept in 2010 (P < 0.01, no difference in slopes) (Fig. 3.2). While \( W_r \) of walleye was significantly different between June of 2009 and June of 2010, there was no difference between \( W_r \) in August of both years. Yellow perch length-weight regressions did not change significantly from early to late summer of 2009, but intercepts differed significantly in 2010 due to an increase in \( W_r \) from June to August (Fig. 3.3). Unfortunately, data for pike were insufficient for regression analysis of length-weight relationships.

Walleye and northern pike were in good condition during early 2009, and substantial body fat reserves were observed upon dissection (Sydney Chow, personal observation). Despite their high fitness in early summer, these two species were slightly underweight in late summer of 2009. Conditions of yellow perch were somewhat different, as \( W_r \) in June of 2009 was only 91 (slightly below the target range and well below the high values recorded for the other species), and values did not further increase until August of 2009 (Fig. 3.3). Over the warmer and longer ice-free season of 2010, body mass generally increased from June to August for all three species. In June of 2010, walleye condition was poor, with a low relative weight of 81, but by August mean walleye condition across lakes reached a relative weight of 105. The seasonal increases in \( W_r \) values for pike and perch were even higher with increases from 85 to 123 and 84 to 117, respectively (Table 3.3).

The majority of walleye populations achieved the target weight within 2010, but in Shannon, Kipabiskau and Fishing Lakes body conditions remained poor. Overall,
Fig. 3.2. Regressions of length by weight revealed a significant decrease in walleye body weight by length from June to August 2009 (above), and an increase in 2010 (below).
Fig. 3.3. Regressions of length by weight revealed no significant change in perch body weight for the full lake set from early to late 2009, and an increase in weight from early to late 2010.
Fishing and Kipabiskau Lakes were below target for all three species (not significant), while stocked walleye represented the only gamefish species in Shannon Lake. Potentially, the lower performance of walleye in these lakes may have been associated with poor water quality, as these lakes did not represent an optimal habitat for walleye. While Shannon and Fishing Lakes had elevated salinities, Kipabiskau and Shannon Lakes were eutrophic to hypereutrophic, based on integrated water column samples of total phosphorus and chlorophyll a. However, no significant differences in fitness were detected among lakes, and linear regressions revealed no predictive relationship between $W_r$ and water chemistry or lake morphometry parameters.

Liver somatic index (LSI) averaged approximately 1 for walleye, 1.15 for northern pike, and 1.3 for yellow perch, indicating that liver weight was relatively normal in these populations (Adams and McLean 1984). LSI did not differ between 2009 and 2010 for any of the species, or between June and August. Furthermore, LSI did not covary with $W_r$ or any of the measured water chemistry or climate parameters.

3.3.3. Stomach contents

Stomach fullness was not significantly different between 2009 and 2010 for any of the three species. Common stomach contents of walleye and pike included small fishes (brook stickleback and fathead minnows) and benthic prey (amphipods and larval insects). Yellow perch consumed zooplankton, benthic prey and small fishes. Approximately 30% of sampled walleye had empty stomachs, and 35% of pike and <1% of perch stomachs were empty. Some differences in stomach fullness between lakes were observed over the study period, but did not correlate with inter-lake differences in fitness or any environmental parameters. Pike and perch in Kipabiskau Lake exhibited
significantly higher benthivory than in other lakes, while walleye in Shannon Lake exhibited a higher degree of benthivory (P < 0.05).

