BIOLOGICAL INDICATORS OF CLIMATE CHANGE: TRENDS IN FISH COMMUNITIES AND THE TIMING OF WALLEYE SPAWNING RUNS IN MINNESOTA

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I dedicate this thesis to my mother and stepdad whose unending support and encouragement played a major role in this accomplishment. I cannot simply put into words how much I appreciate them.

ABSTRACT

I conducted research on two projects to examine effects of climate change on Minnesota's aquatic communities. I used walleye egg-take records from the Minnesota Department of Natural Resources for 12 spawning locations and historical ice-out data to determine if the timing of these events is changing. I used ice-out data instead of temperature for our analyses because historical temperature data is not available and ice-out has been previously related to climate change. Because ice-out has been previously related to climate change, I regressed the dates of first egg-take against ice-out dates to determine if the timing of walleye spawning runs could be a useful biological indicator of climate change. For the second project to determine if fish species abundances are changing in response to climate change, I used historical lake survey records for 34 lakes, each with 15 to 43 years of data, and regressed catch-per-unit-effort (CPUE) against year. I examined species distributions by regressing mean latitude against year. I regressed slopes of CPUE over time against 5 local air temperature variables to determine if changes in abundance were associated with air temperature. I also used stepwise regressions (forward and backward selection) and one-way analysis of variance (ANOVA) to determine if variability in trends could be explained by lake physical and chemical characteristics. Results were reported for 7 species with the strongest trends: Centrarchids (*Micropterus salmoides*, *Micropterus dolomieu*, and *Lepomis macrochirus*); Ictalurids (*Ameiurus melas* and *Ameiurus natalis*); Whitefish (*Coregonus artedi* and *Coregonus clupaeformis*).

For the walleye spawning analyses I found that spawning runs and ice-out are occurring earlier in some lakes but not all. However, there was a strong relationship between first egg-take and ice-out dates, and walleye egg-take appears to provide a good biological indicator of climate change. For the lake survey analysis, centrarchid abundance in lakes was increasing over time, black bullhead abundance was decreasing, and other species were increasing in some lakes and decreasing in others. Slopes of CPUE versus year increased more quickly over time in smaller lakes and more quickly moving east across the state than in larger lakes toward the west. All species' ranges were significantly advancing northward except smallmouth bass and whitefish. Regressions of CPUE versus air temperature showed that centrarchids are increasing in lakes as summer air temperatures increase, and whitefish are decreasing in lakes as air temperatures increase. In summary, the abundances and distributions of these 7 species over time may be responsive to climate change, and trends for species abundances may be influenced by lake characteristics. Centrarchids and bullhead may be good indicators, and thus, further research is warranted. Also, because there is a strong relationship between dates of first egg-take and ice-out, and because ice-out has previously been related to climate change, the timing of walleye spawning runs may be a useful biological indicator of climate change.

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CHAPTER 1

PROLOGUE

Climate change and its effects are important topics that are arousing interests and concerns in fisheries and related disciplines (McGinn 2002: American Fisheries Society Symposium 32). Climate change is affecting physical processes such as altered streamflows and the timing of ice-out with effects on both human infrastructure and biota (Melillo et al. 1993; Magnuson et al. 2000; Walther et al. 2002; Koster et al. 2005; Schindler et al. 2005; Hodgkins and Dudley 2006; Parmesan 2006). Climate change is also affecting biological processes that influence community structure and species composition in aquatic systems (e.g., Gerten and Adrian 2000; Sundby and Nakken 2008; Wingate and Secor 2008). Evidence of climate change and its effects has been documented using a range of both physical and biological responses.

Primarily, climate change is indicated by changes in global average air temperatures, which have increased 0.6°C (± 0.2°C) since the late 1800s (IPCC 2001; Walther et al. 2002). The years 1970-forward have been recognized as a distinct period of increased warming. Local effects have been observed ranging from summer extremes to shorter winters; in the Midwest large heat waves have been recorded more frequently in the period 1980-forward than for any other time period in the past century (U. S. Global Change Research Program, 2009), and the length of the frost-free season is increasing (Easterling 2002; Frich et al. 2002). Lake and stream temperatures are increasing (Johnson and Stefan 2006; Austin and Colman 2007), and ice-out (ice break-up on lakes) is occurring earlier over time (Magnuson et al. 2000; Jensen et al. 2007). Evidence that climate change is affecting biological systems around the world spans both aquatic and terrestrial systems; studies have documented climate-driven range shifts for more than 300 species in terrestrial and aquatic habitats (Parmesan et al. 1999; Parmesan and Yohe 2003; Chu et al. 2005; Hickling et al. 2005). Numerous others have shown that climate variables, such as temperature, influence species reproduction (Reading 1998; Dunn and Winkler 1999, Sundby and Nakken 2008), migration (Bohlin et al. 1993; Both et al. 2005), and abundance (Shuter et al. 1980; Shuter et al. 2002; Wingate and Secor 2008).

Changes in biological systems raise questions about the fate of species affected, and for this thesis I will focus on those related to fisheries. For example, will range expansion of warm-water fish such as bluegill (*Lepomis macrochirus*) or smallmouth bass (*Micropterus dolomieu*) become more frequent in lakes and across regions? Will there no longer be suitable habitat for some cold-water species such as tullibee (*Coregonus artedi*) or lake whitefish (*Coregonus clupeaformis*)? If the answer to the previous two questions is “yes”, will we observe more species extinctions? Some studies have already documented species invasions and predicted local extinctions associated with climate change (Chu et al. 2005; Daufresne and Boet 2007; Rahel and Olden 2008). For example, Stefan et al. (2001) predicted that warming temperatures would reduce the number of lakes in the United States with suitable cold-water fish habitat by up to 45%, and some Canadian studies have shown that one warm-water species, smallmouth bass, is already expanding its range northward as temperatures warm (Shuter et al. 2002, Vander Zanden et al. 2004). The introduction of non-native species could be detrimental to populations of native species in aquatic habitats (Findlay et al. 2000; Jackson and Mandrake 2002). For example, the introduction of a warm-water species to a cool-water habitat could alter predator-prey interactions and as a result, cause reductions in diversity and prey species abundances (Robinson and Tonn 1989; Jackson et al. 2001; Vander Zanden et al. 2004). In a study of competition between Sacramento perch (*Archoplites interruptus*) and bluegill, Marchetti (1999) suggested that introduced centrarchids might be responsible for present and future extirpations of Sacramento perch in California. Jackson (2002) showed that there was a strong negative association between abundances of small-bodied fishes and black basses in south-central Ontario lakes. He also mentioned that changes in fish diversity and prey (small-bodied) species abundances could negatively affect water quality by altering planktonic communities via a trophic cascade. Processes such as these are important to consider for future projections and management of local resources. Moreover, aside from community and ecosystem changes via invasions and extinctions, we should also consider economic effects. Many aquatic species such as walleye (*Sander vitreus*) and largemouth bass (*Micropterus salmoides*) are important commercially and recreationally as a source of food and revenue (i.e. bait and tackle sales, commercial fish sales, etc.) for the economy. Therefore, reductions of these important species could result in negative economic as well as biological consequences (Roessig et al. 2004; Brander 2007).

From examination of previous studies we can see that climate change could significantly affect our aquatic resources. Because of this, it would be useful to have climate change indicators that could help researchers and agencies develop future projections and management plans. Moreover, biological indicators would be particularly useful to natural resource management agencies because they could act as a response variable or a predictor depending on the goal of the analyses. Previous studies have shown that species including Atlantic cod (*Gadus morhua*), the common toad (*Bufo bufo*), and some insects may be good biological indicators of climate change (e.g. Reading 1998; Larocque et al. 2001; Balanya et al. 2006, Sundby and Nakken 2006). For aquatic resources, a good candidate for a biological indicator may be a species that is responsive to climate change in an easily observable manner and is important commercially or recreationally. The availability of long-term records and the chance that the species would continue to be monitored over time would probably be greatest for these species. A good candidate for a biological indicator would also benefit from being economically important so that value is perceived across different components of society, thus making its response to climate change of more interest to various stakeholders.

To find an indicator we must determine if there are changes in aquatic populations that are associated with climate change and determine if the population can be characterized by the attributes discussed previously in order to promote scientifically sound results that will benefit multiple components of society. By following these guidelines, not only may we find a good indicator, but we'll also get some idea of changes we can expect in the future.

My research goals were to identify a good aquatic biological indicator of climate change (Chapter 2) and to examine changes in Minnesota's fish communities associated with climate change and identify additional indicators (Chapter 3). The thesis is organized into chapters with this introductory chapter followed by two chapters written as manuscripts for publication. A concluding (Epilogue) chapter summarizes my overall findings and conclusions. Below I give brief descriptions of each chapter. For chapters 2 and 3 I give likely co-authors for manuscripts in press or to be submitted, and within these chapters I use the plural “we” instead of “I” because these chapters had contributing co-authors.

Chapter 2: Schneider, K. N., R. M. Newman, V. Card, S. Weisberg, and D. L. Pereira. The timing of walleye spawning as an indicator of climate change. Accepted 24 March 2010 for publication in Transactions of the American Fisheries Society.

In Chapter 2, I proposed that the timing of walleye (*Sander vitreus*) spawning runs might be a good biological indicator of climate change, and I examined changes in the timing of walleye spawning and ice-out over time. To determine if walleye spawning was a good indicator, I regressed the date of first egg-take against the date of ice-out. I used egg-take data from 12 hatcheries across Minnesota and ice-out data from lakes within 48 km of each egg-take site. I used ice-out data instead of air temperature for our analyses because walleye often spawn soon after ice-out and because ice-out has been previously related to climate change (Scott and Crossman 1973; Becker 1983; Magnuson et al. 1997; Magnuson et al. 2000; Jensen et al. 2007). I also determined if there were changes in the timing of walleye spawning runs and ice-out over time.

Chapter 3: Schneider, K. S., R. M. Newman, S. Weisberg, and D. L. Pereira. Changes in Minnesota fish species abundance and distribution associated with local climate and lake characteristics. Target journal not yet determined.

In Chapter 3, I examined changes in Minnesota fish communities over time and responses of fish communities to changes in local climate. I analyzed historical Minnesota fisheries lake survey data (gillnet and trapnet) for 34 lakes, each with 15 to 43 years of data, to determine if fish distributions and abundances were changing over time. I also analyzed trends to determine the relationship between five air-temperature variables and fish abundance and to determine if lake physical and chemical characteristics influenced trends in catch-per-unit-effort over time. Results were summarized for 7 fish species with the strongest trends: Centrarchids (*Micropterus salmoides*, *Micropterus dolomieu*, and *Lepomis macrochirus*); Ictalurids (*Ameiurus melas* and *Ameiurus natalis*); Whitefish (*Coregonus artedi* and *Coregonus clupaeformis*).

Chapter 4 is the final chapter where I summarize results from previous chapters (2 and 3), and further discuss the importance and application of these findings for aquatic resource management. Chapter 2 was accepted for publication in Transactions of the American Fisheries Society, and Chapter 3 is undergoing revisions so that it can be submitted to a journal upon completion.

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CHAPTER 2

Timing of Walleye Spawning as an Indicator of Climate Change

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Thank you,

Kristal N. Schneider

CHAPTER SUMMARY

We obtained walleye *Sander vitreus* historical egg-take records for 12 spawning locations from the Minnesota Department of Natural Resources to determine if the timing of walleye spawning runs could be used as an indicator of climate change. We used ice-out data instead of temperature for our analyses because walleye often spawn soon after ice-out, and ice-out has been previously related to climate change. We used linear regressions to determine the relationship between the start of spawning (based on first egg-take) or peak of spawning run (greatest egg-take) and ice-out date and to determine if there were long-term trends in ice-out and date of spawning over time. Linear regressions of the date of first walleye egg-take versus ice-out date showed that for each day ice-out gets earlier, walleye spawning begins 0.5 to 1 day earlier. All but 2 regressions had slopes less than 1. Similar results were found for peak of spawning runs. Regressions of egg-take and ice-out date versus year showed trends toward earlier spawning and earlier ice-out. For regressions of first egg-take versus year (16 total with restricted datasets), significant negative slopes (P<0.1) were observed in 5 out of 16 regressions; for peak egg-take, 6 regressions had significant negative slopes. For regressions of ice-out date versus year, 25 of 26 regressions were negative; there were 9 significant negative slopes (P<0.1). Overall, ice-out and walleye spawning are getting earlier in Minnesota, and the timing of walleye spawning may be a good biological indicator of climate change.

INTRODUCTION

As interest in climate change increases, there is a growing concern for its effects on the distribution and reproduction of species as well as an increasing need for biological indicators of climate change. Defining multiple parameters as indicators of climate change allows us to compare trends that can be used to predict future changes or reconstruct past changes in climate and allows us to choose cost-effective methods to monitor effects of climate change. Past research has documented climate trends by analyzing hydrologic parameters such as freeze and ice-out dates (Robertson et al. 1992; Magnuson et al. 1997; Jensen et al. 2007), climatic variables such as temperature and precipitation (Karl et al. 1996; IPCC 2001), and biological parameters such as changes in algal assemblages (Smol and Cumming 2000), diatom community structure (Kilham et al. 1996), and species distributions (Larocque et al. 2001; Chu et al 2005; Balanya et al. 2006). Indicators such as these help to answer questions from researchers, policy-makers, and the public about future climate projections, the effects of climate change on species and ecosystems, and anthropogenic forces that may be driving climate change.

The purpose of our study was to determine if climate change is affecting an aquatic species that is an important commercial and recreational resource in Minnesota and to determine if that species may be a useful biological indicator of climate change. Biological indicators are important because they provide us with a response that is a function of some stimulus over time instead of just a snapshot that may record a single extreme event (such as one random day with record high temperatures). By choosing walleye *Sander vitreus*, a species important both commercially and recreationally, we were able to obtain long-term records to determine if the timing of walleye spawning runs was related to ice-out and to identify any long-term trends in walleye spawning and ice-out data.

Walleye egg-take for hatcheries in Minnesota started in the late 1800s, and by 1923 seven walleye hatcheries and collection sites were established (Minnesota Department of Natural Resources 1996). Fish trapping sites are used to capture walleye for egg collection. Walleye spawning typically occurs soon after ice-out when ambient water temperatures are between 4-11°C (Scott and Crossman 1973; Wolfert et al. 1975; Becker 1983) and is partly dependent on these conditions and photoperiod to induce gonadal and hormonal changes that prepare the fish for spawning (Hokanson 1977; Malison et al. 1994; Malison and Held 1996). Thus some climate variable(s) likely influence the timing of the spawning run. Earlier studies of fishes have shown that climate change has significant relationships with species range shifts (Chu et al. 2005), recruitment (Shuter et al. 2002), fecundity (Sundby and Nakken 2008), and abundance (Kallemeyn 1987; Wingate and Secor 2008), but few have documented climate change effects on the timing of spawning in fishes.

Air temperature (e.g., mean monthly or maximum daily) has been used frequently in previous studies to examine the effects of climate change on various organisms (e.g. Winkel and Hudde 1997; Reading 1998; Dunn and Winkler 1999; Blaustein et al. 2001; Both et al. 2005). For our study we decided to focus on the relationship between the timing of walleye spawning runs and ice-out instead of air or water temperature. Ice-out is generally described as the time when a lake is free of all ice. We used ice-out because walleye spawning generally occurs soon after ice-out (Scott and Crossman 1973; Becker

1983) and because previous research has documented changes toward earlier ice-out, which may be evidence of climate change (Magnuson et al. 1997; Magnuson et al. 2000; Jensen et al. 2007). We also chose to use ice-out data because it is broadly available geographically and historically (more than 100 years of data in some cases) whereas air and water temperature data are not. In our datasets, temperature (air and water) was not recorded for every day of sampling, and record format was inconsistent across locations. For example, some locations recorded minimum and maximum daily temperatures, but others recorded only one measurement per day. Also, although spawning has been documented to occur when ambient water temperatures are between 4-11°C (Scott and Crossman 1973; Wolfert et al. 1975; Becker 1983) as previously noted, spawning temperature and temperature measurements taken with a thermometer are quite variable. Thus the timing of the spawning run is probably better related to ice-out than temperature. Robertson et al. (1992) suggest that the climate signal is amplified by using ice cover as a response. Based on their analyses, a 1°C change in air temperature should result in a 5.1 ± 0.4 (95% confidence limit) day change in mean ice-out dates. Other research suggests that the timing of ice-out may be a good indicator of climate change because it is strongly correlated with air temperatures (Palecki and Barry 1986; Johnson and Stefan 2006). Previous studies also suggest that the period 1970-onward is a distinct period of warming with increases in temperature occurring at a rate that is nearly double that of the previous period (IPCC, 2001; Walther et al. 2002). In agreement, a shift toward earlier ice-out in North America was documented during that same time period (Robertson et al. 1992; Johnson and Stefan 2006).

In this paper we determine the relationship between the timing of walleye spawning runs and ice-out, and we determine if there are trends in timing and duration of walleye spawning and in the timing of ice-out over time in Minnesota lakes. If the timing of walleye spawning is related to ice-out, it may provide a convenient biological indicator of climate change. Also, an observed relationship between walleye spawning and ice-out may demonstrate how walleye are responding to climate change. This information would be useful in future management plans for aquatic resources and in future climate change studies.

METHODS

We obtained walleye spawning records from the Minnesota Department of Natural Resources (MN DNR) and acquired Minnesota ice-out records from the Minnesota Ice Cover Database, the Minnesota Historical Society, and the Cook Herald News. For three of our spawning locations, we used ice-out data (measured as the number of days ice-out occurred after April 1st; January 1st for time series) from the same lake where walleye spawning data were collected (Table 1). Two spawning sites were in streams that flowed directly into the ice-out lakes, one site was in a system indirectly connected to the ice-out lake, and six sites were in water bodies not connected to the ice-out lakes but within 17 to 48 km. For Lake Sallie we evaluated two different ice-out datasets, Lake Sallie and Detroit Lake (connected to Lake Sallie) because the Detroit Lake ice-out record had 8 more sampled years than the Lake Sallie ice-out record. Statistical analyses were performed using R version 2.5.1, except Microsoft Excel was used to calculate some correlations. All statistical results were judged significant at the $P<0.05$ level unless otherwise stated. ArcGIS 9 (ESRI 2004) was used to map walleye spawning and ice-out locations and to measure the distance between spawning and ice-out data collection sites.

Walleye Spawning Records

Walleye spawning records collected by the MN DNR contained information on egg-take (number of eggs stripped from ripe walleye females) and individual fish counts obtained from twelve walleye egg collection operations conducted by various Minnesota hatcheries from 1938 to 2007 (Table 1). The timing of the walleye spawning runs could be described by the beginning of spawning, peak of spawning, or the end of spawning. From 1987 to 2007, the data recorded included number of walleye captured by sex and reproductive state of females (green, ripe, or spent), along with egg-take on each date. Prior to 1987, data on individual walleyes were generally not recorded, and only data on egg-take were available. Because egg collection quotas were common among hatcheries and tended to halt egg collections before the actual end of walleye spawning runs, we decided to focus on the dates for beginning and peak of spawning only. We wanted to know if we could use these dates interchangeably or if one response was a better indicator of the timing of spawning runs. We also needed to determine if the selected response was correlated with egg-take records so that data prior to 1987 could be used. We chose to use ripe females rather than green or spent females because these fish were ready to spawn.

We first needed to determine if peak capture dates or dates of first capture better described the timing of the spawning run. Coefficient of determination (R^2) values from regressions of the peak of spawning runs versus the start of spawning runs for ripe females ranged from 0.16 to 0.94, and at all but two locations, Otter Tail River and Rice Lake, regressions were significant. On average, peak capture of ripe females occurred 2 to 8 days later than first occurrence of ripe females. When correlations were computed separately across locations for the start of spawning runs and for the peak of spawning runs, correlations were larger on average for the start of spawning versus year than for the peak of spawning versus year. Thus, we focus on dates of first capture of ripe females.

To determine if egg-take (which greatly extended the data set) could be used instead of ripe females, we computed correlations between dates of first egg collection and dates of first ripe female sightings at all locations. They were highly correlated, with correlations (r) ranging from 0.78 to 0.99, and Rice Lake and Otter Tail River were the only locations with correlations less than 0.97. This allowed us to greatly extend our datasets by using egg-take data instead of data on adult walleyes that were typically not available prior to 1987.

Spawning and Ice-out Regressions and Time Series

We regressed the dates for the beginning of walleye spawning runs against ice-out dates for all 12 spawning locations to determine if there was a relationship between the two variables. For these regressions April 1^{st} was designated as day 0 to magnify plots. The slopes and intercepts were compared across latitudes to determine if there were obvious spatial trends and were also compared using the “lmList” function in R (Pinhero and Bates, 2000) to create a list of slopes and intercepts as objects with 95% confidence intervals. T-tests were used to test the null hypothesis at each location that the slope was equal to one. We also regressed dates of peak egg-take versus ice-out to compare trends with first egg-take. To test for serial dependence in the datasets (Oehlert, 2000), the "acf" function in R was used to plot residuals from the regressions of walleye spawning versus ice-out date. We used a Bonferroni correction to control the family-wise error rate and report these results separately for each analysis. To determine if there were long-term trends in the timing of walleye spawning runs, we computed regressions of the beginning of walleye spawning (first egg-take) and the peak of walleye spawning (peak egg-take) versus year for each location. Because Pike and Pine Rivers both had about a twenty year gap in data, regressions were also computed for these locations that restricted the analyses to those years after 1970. We used the "pbinom" function in R to test the probability of getting our observed number of negative slopes.

Although there were likely constraints due to egg-take quotas, we present the results of regressions of peak egg-take versus ice-out and peak egg-take versus year for comparison with first egg-take results. Because changes in dates of first and peak egg-take may also indicate or be influenced by changes in the duration of spawning, we also present the results of regressions of the duration of spawning versus year and the duration of spawning versus ice-out. The duration of spawning was defined as number of days occurring from first to peak egg-take.

To determine if there were long-term trends in ice-out, we computed the regressions of ice-out dates versus year for all locations. Regressions were computed using full ice-out datasets at each location and using ice-out data that were matched to the sampling years represented in the spawning datasets (referred to as "restricted datasets"). More than half of the ice-out locations had records that started around 1970 or later. To determine if significant trends were present for that period, the datasets with longer-term records (prior to 1970) were restricted to the years 1970-onward (referred to as "restricted datasets"). We then used the "pbinom" function in R to test the probability of getting our observed number of negative slopes.