3.3.4. Parasite load

Tapeworm levels were highest in walleye, and significantly more prevalent in 2009 than in 2010 (Fig. 3.4). Population-level parasite prevalence was significantly correlated with salinity in 2009 (r^2=0.93), but not in 2010 (Fig. 3.5). Additionally, salinities were significantly higher in 2009 (P<0.05). No other environmental parameters showed any significant relationships with tapeworm prevalence. Larger walleye (total length > 10 cm) were significantly more likely to host tapeworms (P<0.05). Subsequently, tapeworm loads were also tested as weight-based loads against environmental variables, but this adjustment did not change the general findings. In 2009, female and male walleye had similar rates of tapeworm infection, but when infected, females hosted significantly more tapeworms (p<0.05). In 2010, only female walleye were infected.
Fig. 3.4. Female walleye (gray bar) exhibited a significantly higher mean tapeworm count than males (hatched bar) in both years. Overall tapeworm counts were significantly higher in 2009 than 2010. No males were infected in 2010.
Fig. 3.5. Proportion of walleye populations infected with tapeworms was significantly associated with salinity in 2009 ($r^2 = 0.934$), but not in 2010. Shannon Lake, excluded from the analysis, is shown in white.
3.4. DISCUSSION

Game fish fitness and parasite load, among walleye in particular, correlated significantly with changes in salinity and temperature over the two year study. Accordingly, temperature and precipitation were related to the fitness of ambient fish populations. Furthermore, the changes in fish condition and parasite load were even detectable on short-term (annual) time scales. Surprisingly, no other factors known to predict fish habitability were influential in this study. Potentially, environmental parameters such as nutrient concentrations, lake depth, Secchi depth and algal biomass established the habitability thresholds of the lakes by increasing winterkill risk, but had no observable effects on ambient fish populations during summer. In this case, no effects would be observable below the threshold for winterkill. This is in contrast to other gamefish populations, which have shown seasonally reduced condition along with lower Secchi depth (Craig and Babaluk 1989), poor growth with small lake surface area (Cena et al. 2006), and changes in recruitment relative to lake depth, volume and Chl-α (Mehner et al. 2005). Nevertheless, the impacts of lake morphometry and trophic state on a landscape scale are critical, but are more likely to control the inhabitability of lakes for fishes, rather than controlling their condition in those lakes that have established fish communities. Therefore, established gamefish of this region are likely to be more strongly impacted by natural variability of weather conditions and climate change, as both temperature and precipitation are directly linked to climate and hydrology.

3.4.1. Body condition

The poor fitness values in June of 2010 were likely a result of the shorter growing season and less optimal temperatures during 2009. In 2009, many more days were above
and below the optimal thermal range for walleye growth, which likely resulted in the
decline of body condition from June to August. Temperature has a direct effect on fish
bioenergetics, increasing the metabolic rate of fish (Kitchell et al. 1991). Assuming that
adequate prey is available, high temperatures will result in weight gain up to a critical
threshold, beyond which it is physically impossible to sustain body mass. High
temperatures have not only been shown to induce thermal stress but also reduce overlap
of walleye with warm water prey species at temperatures above 22°C, even in polymictic
lakes (Kocovsky and Carline 2001, Quist et al. 2002). However, a warmer spring and fall
could compensate for summer growth losses if summer temperatures remain sublethal
(Quist et al. 2002).

In 2010, the number of days in the optimal thermal range were well above-
average, resulting in a substantial improvement in condition over the 2010 growing
season. These trends were uniform across the target size range, despite findings in other
studies that temperature effects can be size-dependent (Carginelli and Gross 1997,
Gabelhouse 1991). It is noteworthy that mostly young of the year (YOY) fish, which
were not included in this study, may experience high over-winter mortality and condition
decline relative to older conspecifics (Pangle et al. 2004). Hence, the lack of size-
dependency was not a concern.

While dietary proportions of fish and benthic prey varied among lakes, this did
not have an apparent effect on body condition. Paradis et al. (2006) found that walleye
maintained similar body condition regardless of dietary composition, but grew fastest on
a piscivorous diet. Unfortunately, this effect could not be tested here, as not all fishes
could be aged. Furthermore, food availability and bottom-up effects were not likely to
have impacted the condition of fishes. Almost no perch were found with empty stomachs, indicating that food was not limiting (Knight et al. 1984). For walleye and pike, only 30 to 35% of specimens had no detectable food in their stomach, which is fairly common for species that have a higher degree of piscivory and therefore rely on less frequent meals of larger prey items (Chapman et al. 1988).