The "lowess" function in R, an algorithm based on the Ratfor original by W.S. Cleveland (1981), was used to compute a LOWESS smooth (SPAN=2/3) for each time series (spawning and ice-out). These were then compared to the linear regressions by computing the G-test statistic for lack of fit in R (Weisberg, 2005) to determine if the LOWESS smooth improved the fit. All time series datasets were tested for autocorrelation using the "acf" function in R, and a Bonferroni correction was used to control family-wise error rate.

RESULTS

Relationship Between Spawning and Ice-out

The timing of walleye spawning runs was highly correlated with the timing of ice-out, and there was no evidence of autocorrelation. Slopes from linear regressions of first egg-take versus ice-out date were significant at all locations, and all R^2 values were greater than 0.30 (Table 2, Figure 1). After a Bonferroni correction, 10 of 13 regressions were significant; only Bucks Mill, Otter Tail River, and Rice Lake were not significant. The relationships described by linear regression suggested that walleye spawning gets half a day to one day earlier for each day that ice-out gets earlier (Table 2). All but 2 locations, Lake Koronis and the St. Louis River, had slopes significantly less than 1 (t-tests H_0: Slope=1). We found no obvious trends across Minnesota latitudes to explain the differences in slopes.

Regressions of peak egg-take versus ice-out date showed similar results (Table 2); Bucks Mill and Rice Lake were not significant after a Bonferroni correction. However, the slope for Otter Tail River, which wasn't significant in first egg-take regressions, was significant using peak egg-take. The slopes for peak egg-take were usually similar to (differences of 0.02 to 0.33), but lower than the slopes for first egg-take at all locations except Little Cut Foot Sioux Lake, Bucks Mill, and Otter Tail River (Table 2). For regressions of the duration of spawning versus ice-out, significant negative slopes ($P<0.1$) were observed for Boy River, Dead River, Little Cut Foot Sioux Lake, Rice Lake, and St. Louis River. After a Bonferroni correction, only regressions from Boy River and Dead River were significant.

Spawning and Ice-out Time Series

The regressions of first egg-take versus year revealed significant negative slopes at Otter Tail River and at Lake Koronis (Figure 2, Table 3). Marginally significant ($P<0.1$) negative slopes were observed at Lake Sallie and for the restricted Pine River and Pike River datasets (Table 3). After a Bonferroni correction, Lake Koronis was the only location where the regression of first egg-take versus year was significant ($P<0.0063$). However, the probability of getting 14 negative slopes out of 16 was 0.0018. The LOWESS function improved the fit of the data ($P<0.05$) compared to linear regression at only Pike River, Pine River, and Rice Lake, which implied that data were well represented by the fit of the linear regressions at most locations. For peak egg-take regressions, significant ($P<0.05$) negative slopes were observed for Big Lake Creek, Lake Koronis, Otter Tail River, and for the restricted (1971-2007) Pine River dataset (Table 3).

Marginally significant (*P*<0.1) negative slopes were observed from Little Cut Foot Sioux and Pine River. After a Bonferroni correction, no regressions of peak egg-take versus year were significant, however, the probability of getting 14 of 16 negative slopes due to chance was 0.0018.

For regressions of the duration of spawning versus year, significant negative slopes (P<0.1) were observed for Big Lake Creek, Little Cut Foot Sioux Lake, and Pine River. A significant positive slope was observed at Lake Sallie. After a Bonferroni correction, there was one significant negative slope (Big Lake Creek) and one significant positive slope (Lake Sallie).

For ice-out regressions there were 25 negative slopes and 1 positive slope (Table 4). Significant negative slopes (*P* < 0.1) were observed in 8 of 26 regressions (Table 4, Figure 3). No slopes were significant with the Bonferroni correction (*P*<0.0038). However, even if there were no significant relationships between ice-out date and year, the probability of getting 25 negative slopes out of 26 regressions was <0.0001. Linear regressions described the ice-out datasets better than LOWESS fits at most locations (Figure 3). Lack of fit G-test statistics to test if the LOWESS improved the fit compared to linear regressions were only significant (*P*<0.05) for Lake Vermilion (full dataset) and for the Lake Vermilion dataset that was restricted to the range of years represented in the Pike River egg-take dataset.

DISCUSSION

There was a significant positive relationship between the timing of walleye spawning runs and ice-out at all locations. Even with the Bonferroni correction, 10 of 13 regressions for start of the runs were significant. Walleye spawning runs started 0.5 to 1 day earlier for every day ice-out occurred earlier. Although it is typically reported that spawning occurs soon after ice-out (see Scott and Crossman 1973; Wolfert et al. 1975; Becker 1983), our results indicate that in many cases the spawning run may be initiated just before ice-out. This may be a result of using the first occurrence of ripe females (or eggs) as an indicator of the start of spawning runs (i.e. individual vs. population response). The peak occurrence of ripe females and peak egg-take occurred 0 to 25 days after the first sighting of ripe females and first egg-take. The first sighting of ripe females and first egg-take occurred 20 days before to 27 days after ice-out (average of 3.3 days after ice-out). Neither spawning habitat (river versus lake spawning), nor location (location of egg-take site or distance to corresponding ice-out location) could explain the higher slopes at St. Louis River and Lake Koronis (slopes not significantly different from 1), which may mean that other lake characteristics are affecting slopes. Photoperiod and prior thermal history also determine timing of spawning (see Hokanson 1977; Malison et al. 1994; Malison and Held 1996) and likely constrain the dates of spawning.

Previous studies have shown a strong relationship between ice-out and air temperature (Palecki and Barry 1986; Robertson et al. 1992; Johnson and Stefan 2006), and temperature has significant relationships with life history traits of fishes (Bohlin et al. 1993; Shuter et al. 2002; Sundby and Nakken 2008). In a study of the effects of temperature and climate change on year-class production of fishes in the Great Lakes Basin, Casselman (2002) noted that although the time of spawning in lake trout *Salvelinus namaycush*, a cold-water fish, had been relatively consistent over time, an increase in fall temperatures at spawning time had a negative impact on year-class strength. Casselman also observed that year-class strength of northern pike *Esox lucius*, a cool-water fish, showed a curvilinear relationship with July-August temperatures and a similar reduction at high temperatures but observed a general positive effect for smallmouth bass. Moreover, Sundby and Nakken (2008) observed that increasing temperatures induced a northward shift of spawning areas and an increase in fecundity for Arcto-Norwegian cod *Gadus morhua*. Studies of walleye have shown that temperature affects the production and yield of walleye (Christie and Regier 1988; Schupp 2002) and that the timing of walleye spawning depends on water temperature and location (Scott and Crossman 1973; Hokanson 1977; Becker 1983), but the exact relationship between the timing of walleye spawning and temperature has not been well documented. Because our results show that there is a strong relationship between the timing of walleye spawning runs and ice-out, and ice-out has extensive evidence for its use as an indicator of climate change (e.g., Magnuson et al. 2000; Johnson and Stefan 2006), we believe the timing of walleye spawning is a useful biological indicator of climate change.

As with many sampling procedures, there is potential for sampling bias. For example, it's possible that the relationship observed between dates of first egg-take and ice-out is a result of sampling constraints (i.e., if sampling does not begin until after ice-out). However, in our study only 3 of 13 regressions paired egg-take data with ice-out data from the same location, and out of 10 spawning datasets with adequate records, only 23% of first egg-take dates occurred on the first day of sampling. Also, slopes from regressions of peak egg-take versus ice-out date were significant and similar to slopes from first egg-take regressions (Table 2). Peak egg-take occurred 0 to 25 days (mean 5.8

days) after first egg-take; 3% of peak egg-take dates were the same date as first egg-take, and 5% of peak egg-take dates were the day after first egg-take. Furthermore, although spawning duration was negatively related to ice-out for 5 lakes, there was no relation in the other 8 comparisons and no suggestion that duration was constrained by inability to sample spawning fish due to the presence of ice. These results suggest that spawning is related to ice-out but it is unlikely that sampling constraints due to the timing of ice-out were driving the relationships.

The negative relationship of spawning duration with ice-out date at some lakes may reflect biological constraints. With later ice-outs most fish may have mature gametes and be ready to spawn, but with earlier ice-out more individual variation in maturation may be seen. Earlier ice-out therefore might be expected to result in extended spawning runs, however, there was no indication that run duration was generally increasing in Minnesota; duration was increasing at Big Lake Creek and decreasing at Lake Sallie with no change at the other 10 locations. Further consideration of the implications of increased duration of spawning with earlier ice-out is warranted.

Regressions of start of walleye spawning versus year indicated that walleye spawning is getting significantly earlier at some locations in Minnesota, but not all. If we applied a Bonferroni correction, only 1 (Lake Koronis) of 16 regressions would be significant. However, the probability of getting 14 negative slopes out of 16 regressions was very low (0.0018). Similar results were seen with peak of spawning. Walleye spawning regressions with more than 30 years of data contributed 80% of significant negative slopes. Four of the 5 significant regressions were for lakes where spawning records started in 1970 or later. Otter Tail River was the only significant relationship with records prior to 1970. We were unable to detect any spatial trends that would explain variability in relationships among locations.

The trends that we documented in earlier spawning over time could have resulted from artificial selection by stocking artificially hatched walleye fry into these lakes. A MN DNR policy requires that 10% of hatchery production be returned to the waters where the parental fish came from (MN DNR 1997). This policy is intended to compensate for natural production that the artificially hatched fish would have provided if they were not intercepted in the spawn-taking operation. Egg-take at some hatcheries may have been biased toward earlier spawning fish in some years and locations because the operations of trapping and artificially fertilizing fish were often terminated after hatchery production needs (i.e. egg quotas) were met. However, for selection to occur, the stocked recruits would need to make up a greater proportion of the spawning population than did naturally hatched and recruited fish. Although there is potential for some selection bias to arise from this mechanism, it is unlikely that the artificially hatched and stocked fish would contribute disproportionately to the spawning population, especially in spawning runs emanating from the larger lakes where a smaller proportion of the spawning biomass will be intercepted by the spawning run trap.

For ice-out, our results were consistent with previous studies that documented ice-out occurring earlier over time (Schindler et al. 1990; Robertson et al. 1992; Magnuson et al. 2000; Johnson and Stefan 2006). In our study, 25 of 26 regressions were negative, and although a Bonferroni correction would result in no significant regressions, the probability of getting 25 negative slopes out of 26 regressions was very low (<0.0001). Ice-out regressions with more than 30 years of data contributed 75% of significant negative slopes. Six of the 9 significant regressions were for locations where ice-out records started in 1970 or later; Lake Koronis, McDonald Lake restricted to Dead River walleye sampling years, and McDonald Lake restricted to Otter Tail River walleye sampling years were the only significant relationships with records prior to 1970. Some literature (IPCC, 2001; Walther et al. 2002) suggests that 1970-forward is a period of distinct warming that is occurring at rates nearly double those of previous years. There was some indication of accelerating ice-out in our datasets.

Our results suggest that the timing of walleye spawning runs can be used as a biological indicator of climate change because it has a strong relationship with ice-out. Both walleye spawning and ice-out in Minnesota seem to be occurring earlier over time. Although all slopes were not negative and those that were negative were not all significant, both variables (spawning and ice-out) show mostly negative trends over time. Moreover, the very low likelihood of getting so many negative slopes and few positive slopes for both spawning and ice-out suggest the trends are real. Finding no relationship between two variables (egg-take and year or ice-out and year) can reflect either that no such relationship exists, or that the design, either through the variation in the values of the predictors or the sample size, is such that the power of detecting a significant relationship is low for any particular location. That the signs of almost all the coefficients were in the expected direction (moving toward earlier egg-take and ice-out) is indicative that power of detection was too low to detect a significant relationship in any particular lake or river, but taken as a whole, the test we used on the signs of the coefficients suggests against the hypothesis of independence.

Aside from being used as an indicator of climate change, the relationship between walleye spawning and ice-out may provide information about how climate change could affect walleye populations. One potential consequence of earlier spawning may be a mismatch in the timing of larval walleye abundance and peak prey availability, assuming prey populations do not respond to climate change by hatching earlier. This mismatch could cause negative consequences for walleye populations, and should perhaps be examined in future studies. Gotceitas et al. (1996) showed that larval Atlantic cod *Gadus morhua* tended to exhibit poorer growth and survival when there was a temporal mismatch in peak larvae abundance and peak prey availability compared to match conditions. This type of interaction has also been documented outside of the laboratory. Winder and Schindler (2004) found that there was a temporal mismatch in diatom and zooplankton blooms due to differences in sensitivity to warming in Lake Washington. *Daphnia* densities declined because the peak diatom bloom occurred too early to allow for maximum foraging by *Daphnia* populations. Because zooplankton availability significantly influences the survival and growth of larval walleye (Mayer and Wahl 1997; Hoxmeier et al. 2004), a temporal mismatch between peak larvae abundance and peak zooplankton (or other prey) availability may also significantly affect walleye populations. Additionally, change in the timing of walleye spawning runs may also affect recruitment if there is a temporal mismatch between the timing of peak larval emergence and optimal discharge events. There is strong evidence that discharge affects larval walleye survival (Becker 1983; Mion et al. 1998; Jones et al. 2006) and that discharge events may be significantly affected by climate change (Middelkoop et al. 2001; Peterson et al. 2002; Graham 2004).

We have presented evidence that the timing of walleye spawning runs may be a good biological indicator of climate change that could also provide insight into how climate change is affecting walleye populations. The timing of walleye spawning runs is a convenient indicator because walleye are an important sport and commercial fish that are continually monitored and managed in Minnesota. Further research investigating lake and river characteristics is needed to identify factors that could be influencing the relationship between the timing of walleye spawning and ice-out. This information would be useful for developing models to reliably predict the timing of walleye spawning. It would also be useful for creating a universal climate change model instead of several models that vary based on individual locations.

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Table 1. Summary of spawning locations and associated ice-out locations in Minnesota. Distance from spawning location to associated ice-out location was measured, and the number of years (N pairs) were counted where both spawning and ice-out data were available. Sampling range of years for both spawning and ice-out records is shown. The overlap range represents the range of years when spawning and ice-out data were both available, and superscripts identify the type of connectivity, if any, between spawning and ice-out locations. Synthetic records for Rice Lake were created by neighbor-lake modeling.

Spawning location	Spawning range (years)	Ice-out location	Ice-out range (years)	Site-to-site distance (km)	N pairs	Overlap range
Big Lake Creek	1971-2006	Big Turtle Lake[4]	1965-2008	21.86	29	1971-2005
Boy River	1970-2006	Long Lake (Cass)[4]	1974-2008	14.25	32	1974-2005
Bucks Mill	1985-1993	Long Lake[3] (Becker)	1980-2003	10.49	9	1985-1993
Dead River	1966-2007	McDonald Lake[4]	1968-2005	18.56	35	1969-2005
Lake Koronis	1996-2007	Lake Koronis[1]	1950-2005	NA	8	1996-2007
Lake Sallie	1971-2007	Lake Sallie[a]	1970-2007	NA	29	1971-2007
Lake Sallie		Detroit Lake[c]	1970-2007	1.2	37	1971-2007
Little Cut Foot Sioux L.	1942-2007	Leech Lake[d]	1936-2007	48.10	61	1942-2007
Otter Tail River	1954-2002	McDonald Lake[d]	1968-2005	19.91	24	1971-2002
Pike River	1938-1946, 1971-2007	Lake Vermilion[b]	1906-2007	10.23	44	1938-2007

Table 1 (continued).

Pine River	1925-1942, 1970-2006	Lake Edna[d]	1980-2005	17.33	26	1980-2005
		Ponto Lake[d]		20.72		
		Gull Lake[d]		26.99		
Rice Lake	1987-2007	Rice Lake[a] (& synthetic)	1962-2005	NA	10	1987-2005
St. Louis River	1992-2006	Fond du Lac[b]	1996-2007	< 1	11	1996-2006

[a] Same location as egg-take

[b] Egg-take location runs into ice-out lake

[c] Connected to egg-take site through a system of lakes and streams

[d] No connection to egg-take location

Table 2. Summary of linear regressions of first and peak egg-take versus ice-out date. The y-intercept, slope, R^2, P-value, and number of years with egg-take and ice-out data (N) are shown for each location. The number of years with egg-take and ice-out data are the same for both first and peak-eggtake at each location. The origin is April 1.

Spawning location	Ice-out location		Y-intercept	Slope	R^2	*P*	N (pairs)
St. Loius River	*Fond du Lac*	First Egg-take	0.47	1.095	0.918	<0.001	10
		Peak Egg-take	5.83	0.912	0.809	<0.001	
Lake Koronis	*Lake Koronis*	First Egg-take	4.95	0.906	0.809	0.002	8
		Peak Egg-take	8.05	0.829	0.890	<0.001	
Little Cut Foot Sioux	*Leech Lake*	First Egg-take	3.17	0.731	0.739	<0.001	61
		Peak Egg-take	7.85	0.752	0.834	<0.001	
Boy River	*Long Lake (Cass)*	First Egg-take	5.5	0.631	0.806	<0.001	32
		Peak Egg-take	18.01	0.301	0.422	<0.001	

Table 2 (continued)

Pike River	*Lake Vermilion*	First Egg-take	2.31	0.629	0.556	<0.001	44
		Peak Egg-take	9.2	0.564	0.604	<0.001	
Pine River	*Edna, Ponto, and Gull*	First Egg-take	2.92	0.598	0.476	<0.001	24
		Peak Egg-take	10.99	0.470	0.439	<0.001	
Big Lake Creek	*Big Turtle Lake*	First Egg-take	7.54	0.570	0.692	<0.001	29
		Peak Egg-take	15.19	0.485	0.635	<0.001	
Lake Sallie	*Lake Sallie*	First Egg-take	4.17	0.567	0.675	<0.001	29
		Peak Egg-take	10.6	0.476	0.462	<0.001	
Lake Sallie	*Detroit Lake*	First Egg-take	4.62	0.537	0.713	<0.001	36
		Peak Egg-take	10.86	0.468	0.552	<0.001	

Table 2 (continued).

Dead River	*McDonald Lake*	First Egg-take	5.79	0.567	0.668	<0.001	35
		Peak Egg-take	17.72	0.355	0.486	<0.001	
Rice Lake	*Rice Lake / Synthetic*	First Egg-take	8.11	0.566	0.567	0.012	10
		Peak Egg-take	10.88	0.56	0.556	0.021	
Bucks Mill	*Long Lake (Becker City)*	First Egg-take	5.29	0.492	0.472	0.041	9
		Peak Egg-take	5.8	0.733	0.574	0.018	
Otter Tail River	*McDonald Lake*	First Egg-take	12.37	0.394	0.319	0.004	24
		Peak Egg-take	16.49	0.466	0.398	<0.001	

Table 3. Summary of linear regressions of first and peak egg-take versus year. The y-intercept, slope, *P*-value, and number of years with egg-take data (N) are shown for each spawning location. The number of years with egg-take data is the same for both first and peak egg-take at each location. Years for restricted regressions are given in parentheses.

Spawning location	Y-intercept	Slope	*P*	N
Big Lake Creek				
First Egg-take	135.36	-0.013	0.891	33
Peak Egg-take	384.04	-0.180	0.030	
Boy River				
First Egg-take	240.07	-0.067	0.453	37
Peak Egg-take	193.45	-0.040	0.608	
Bucks Mill				
First Egg-take	-692.71	0.400	0.433	9
Peak Egg-take	-1351.49	0.733	0.277	
Little Cut Foot Sioux L.				
First Egg-take	195.50	-0.042	0.363	66
Peak Egg-take	268.20	-0.076	0.058	
Little Cut Foot Sioux L. (1970-2007)				
First Egg-take	474.13	-0.182	0.108	38
Peak Egg-take	380.28	-0.132	0.158	
Dead River				
First Egg-take	238.50	-0.067	0.388	39
Peak Egg-take	308.23	-0.098	0.094	

Table 3 (continued).

Lake Koronis				
First Egg-take	3540.21	-1.714	0.005	8
Peak Egg-take	2779.29	-1.333	0.024	
Lake Sallie				
First Egg-take	419.29	-0.158	0.053	37
Peak Egg-take	153.62	-0.022	0.789	
Otter Tail River				
First Egg-take	442.60	-0.168	0.037	32
Peak Egg-take	703.73	-0.297	0.006	
Otter Tail River (1971-2002)				
First Egg-take	474.20	-0.184	0.213	23
Peak Egg-take	561.76	-0.225	0.147	
Pike River				
First Egg-take	152.69	-0.022	0.640	46
Peak Egg-take	135.65	-0.011	0.788	
Pike River (1971-2007)				
First Egg-take	493.09	-0.193	0.070	36
Peak Egg-take	362.40	-0.125	0.153	
Pine River				
First Egg-take	122.36	-0.009	0.781	55
Peak Egg-take	212.04	-0.051	0.085	

Table 3 (continued).

Pine River (1970-2006)				
First Egg-take	527.90	-0.213	0.061	37
Peak Egg-take	507.76	-0.200	0.027	
Rice Lake				
First Egg-take	-218.55	0.160	0.484	12
Peak Egg-take	-224.41	0.164	0.469	
St. Loius River				
First Egg-take	788.60	-0.339	0.383	15
Peak Egg-take	669.26	-0.279	0.427	

Table 4. Summary of linear regressions of ice-out date versus year for full and restricted datasets. The y-intercept, slope, *P*-value, and number of years with ice-data (N) are shown for each location. Parentheses indicate datasets restricted to a range of years or restricted to years sampled at the corresponding spawning location. Brackets indicate county names for lakes with identical names. Synthetic records for Rice Lake were created by neighbor-lake modeling.

Ice-out location	Y-intercept	Slope	*P*	N
Big Turtle Lake	383.00	-0.137	0.192	42
Big Turtle Lake (Big Lake Creek)	401.52	-0.146	0.387	30
Big Turtle Lake (1970-2007)	388.19	-0.139	0.276	37
Detroit Lake	558.91	-0.227	0.064	38
Detroit Lake (Lake Sallie)	509.32	-0.202	0.121	37
Edna, Ponto, and Gull	-124.09	0.116	0.500	26
Fond du Lac	1255.88	-0.573	0.283	12
Fond du Lac (St. Louis River)	1690.70	-0.791	0.211	11
Lake Koronis	437.74	-0.169	0.027	56
Lake Koronis (Lake Koronis)	2964.18	-1.429	0.041	8
Lake Koronis (1970-2005)	680.02	-0.291	0.084	36
Lake Sallie	512.55	-0.204	0.101	30
Lake Sallie (Lake Sallie)	551.48	-0.223	0.095	29
Leech Lake	256.29	-0.071	0.137	72

Table 4 (continued).