3.4.2. Parasite load

While salinity did not correlate with body condition, there was a significant increase in parasite load and prevalence in walleye corresponding with increasing salinity in 2009. The insignificant relationship between salinity and parasite load in 2010 may have been due to the concurrent freshening of all lakes between years. In 2009 salinities exceeded 2.0 g L\(^{-1}\), whereas in 2010 they were all below 1.5 g L\(^{-1}\) in all lakes. Tapeworm levels were correspondingly low across all lakes in 2010. The strong correlation between parasite load and an environmental stressor (salinity) was not surprising. Environmental stress and pathogenicity are believed to act synergistically (Marcogliese et al. 2005); however, fitness effects of this parasite and environment interaction were beyond the scope of this study. If the here identified threshold of 1.5 g L\(^{-1}\) salinity is universal or region-specific will have to be evaluated in future studies. Koel and Peterka (1995) identified a threshold between 1 and 2 g L\(^{-1}\) sodium sulfate for walleye hatching success; however, thresholds for effects of salinity on immune function in walleye are not documented.

Several alternative explanations for the discrepancy in parasite load between years could not be directly evaluated here. The interannual difference in temperature may have had some effect on cestode life cycles; however, this seems unlikely as eggs are often
stimulated to hatch by warmer temperatures (Wright and Curtis 2000), and 2010 experienced warmer temperatures overall. It is also plausible that selective mortality of infected hosts occurred between years, although this would not fully explain the apparent lack of new infections in 2010. I therefore hypothesize that salinity-induced immunocompromisation of the host is the most likely explanation for the salinity and parasite load correlation in 2009 and the significant interannual difference in parasite load.

3.4.3. Species-specific differences

Despite the similar general trends across species, I detected several differences among walleye, pike and perch. Walleye were a significantly greater definitive host for tapeworms in this system as in others (Muzzall and Haas 1998), and was the only species that exhibited a change in tapeworm load and prevalence in response to environmental salinity. Pike and perch exhibited such low parasite load in both years that this data could not be analyzed. Most likely, the cause for different parasite prevalences is due to dietary preferences, which include a larger benthic composition (Beaudoin et al. 1999, Hayward and Margraf 1987). Pike and perch are therefore less exposed to vertical transfer of parasites from pelagic prey (Marcogliese 2002). Yellow perch were apparently least selective in regard to prey, as their stomachs were full significantly more often than those of pike and walleye, which is like associated with their lower trophic position (Cooper and Wissel 2012a).

Overall, walleye seemed to be the most vulnerable species to observed environmental changes based on its greater intra-annual and inter-annual changes in fitness and parasite load, followed by pike and perch. Hence, while stocking efforts maintain walleye populations in these lakes, their overall resilience is low relative to
populations of naturally occurring fish species. In fact, the single-source stocking approach for walleye may have detrimental effects on these populations by inviting larger parasite loads (Poole and Dick 1985) and reducing mean body weight (Li et al. 1996).

3.4.4. Anticipated future effects of climate change

Overall growth rates of fishes will likely improve if climate change would only prolong the duration of summer without increasing maximum temperatures. Yet, the predicted increase of 5°C by 2050 relative to current maximum temperatures (Barrow 2009) will likely result in severe metabolic deficits in walleye and other fish species. Observations of walleye in more southern lakes of the Great Plains indicate that increases in summer temperatures result in growth declines; yet, simultaneous warming in spring and fall may actually increase total growth over the whole year (Quist et al. 2002).