Leech Lake (1970-2007)	533.39	-0.210	0.069	38
Long Lake [Cass]	239.97	-0.066	0.640	34
Long Lake [Becker]	120.84	-0.007	0.974	24
McDonald Lake	486.45	-0.191	0.125	38
McDonald Lake (Dead River)	580.99	-0.238	0.082	35
McDonald Lake (Otter Tail River)	912.34	-0.405	0.007	27
Rice Lake (and synthetic)	372.96	-0.137	0.225	43
Rice Lake (1970-2005)	563.48	-0.233	0.042	36
Lake Vermilion	130.30	-0.0064	0.846	89
Lake Vermilion (1970-2007)	467.03	-0.176	0.106	38
Lake Vermilion (Pike River)	468.72	-0.177	0.243	32

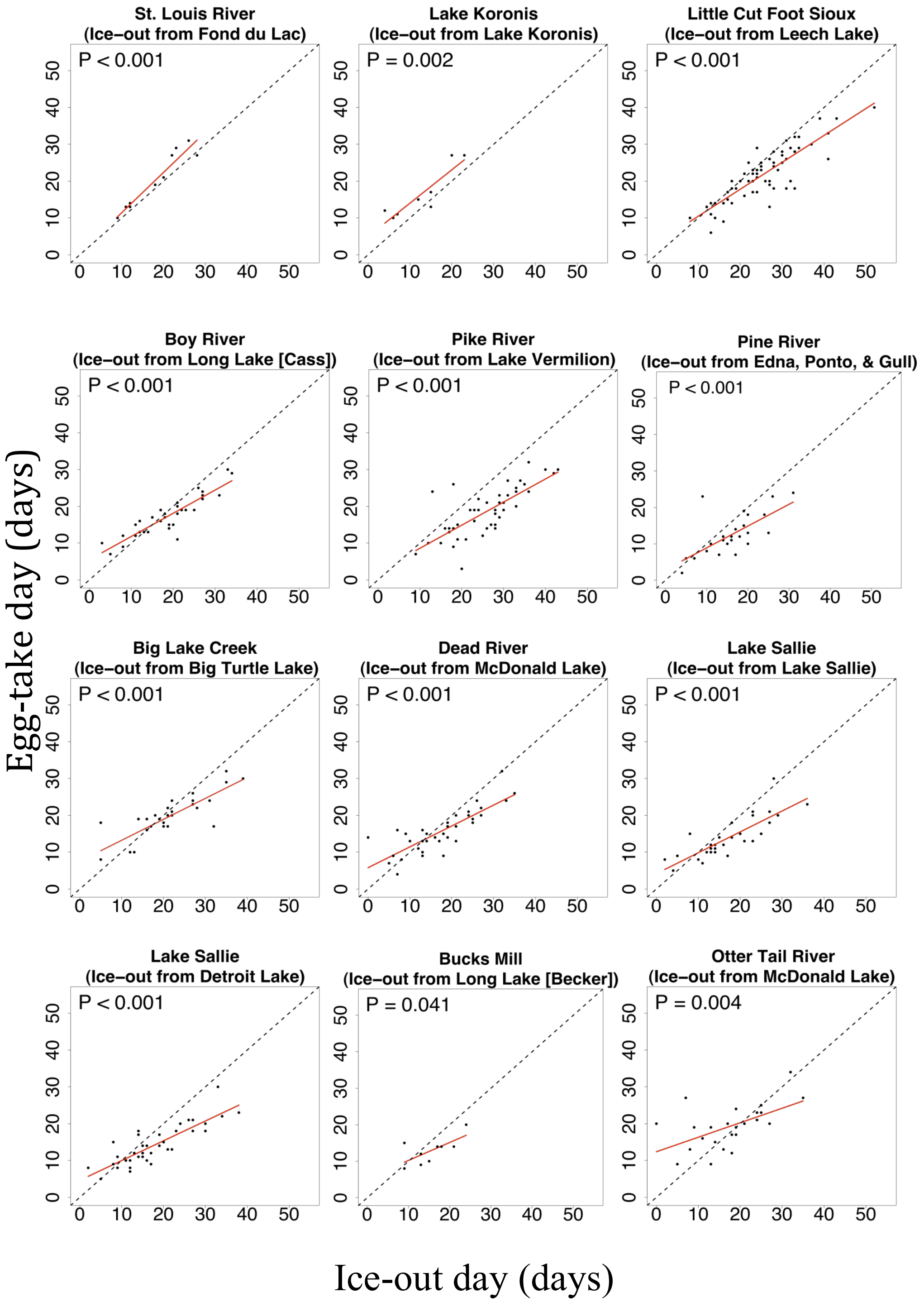

Figure 1. Regressions of first day of egg-take versus ice-out day in order of decreasing slope. All slopes were significant at the 0.05 level. The solid line is the linear regression. The dashed line is y=x. Each point represents one year, and the origin is April 1st.

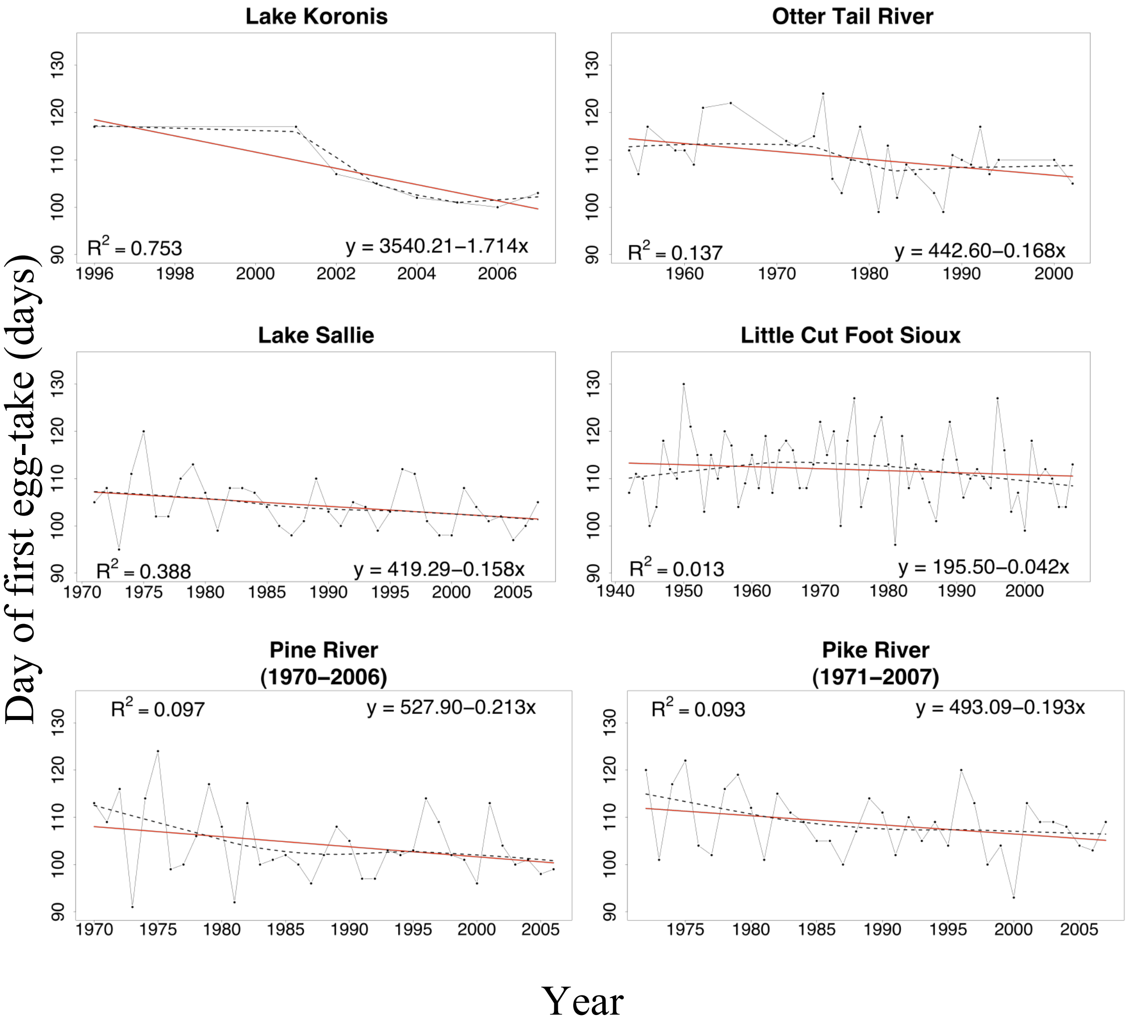

Figure 2: Example relationships of walleye first egg-take versus year. First egg take is recorded as the number of days from 1 January. The solid line is the linear regression, and the dashed line is the LOWESS fit. The linear regression was a better fit than the LOWESS smooth at all locations shown except Lake Koronis. All slopes shown except Little Cut Foot Sioux Lake were significant at the 0.1 level. Little Cut Foot Sioux Lake is shown as an example of a long-term time series that didn't have a significant slope.

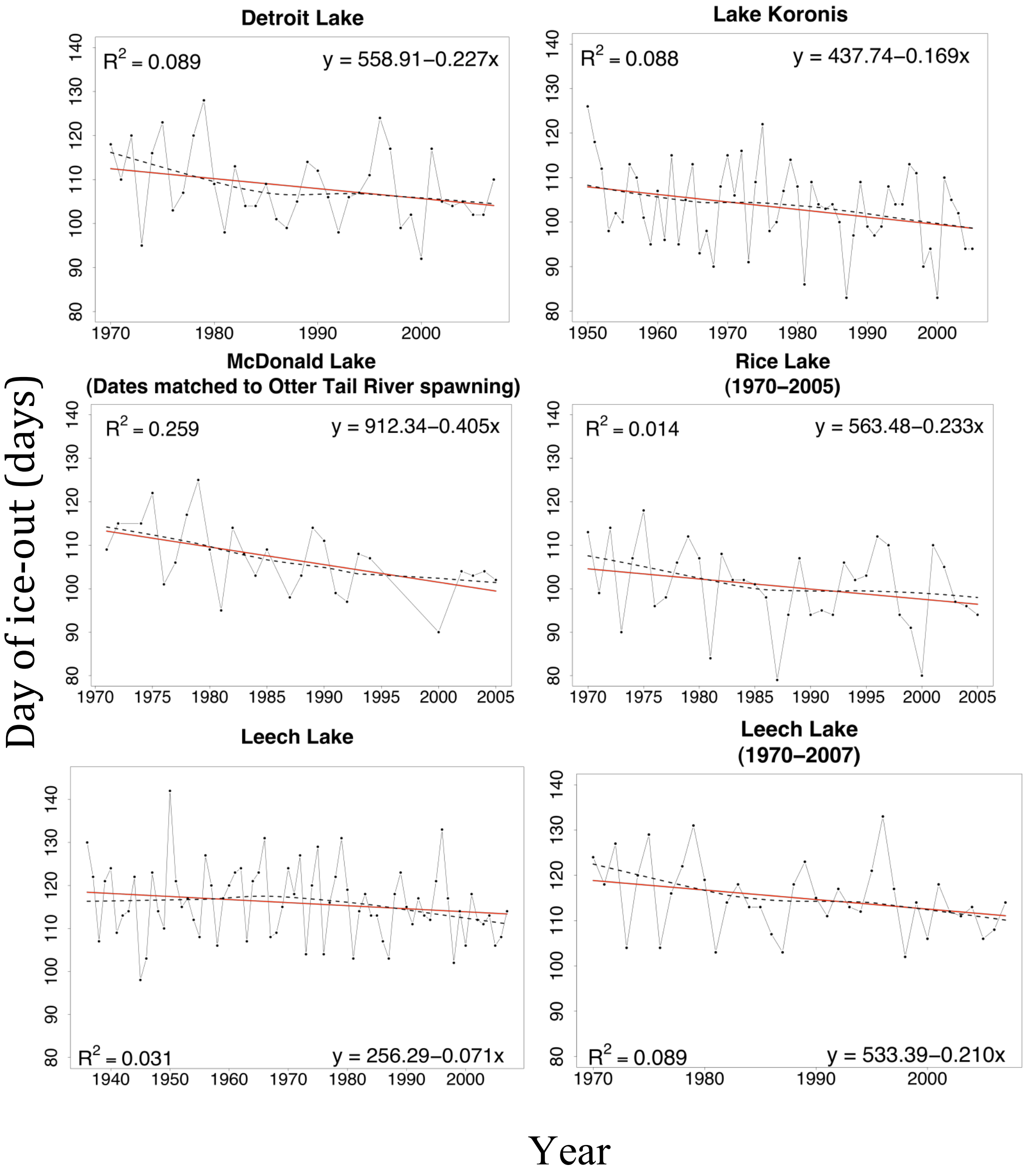

Figure 3. Example regressions of ice-out date over time. Ice-out is recorded as the number of days from 1 January. The solid line is the linear regression, and the dashed line is the LOWESS fit. All slopes shown except Leech Lake (full dataset) were significant at the 0.1 level. The Leech Lake time series is shown as an example of a long-term dataset that didn't have a significant slope. The LOWESS smooth did not improve the fit of the data compared to linear regression for all time series shown.

CHAPTER 3

Changes in Minnesota fish species abundance and distribution associated with local climate and lake characteristics

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CHAPTER SUMMARY

We analyzed historical Minnesota fisheries lake survey data (gillnet and trapnet) for 34 lakes, each with 15 to 43 years of data, to determine if fish distributions and abundances were changing over time. We then analyzed trends to determine effects of local climate on fish abundance and to determine if lake characteristics influenced trends in catch-per-unit-effort (CPUE) over time. Seven fish species from three families showed the strongest trends: centrarchids (*Micropterus salmoides*, *Micropterus dolomieu*, and *Lepomis macrochirus*); ictalurids (*Ameiurus melas* and *Ameiurus natalis*); whitefish (*Coregonus artedi* and *Coregonus clupaeformis*). We used simple linear regression to analyze CPUE over time, and we regressed mean latitudes of species occurrence against year to determine if ranges were advancing northward or contracting. Linear regressions were used to analyze the relationship between fish species' CPUE by lake and the following 5 temperature variables: maximum 7-day max temperature, average annual temperature, average summer temperature, average winter temperature, and degree-days above 5°C. We used stepwise regressions to determine if variability in slopes of CPUE vs. year could be explained by lake surface area, maximum depth, latitude, or longitude, and ANOVA to determine if variability in slopes could be explained by Schupp's lake classes. Linear regressions of CPUE vs. year indicated that centrarchid abundance was increasing, black bullhead (*Ameiurus melas*) abundance was decreasing, and other species were increasing in some lakes and decreasing in others. The ranges of all species were significantly advancing northward except smallmouth bass and whitefish. Regressions of CPUE versus air temperature showed that bass and sunfish were increasing in lakes as summer air temperatures increased, and whitefish were decreasing in lakes as air temperatures increased. Location, lake surface area, and lake class may explain some variability in slopes of CPUE versus year. In summary, temporal trends in the abundance and distribution of some centrarchids, ictalurids, and whitefish may be responding to climate change, and trends may be affected by lake characteristics.

INTRODUCTION

Climate change is expected to affect aquatic ecosystems around the world. Studies of the potential effects of climate change on fish have predicted a northward shift in species distributions (Magnuson et al. 1990; Meisner 1990; Stefan et al. 2001; Chu et al. 2005), and some studies have already documented occurrences of climate-related distribution shifts in fishes (Jackson and Mandrak 2002; Perry et al. 2005; Sundby and Nakken 2008). In a study of reef fish assemblages in the Southern California Bight, Holbrook et al. (1997) observed an increased abundance of southern species and a decreased abundance of northern species with the onset of ocean warming. In France, Daufresne and Boët (2007) similarly observed a significant increase in southern fish species and an increase in the proportion of warm-water species in large rivers that was related to water warming.

Most of the studies cited above observed a relationship between changes in water temperature and changes in fish communities (e.g., increased temperatures led to increased fishes from warmer areas). In Minnesota, lake and stream temperatures are increasing (Johnson and Stefan 2006; Austin and Colman 2007), and ice-out is occurring earlier (Magnuson et al. 2000; Jensen et al. 2007; Schneider et al. In press). Because of these changing conditions and the relationships previously observed between fish communities and water temperatures, climate change may have profound effects on fish communities in Minnesota. However, fish species composition and abundance is often influenced by other chemical and physical characteristics of the lake environment they inhabit (Tonn and Magnuson 1982; Robinson and Tonn 1989; Rodriguez and Lewis Jr. 1997). For example, Marshall and Ryan (1987) showed that mean depth influenced salmonid and percid abundance in Northwest Ontario, and Jackson and Harvey (1989) showed significant correlations between species richness and lake area in the Laurentian Great Lakes basin of Ontario. Thus, fish responses to climate change may be influenced by lake physical and chemical characteristics.

In this study we address 3 questions. (1) Are fish species distributions and relative abundances changing in Minnesota (e.g., are southern species increasing in northern lakes?), and (2) are changes in distributions and abundances related to climatic variables? Also, because lake physical and chemical characteristics are important factors that influence species composition (e.g., Jackson and Harvey 1989; Rodriguez and Lewis Jr. 1997), (3) could location of the lake and other lake physical and chemical properties affect observed trends in abundance and distribution?

METHODS

We obtained fisheries lake survey data from the Minnesota Department of Natural Resources (MN DNR) for 4,145 lakes with data ranging from 1940 to 2007. We initially chose to analyze 20 lakes sampled annually with 18 or more years of gillnet data (Table 1) and 20 lakes with 15 or more years of trapnet data (Table 2). There were 34 individual lakes within this subset because some lakes had both gillnet and trapnet data. Gillnet data ranged from 1941-2007, and trapnet data ranged from 1948-2007. The fisheries surveys used standardized sampling methods (MN DNR 1993) to collect information about fish communities (i.e., species present, number of individuals captured, etc.,) and lake physical and chemical properties. Nets were set overnight during the summer and emptied the next day. Gillnets were 76.20-m long and 1.83-m deep and constructed of #104 twisted nylon fibers. Each net had five 15.2-m panels of varying size bar mesh (1.9, 2.54, 3.18, 3.81, and 5.08 cm), and effort was based on the size of each lake (e.g. 9 nets were used for lakes with areas from 1.2 to 2.4 km^2 and 15 nets were used for lakes larger than 6 km^2). Trapnets were constructed of 1.9-cm nylon mesh and were 12.19-m long and about 1.07-m deep with two 1.83 m X 0.91 m frames and six 76.2-cm hoops. Throat openings were about 12.7-cm diameter (MN DNR 1993).

We analyzed catch-per-unit-effort (CPUE) to determine if species were changing in abundance within lakes, expanding their ranges into new lakes, or disappearing from other lakes. To determine if there were significant trends in species abundances, we computed linear regressions of CPUE versus year by gear, lake, and species. We also examined the percentage and distribution of lake surveys each species appeared in over time by partitioning data so that the total number of surveys was evenly distributed between 5 time periods: 1940 to 1970, 1971 to 1980, 1981 to 1990, 1991 to 2000, and 2001 to 2008. To graphically examine changes in fish communities, we plotted species occurrence over time by lake for gillnets and for trapnets. To determine if species distributions were significantly advancing northward or southward, we averaged latitudes from the lakes each species occurred in each year and regressed the mean latitude against year.

To determine if changes in abundance (and indirectly, changes in distribution) were affected by climatic variables, we chose 5 air temperature variables to analyze. Air temperature was used instead of water temperature because of its broad distribution and availability of long-term records. We obtained air temperature data from National Weather Service Cooperative daily measurements (Zandlo 2008) from weather stations within 45 km of our lakes. We used the following temperature variables in regressions by species to determine if there was a relationship between CPUE and air temperatures across lakes: maximum 7-day maximum (max) temperature each year, average annual temperature, average summer temperature (June-August), average winter temperature (November-March), and degree days above 5°C.

Some of the variability in trends of abundance over time (and in relationships between CPUE and temperature) may be explained by lake characteristics. To investigate this, for each species we computed stepwise regressions that examined the relationship between the slope of CPUE over time and the following independent variables: maximum lake depth, lake location (latitude and longitude), and lake surface area. The full model was:

$$\text{Slope} = \beta_0 + \beta_1\text{MaxD}+\beta_2\text{X\_UTM} + \beta_3\text{Y\_UTM} + \beta_4\log(\text{Area})$$

Slope was the slope from regressions of CPUE versus year for each lake. β_0 was the intercept, and MaxD was the maximum depth of each lake. X_UTM and Y_UTM were the Universal Transverse Mercator (UTM) coordinates for the location of each lake, and log(Area) was the natural log of lake surface area. We used both forward selection and backward elimination and chose models by selecting regressions with the smallest AIC (Akaike Information Criterion). We also used one-way ANOVAs to determine if slopes of CPUE over time for each species varied with Schupp's (1992) lake classes. Schupp's lake classes are based on 8 physical and chemical variables: area, maximum depth, littoral area (percentage), total alkalinity, Secchi depth, the Morphoedaphic Index (MEI), Carlson's Trophic Status Index (TSI), and shoreline development factor. Because our dataset was relatively small and there are 44 lake classes, we used both Schupp's lake classes and a variation of Schupp's classes that grouped the 44 classes into 9 groups (referred to as Schupp's groups) that were the result of a K-means cluster analysis (Schupp unpublished).

RESULTS

Abundance and distribution

Significant relationships ($P < 0.10$) from regressions of CPUE versus year by species were observed in 28 lakes (N = 34). Centrarchids showing trends most frequently were largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), and bluegill (*Lepomis macrochirus*). Largemouth bass distribution and abundance in Minnesota lakes has been increasing over time. Before 1980, largemouth bass appeared in less than 31% of Minnesota lakes surveyed by the MN DNR (Table 3). By the next time period (1981 to 1990), the percentage of lakes with largemouth bass records doubled to 62% and largemouth persisted in > 50% of lakes through 2008 (Appendix B). For regressions of largemouth bass gillnet and trapnet CPUE versus year, there were 20 positive slopes and 10 negative slopes; there were 3 significant positive slopes ($P < 0.1$) and 2 significant negative slopes. In addition to increased abundance within and among lakes, the regression of largemouth bass mean latitude versus year (Figure 1) showed that largemouth were expanding their distribution northward in Minnesota (Appendix A1) by about 2.3 km each year ($P < 0.001$).