Simulations predict that maximum lake temperatures in southern Saskatchewan will increase to about 25 to 30 °C by the year 2100, relative to current maxima of 20 to 25 °C (Sharma et al. 2007). Current temperature maxima bracket the thermal optimum for walleye (22 °C), while future conditions would not only go beyond the thermal optimum, but would also reach or even exceed the bioenergetic (lethal) limit of adults (27 °C). While walleye and yellow perch have similar optimal thermal ranges (Kitchell et al. 1977), perch aren’t as detrimentally affected by suboptimal temperatures (Huh et al. 1976). Based on this information, perch should not be as negatively impacted by climate warming. Unfortunately, pike samples were not adequate in 2009 to measure the impact of temperature on growth, but since their thermal optimum is also similar to walleye (Christie and Regier 1988), this species is also like to be natively impacted in the future, though it is unclear to what extent.
Among the three piscivorous species, walleye appeared most vulnerable to climate change in these lakes. In addition to their fitness correlations to temperature and salinity changes, only walleye exhibited a high parasite load. Walleye body condition was overall less variable among lakes and over time than for the other two game fish species, potentially due to the low inter-lake genetic variability of this species as a result of single-source stocking (Starks, unpublished data). Because of their popularity as game and commercial fish species, identifying and prioritizing more optimal habitats for their maintenance should be a priority. Small lakes such as those studied here may not be suitable in the long term, and more potentially resilient species such as northern pike and yellow perch are likely to replace walleye in small lakes (which would largely also be the current scenario in the absence of stocking). Larger and deeper freshwater lakes that would be more suited to support walleye are rare in the prairie region (Last and Ginn 2005), but might be a prime habitat in northern, boreal parts of Saskatchewan, especially as temperature increase.

In systems other than endorheic prairie lakes, lake size, genetics and diet, vary much more than in this dataset (Cena et al. 2006), while hydrology is less variable (Pham et al. 2008, Winter and Rosenberry 1998). Temperature and salinity were relevant to fitness of game fishes in Saskatchewan prairie lakes, but lakes that are thermally stratified and less prone to salinization are unlikely to be negatively impacted by climate change to the same degree as prairie lakes (Adrian et al. 2009). Nevertheless, this study clearly indicates that endorheic systems, such as prairie lakes have a high capacity as model system to study early impacts of climate change on lake ecosystems. This is particularly true, since the two study years fell into a relatively wet period and the observed changes
in climate and water chemistry did not reflect the typical gradients that can occur in this system. Hence, longer-term studies will likely identify even stronger effects on fish fitness.
4. CONCLUSION

4.1 SYNTHESIS

Species assemblages in endorheic lakes of southern Saskatchewan are highly diverse due to the extreme inter-lake variability in environmental parameters and trophic interactions (Cooper and Wissel 2012b). This study revealed that regular drought events such as the recent subdecadal drought functioned as an environmental filter to define fish community composition in prairie lakes, and divided lakes into fairly discrete clusters of fishless, planktivorous (plus benthivorous) and piscivorous (plus planktivorous) fish communities. Environmental variables most relevant to fish community composition were nutrient concentrations and lake depth, which are strongly associated with winterkill risk. Zooplankton responded to fish predation pressure with a reduction in overall quantity and biomass during wet periods, rather than a change in species composition. These observations offer an interesting contrast to other lakes which may stratify to reduce habitat thermal habitat overlap of zooplanktivorous fishes with their zooplankton prey, thereby reducing predation pressure (De Stasio et al. 1996).

While environmental variables, such as lake morphometry, nutrient levels and salinity have been described to be important for defining fish community composition (Cooper and Wissel 2012b, Mehner et al. 2005), surprisingly few of these variables produced visible sub-lethal effects for walleye, perch and pike in my study system. For prairie lakes, seasonal and interannual temperature variation significantly affected body condition of these species, while the large environmental differences among lakes had no influences. Furthermore, salinity had a significant positive correlation with parasite load, but this effect was only detected for walleye populations. In climate change scenarios
(Barrow 2009), variables that induce sub-lethal effects (temperature and salinity) are predicted to change more uniformly across lakes than most other variables, indicating that climate change effects on fish health would be fairly consistent between lakes in this ecoregion.