Regressions of smallmouth bass CPUE versus year also showed increasing abundance over time. There were 14 positive slopes and 2 negative slopes; eight positive slopes were significant ($P < 0.1$). Although smallmouth seemed to be increasing in individual lakes, the percentage of surveyed lakes with smallmouth bass remained between 26-38% over time (Table 3). There were no obvious changes in smallmouth bass ranges in Minnesota (Appendix A2), and the regression of mean latitude versus year (Figure 1) was positive but not significant ($P = 0.82$).

Bluegill abundance also significantly increased over time in Minnesota. Regressions of bluegill CPUE versus year, showed 31 positive slopes and 4 negative slopes; sixteen positive slopes were significant and 2 negative slopes were significant ($P < 0.1$). Bluegill were in 58% of surveyed lakes throughout the first 30 years of sampling, but they are now found in 85% of surveyed lakes (Table 3). In addition to increased abundance, bluegill also seemed to be advancing northward (Appendix A3). There was a significant positive relationship ($P < 0.001$) between mean latitude and year that indicated bluegill distributions were expanding northward by about 2.4 km each year (Figure 1).

There were also changes in bullhead abundance and distributions (Appendix A4 and B5). For regressions of black bullhead CPUE versus year, there were 8 positive slopes and 27 negative slopes; there was 1 significant positive slope and 11 significant negative slopes ($P < 0.1$). Although regressions of CPUE versus year indicated mostly decreasing abundances, the number of lakes with recorded black bullhead occurrences was increasing prior to 2001. Black bullhead were in 58% of surveyed lakes (Table 3) during the first period of sampling (1940-1970). Their occurrence increased over the next 20 years; they occurred in 85% of lakes from 1991 to 2000 before decreasing to 65% in the last time period (2001 to 2008). The regression of mean latitude versus year had a significant positive slope ($P < 0.001$) that indicated black bullhead distributions were expanding northward by about 2.6 km per year (Figure 1).

Yellow bullhead showed similar trends for distribution but not abundance. Regressions of CPUE versus year suggested that yellow bullhead were increasing in about half of the sampled lakes and decreasing in the other half; there were 14 positive slopes (6 significant) and 12 negative slopes (3 significant) ($P < 0.1$). Yellow bullhead occurred in only 32% of surveyed lakes (Table 3) during the first period of sampling. Occurrences of yellow bullhead increased to 62% of surveyed lakes from 1991 to 2001 and remained at 56% of lakes from 2001-2008. Regressions of mean latitude versus year suggested that yellow bullhead distributions were expanding northward by about 1.6 km per year (Figure 1).

Black bullhead and yellow bullhead have different temperature and habitat preferences so that one is known to replace the other under certain conditions (Scott and Crossman 1973; Becker 1983; Hubbs and Lagler 2004). Yellow bullhead have a higher thermal maximum (Reynolds and Casterlin 1978; Carveth et al. 2006) than black bullhead (Black 1953; Cvancara et al. 1977; Kayes 1977), and because of this, the replacement of one species by the other may be a response to climate change. To determine if one species was replacing the other, we regressed the ratio of yellow to black bullhead against year. Our results indicated that ratio of yellow to black bullhead increased over time. There were 21 positive slopes and 5 negative slopes; 10 positive slopes were significant and there were no significant negative slopes.

Tullibee showed less evidence of changes. For regressions of CPUE versus year, there were 7 positive slopes and 7 negative slopes; there was 1 significant positive slope and 2 significant negative slopes ($P < 0.1$). Tullibee occurred in 26% of surveyed lakes (Table 3) during the first time period (1940 to 1970) and in 30 to 35% of lakes from 1971 to 2008. There was no evidence of tullibee range expansion or contraction across Minnesota latitudes (*P* = 0.856) (Figure 1, Appendix A6).

Lake whitefish were increasing in some locations and decreasing in others. For regressions of CPUE versus year, there were 6 positive slopes and 5 negative slopes; there were 4 significant positive slopes and 3 significant negative slopes ($P < 0.1$). Lake whitefish occurred in an increasing percentage of surveyed lakes over time (from 10 to 27%; Table 3), but there was no evidence of range expansion or contraction across Minnesota latitudes (*P* = 0.116) (Figure 1, Appendix A7).

Relationships with temperature

To assess relationships between CPUE and air temperature variables, regressions of CPUE versus each temperature variable were computed by species for each lake and gear type. For regressions of largemouth bass CPUE versus temperature for each lake, most significant ($P<0.1$) positive relationships were observed using maximum 7-day max temperature, average summer temperature, and degree-days above 5°C (Table 4). Most significant negative relationships were from using average annual and average winter temperatures. For regressions of smallmouth bass CPUE versus temperature, most significant positive slopes were observed using each temperature variable except average winter temperature (Table 4), which had 1 positive and 1 negative relationship. For bluegill, significant positive slopes occurred more often than significant negative slopes in all regressions of CPUE versus each temperature variable. Overall, centrarchid CPUE responded positively to warming temperatures.

For regressions of black bullhead CPUE versus temperature, most significant positive slopes were observed in regressions of CPUE versus maximum 7-day max, and most negative slopes were observed in regressions with average annual temperature (Table 4). Black bullhead regressions with other temperature variables resulted in equal numbers of significant positive and negative relationships (e.g. 1 positive slope from one lake and 1 negative slope from another lake). For regressions of yellow bullhead CPUE versus temperature, more significant negative slopes than positive slopes were observed with average summer temperature and degree-days above 5°C (Table 4). More significant positive slopes than negative slopes were observed with average winter temperature. Regressions with all other temperature variables resulted in equal numbers of significant positive and negative slopes.

Regressions of tullibee CPUE versus temperature showed few significant positive relationships with air temperature variables, and no significant relationships were observed with average winter temperature. For all variables except average annual temperature, the significant slopes were negative (Table 4). For regressions of lake whitefish CPUE versus temperature, most significant positive slopes were observed with average annual and average summer temperature, and most significant negative slopes were observed in regressions with maximum 7-day max and average winter temperature (Table 4). Overall, whitefish CPUE responded negatively to warming temperatures.

Relationships with lake characteristics

To determine if lake characteristics were influencing the trends in abundance, slopes from the regressions of CPUE versus year were regressed against lake characteristics. In general, location and lake surface area seemed to influence slopes of centrarchid CPUE versus year, however, for largemouth bass, no lake characteristics explained variability in trends. For smallmouth bass, regressions suggested that lake surface area, latitude, and longitude explained some variability in slopes (Table 5). All three were associated with more negative slopes of smallmouth bass CPUE over time. ANOVAs were significant for both Schupp's lake classes and Schupp's groups. Greater significance (lower p-value) was observed in ANOVAs using Schupp's lake class. For bluegill, stepwise regressions suggested that lake surface area might explain some variability in slopes of CPUE versus year (Table 5); the relationship between surface area and slopes of bluegill CPUE over time was negative. ANOVAs suggested that lake groups (not Schupp's 44 individual classes) might explain some variability in slopes of bluegill CPUE over time.

For black bullhead, lake surface area and latitude explained some variability in the slopes from regressions of CPUE versus year (Table 5). Slopes were more positive as latitude increased and more negative as lake surface area increased. ANOVA's suggested that slopes also varied by Schupp's lake classes and lake groups; greater significance was observed using Schupp's groups. No variability in yellow bullhead slopes could be explained by the lake characteristics we chose for this study or by lake classes.

DISCUSSION

Fish thermal niches are typically established for physiological, ecological, and reproductive optimal performance (Coutant 1987), and because their distributions vary by temperature (Brandt et al. 1980; Holbrook et al. 1997; Daufresne and Boët 2007), changes in species ranges may be indicative of climate change. Studies have also shown that abundance or CPUE may change in response to climate change (Meisner et al. 1987; Willis and Magnuson 2006). In our study, centrarchids were increasing in abundance (Appendix B) and expanding their ranges northward in Minnesota over time, and these changes were associated with air temperatures. Other studies have documented relationships between centrarchid thermal structure and air temperatures (Schlesinger and Regier 1982, Sharma et al. 2007), and except for smallmouth bass, our results were consistent with other studies that predict warm-water and southern species will expand their ranges northward as temperatures increase (Jackson and Mandrak 2002; Chu et al 2005). Several Canadian studies have shown that smallmouth bass are expanding their ranges northward in Canada (Shuter et al. 2002, Vander Zanden et al. 2004). The lack of a significant change in Minnesota smallmouth bass distributions may be a result of their already widespread occurrence in Minnesota lakes by the 1940s (Appendix A2) and the absence of records prior to that time period. Changes in largemouth bass and bluegill populations were associated with increases in summer air temperatures and are likely due to warmer temperatures creating additional suitable habitat available to promote increases in abundance and northern range expansions (Regier and Meisner 1990; Chu et al. 2005; Sharma et al. 2007).

Analysis of ictalurid abundance and distribution showed varying results. Black bullhead were generally decreasing in lakes, and yellow bullhead were increasing in some lakes but decreasing in others. Both species' distributions were advancing northward. Changes in temperature may also be influencing changes in bullhead abundances by altering the amount of available suitable habitat as mentioned previously. Their temperature preferences and sensitivities to different temperature variables may explain the varying trends in CPUE over time. Yellow bullhead have a higher thermal maximum than black bullhead (Reynolds and Casterlin 1978; Carveth et al. 2006) and thus may tolerate warmer temperatures and for longer periods of time than black bullhead. This is a reasonable assumption for a period of warming considering that black bullhead were expanding their ranges northward more quickly than yellow bullhead (2.6 km/yr versus 1.6 km/yr respectively), and although yellow bullhead seemed to have variable changes in abundance, the majority of black bullhead abundances were decreasing.

There was no evidence of range contraction or expansion by cold-water species (whitefish), and their abundances were increasing in some lakes and decreasing in others. However, this does not necessarily indicate a lack of response to climate change. Whitefish (tullibee and lake whitefish) relationships with air temperatures were mostly negative, but lake whitefish abundances responded positively to average annual and average summer temperatures. Meisner et al. (1987) reported increases in whitefish abundance related to increased temperatures, and Fang et al. (2004) projected an increase in the good-growth period for cold-water species by up to 42 days in some of Minnesota's deep stratified lakes and a decrease in the good-growth period in medium-depth lakes. On the other hand, although we found no evidence of trends in 12 tullibee lakes, Jacobson *et al*. (unpublished) reported decreases in mean abundances of tullibee (cisco) statewide in Minnesota that coincided with increases in temperatures. Other than reduced good-growth periods, decreases in abundance may be due to local mortality events caused by reductions in suitable thermal habitat for cold-water fish, which could be further amplified by lethal combinations of oxygen and temperature (Regier and

Meisner 1990; Jacobson et al. 2008). Continued assessment of the response of tullibee and whitefish to climate change is warranted.