4.2 FUTURE RESEARCH DIRECTIONS

This study was designed to assess the effects of a subdecadal climate shift on adult fish population and zooplankton assemblages in small endorheic lakes, and evaluate the potential of these lakes as a model system for ecosystem responses to climate change. While the environmental conditions in my study lakes generally encompasses a large variability for the most important parameters, a larger sample size with more evenly distributed values for depth, surface area and water chemistry parameters could establish that factors other than temperature and salinity are also relevant for determining fish health in these prairie lakes. For example, lakes with sufficient depth could eliminate both winterkill risk and thermal variation that dominate smaller lakes, potentially revealing more subtle underlying effects of water chemistry or seasonal thermal stratification.

Further, the sub-lethal effects on fish identified here were only examined for mature adults. Sub-lethal and partially lethal effects are known to vary across life stages and are often more pronounced at earlier life stages (Mélard et al. 1996). In particular, salinity, suspended sediments or altered temperatures can substantially reduce egg hatching rates (Koel and Peterka 1995, Paxton et al. 2004). Tapeworm parasite load is likely an exception, as parasite loads tend to increase with age (Zelmer and Arai 1998).
Also, a study of all age-classes over multiple years could reveal generational effects that may cause significant demographic shifts over time (Ficke et al. 2007).

This research is helpful for understanding the nature of climate response in climate-stressed lakes. Yet, for better lake management, it would be important to develop quantitative models the future responses of prairie lake communities to climate change. This will require a longer data set as well as an assessment of fish biomass to complement the existing more detailed zooplankton data. Although it was apparent that drought conditions more accurately predicted species composition, the absence of reliable biomass and abundances of fished prevented a more detailed analysis of population response to climate. Shifts in relative abundances of species, as well as shifts in biomass and increases or declines in recruitment numbers are well-documented in other systems (Christie and Regier 1988, Pangle et al. 2004, Paxton et al. 2004), but little information is currently available on this topic for these ecosystems. Once a better data structure exists, a temporal predator-prey modeling approach such as MAR could be an effective option to predict trophic interactions between piscivores, planktivores and zooplankton for climate-change scenarios (Hampton et al. 2006).

4.3 GENERAL CONCLUSIONS

Endorheic prairie lakes served as an excellent model system due to their high hydrologic sensitivity to climate and tendency to regularly experience cyclical climate extremes (Last and Ginn 2005). This allowed for the detection of significant climate responses over a relatively brief (intradecadal) period of time. Similarly, interannual variation in temperature and winter length was substantial enough to reveal its sub-lethal
effects on fish populations. This high degree of natural variability provides valuable information for predicting effects of future environmental change.

Furthermore, this study successfully encapsulated environmental and trophic effects at the community to intraspecific levels. Fish communities were assessed based on trophic position, while zooplankton were evaluated in terms of species abundances, and sub-lethal effects were assessed for three piscivorous fish species. Such a comprehensive analysis facilitates evaluation of the relative importance of these factors and how they may act in concert.

This study revealed that observations about ecosystem response to disturbances may not be universal. In this system, only fishes were directly affected by water chemistry changes, while zooplankton were primarily regulated by predation. Further, lake chemistry parameters differed more during drought, while many other systems responded synchronously in times of environmental stress (Vogt et al. 2011, Webster et al. 2000). Also, lake communities differed more during drought, suggesting that landscape-level diversity is heightened by disturbance in this system, despite typically being lowered by systematic disturbance in others (Balata et al. 2007, Chase 2007).

Aside from these differences, it is clear that this system, like many others, would likely be detrimentally affected by changes in climate, resulting in reduced trophic complexity and lower species diversity within fish and zooplankton communities. Similarly, fish communities would experience physical stress in more extreme environments. Conservation of these valued and threatened species is therefore essential across all systems; however, differences in the underlying mechanisms of change require that model systems be identified.
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