Lake characteristics

Some of the variation in abundance and distribution trends may be explained by lake characteristics. Jackson (2002) showed that lake surface area was significantly associated with total species richness in south-central Ontario. Whittier and Kincaid (1999) showed that lake area and depth were significantly related to species richness in northeastern USA, and that correlations between lake characteristics and species richness were highest for lake area. For our study, some lake characteristics explained variation in abundance and distribution trends. For smallmouth bass, abundance generally increased more in smaller lakes and moving southeast across the state. For bluegill, larger increases in abundance typically occurred in smaller lakes. Consistent with other studies (e.g. Marshall and Ryan 1987; Robinson and Tonn 1989; Rodriguez and Lewis Jr. 1997), it's not surprising that these lake characteristics influenced CPUE over time, but why was CPUE increasing more rapidly given these conditions? Perhaps fish abundances aren't decreasing in larger lakes, but instead are only increasing in smaller lakes in our sample. For bass and sunfish, smaller, southern lakes may provide more good-growth habitat than larger, northern lakes (Bennett 1978, Schindler et al. 1996; King et al. 1999). Also in regard to location, CPUE was increasing in lakes further east that were typically clearer than other lakes. Clearer lakes tend to have deeper epilimnia than lakes with shallower secchi depths (Mazumder and Taylor 1994; Fee et al. 1996), thus providing more good-growth habitat for warm-water species when temperatures are warming.

For black bullhead, CPUE over time increased more in smaller lakes, and their range is expanding northward across Minnesota. Because black bullhead prefer warm temperatures (Cvancara et al. 1977; Kayes 1977), smaller lakes would probably provide more optimum habitat as temperatures increase over time than large lakes (see explanation above). However, the negative relationship with surface area may be an artifact of black bullhead abundances decreasing in most lakes and our sample size consisting of predominantly larger lakes (mean = 34,070 acres, min. = 18 acres, max = 305,907 acres). The lake characteristics we chose for our study did not explain any variation in yellow bullhead abundance over time. It's possible that some other factor (e.g. sampling effort, land use, interactions with black bullhead, etc…) may be influencing changes in yellow bullhead populations, or that lake class may be important, but our dataset lacked influential classes. On the other hand, it could mean that yellow bullhead are simply less sensitive to environmental changes than black bullhead, and the increasing ratio of yellow to black bullhead over time may be occurring because yellow bullhead populations may be less restricted as they advance northward.

For tullibee (cisco), no lake characteristics explained variation in abundance over time, which was decreasing in some lakes and increasing in other lakes. We may not have had enough data to get a strong response, or perhaps the limited distribution of tullibee lakes in our samples restricted the variation in lake characteristics. Our records from tullibee lakes only covered 3 lake classes, and no tullibee have shown up in new lakes (lakes without tullibee previously) since the 1980s (Appendix B6). Perhaps tullibee ranges began constricting to the northern-most part of their range in years not well represented by our records. Effects of climate change on species have been documented around the world since the earliest part of the twentieth century (Parmesan 2006), and Jacobson et al. (2008) have documented tullibee lake mortality events in north-central Minnesota. They reported that 16 north-central Minnesota lakes experienced tullibee midsummer mortality events in 2006, and in all of these mortality event lakes, tullibee had only two choices of habitat: cool hypoxia or normoxia at lethally warm temperatures. In our lakes, it's possible that temperature changes were great enough to allow centrarchids to increase their production but not enough yet to cause tullibee extirpations.

For lake whitefish, no variability in slopes of CPUE versus year could be explained by lake characteristics or lake class. For this species, the strongest response to climate change may be in the colder regions of Northeast Minnesota. In these regions, warming temperatures may not increase water temperatures enough to cause summer kill, but instead could alter important processes such as the timing of ice-out and spawning so that temperatures are closer to optimum and the good-growth season is extended (Fang et al. 1999; Stefan et al. 2001, Fang et al. 2004, Schneider et al. in press). In our dataset, lake whitefish were documented in only five lakes from this region, and only three had records prior to 1980 (Appendix A7). The small sample size (only 10 lake whitefish lakes) and relatively short timespan of the data probably limited the power to detect significant relationships.

Additional considerations: sampling effort, stocking, and land use

It is important to note a few possible sources of variation in abundance and distribution data. One potential source of variation in trends we observed could be from the timespan of the data and the sample size (Wiley et al. 1997). In our dataset, sampling effort varied by lake, and the number of lakes surveyed per year varied over time. This could cause variation in CPUE estimates and a lack of significant trends or false detection of trends. To investigate changes in the number of lakes surveyed per year, we regressed the mean latitude of lakes surveyed (both gillnet and trapnet) against year (Appendix C). The slope was significant (1.51km/year; $P < 0.05$) and suggests that some of the change in species' distributions may be due to changes in the number (and location) of lakes surveyed over time. However, in regressions of each species mean latitude versus year, all slopes were greater than 1.51 (significant slopes ranged from 1.60 to 2.59) and were more significant ($P < 0.001$) than the regression of mean latitude of surveyed lakes versus year.

Sampling effort within individual lakes may also influence trends. In 1993 there was a change in sampling effort that increased the number of nets used in many Minnesota lakes (MN DNR 1993), and an increase in effort could potentially bias records of fish abundance over time. To investigate changes in effort within lakes we examined box plots and computed t-tests for two subsamples of each dataset by lake and species: CPUE from 1983 to 1992 and CPUE from 1993 to 2002. We found no evidence to suggest that observed trends were a function of changing effort within lakes.

Stocking may also play an important role in structuring fish communities. Radomski and Goeman (1995) compared species presence and absence data in Minnesota and showed that species richness within stocked lakes was positively correlated with the number of years stocked ($P < 0.05$). However, they also observed a decrease in community diversity (across-lake diversity) that corresponded with extensive fish stocking. For our lakes, we know that Rebecca (Dakota County), Big Stone, Cass, Leech, Vermilion, and Winnibigoshish have been stocked in the past 10 years with walleye, lake whitefish, or smallmouth bass. During the last 10 years, some of the 7 species used for this study decreased in these lakes and some increased. There doesn't appear to be a direct effect on the species stocked because lake whitefish significantly increased in Cass Lake but decreased in Leech Lake, and there was no significant change in smallmouth bass abundance in any of those five lakes. However, without analyzing the entire fish community in each lake (we chose to run analyses on only 7 of about 70 species occurring in lake survey records) it's unclear if stocked species significantly influenced the changes observed in our study. Further analyses on stocking and diversity in Minnesota lakes would useful to determine if there have been changes in within-lake and across-lake diversity that have influenced populations in this study.

Land use is another factor that may affect fish communities. Evans et al. (1996) linked lake trout, lake whitefish, and lake herring declines in Lake Simcoe, Canada to phosphorous loading in lakes caused by changes in land use. Similarly, Harding et al. (1998) showed that past land use was an important factor in determining present species diversity in streams. Wagner et al. (2006) showed that lakeshore development affected the probability of black bass nest success; nest success decreased with increasing lakeshore development. Numerous other studies have identified ways that land use has altered aquatic habitats that in turn affected resident fish communities (Rodomski and Goeman 1995; Whittier and Kincaid 1999; Wang et al. 2001; Jennings et al. 2003).

Additional research is needed to determine other factors that may be responsible for the relationships observed in our analysis. From this study and examples from others, we showed that there is growing evidence of species range expansions in temperate lakes and changes in abundance that are associated with local climate and lake characteristics. Most notable may be the expansion of ranges and increase in abundances of centrarchids. Numerous studies have predicted or documented substantial population declines of cyprinid and other small-bodied fish, which are important prey species, after bass or bluegill introductions (Marchetti 1999; Findlay et al. 2000; Jackson 2002; Jackson and Mandrak 2002; Vander Zanden et al. 2004; Sharma et al. 2007). From a management perspective, these changes could shift sport fisheries in Minnesota, and thus, shift fisheries management from historical sport fish, such as walleye, to sport fish more recently appearing in lakes, such as bass. In some areas, management has already shifted to include centrarchids, which have been stocked in more than 500 Minnesota lakes since the late 1980s (MN DNR Section of Fisheries, public stocking records, October 8, 2009). Angler perspectives about desirable species may also change if invasive species such as bass become the more common and popular sport fish.

Fisheries management agencies in Minnesota may face many challenges in the future if warming trends continue. Therefore, it’s important that management agencies consider the effects of climate change and other variables that are driving or influencing these changes. Information from this and other studies about how temperature and lake characteristics influence fish species abundance and distributions will benefit state and local agencies as they develop future management plans for Minnesota’s aquatic resources. The ability to define these relationships will become even more important if we continue to observe trends of warming temperatures.

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Table 1. Lakes with 18 or more years of standard gillnet data. Lake name, county, gear type, sampling range in years, and the number of years sampled (N) are shown. Asterisks indicate lakes with both gillnet and trapnet data.

Lake name	County	Sampling range (years)	N (years)
Pepin	Goodhue	1965-2007	43
Vermilion*	St. Louis	1941-2007	34
Mille Lacs	Mille Lacs	1972-2007	33
Namakan	St. Louis	1962-2007	33
Lake of the Woods	Lake of the Woods	1968-2007	30
Sand Point	St. Louis	1970-2007	29
Kabetogama	St. Louis	1980-2007	26
Rainy	St. Louis	1980-2007	26
Cass	Beltrami	1983-2007	25
Leech	Cass	1983-2007	25
Red	Beltrami	1984-2007	24
Winnibigoshish	Cass	1983-2007	24
Fox*	Martin	1981-2007	22
Green*	Kandiyohi	1956-2007	22
Lac Qui Parle	Lac Qui Parle	1956-2007	22
Traverse*	Traverse	1971-2007	21
Big Stone*	Big Stone	1971-2005	20
Cut Foot Sioux	Itasca	1975-2007	18
James	St. Louis	1973-2007	18
Pine*	Cook	1960-2004	18

Table 2. Lakes with 15 or more years of standard trapnet data. Lake name, county, gear type, sampling range in years, and the number of years sampled (N) are shown. Asterisks indicate lakes with both gillnet and trapnet data.

Lake name	County	Sampling range (years)	N (years)
Vermilion*	St. Louis	1953-2007	23
Fox*	Martin	1981-2007	22
Green*	Kandiyohi	1956-2007	22
Rebecca	Hennepin	1954-2005	19
Big Stone*	Big Stone	1971-2005	18
Round	Hennepin	1976-2006	18
Clear	Waseca	1982-2005	17
Lura	Blue Earth	1972-2004	17
Olson	Washington	1960-2005	17
Traverse*	Traverse	1971-2005	17
Winona	Winona	1953-2006	17
Ash	St. Louis	1957-2002	16
Pine*	Cook	1960-2004	16
Crooked	Anoka	1951-2004	15
DeMontreville	Washington	1961-2005	15
Elephant	St. Louis	1962-2006	15
Jane	Washington	1950-2007	15
Owasso	Ramsey	1948-2006	15
Rebecca	Dakota	1961-2006	15
Snelling	Hennepin	1960-2003	15

Table 3. Percentage of lakes that each species occurred in lake surveys for the given time period. N is the number of surveys (both gillnet and trapnet data) per year for the given time period.

Species	1940-1970	1971-1980	1981-1990	1991-2000	2001-2008
	N = 19	N = 26	N = 34	N = 34	N = 34
Centrarchidae					
Bluegill	57.9%	65.4%	70.6%	82.4%	85.3%
Largemouth Bass	31.6%	30.8%	61.8%	70.6%	58.8%
Smallmouth Bass	36.8%	26.9%	32.4%	35.3%	38.2%
Ictaluridae					
Black Bullhead	57.9%	57.7%	79.4%	85.3%	64.7%
Yellow Bullhead	31.6%	30.8%	52.9%	61.8%	55.9%
Salmonidae					
Tullibee	26.3%	30.8%	35.3%	35.3%	35.3%
Lake Whitefish	10.5%	11.5%	23.5%	26.5%	26.5%

Table 4. Counts (N) of significant slopes (*P*<0.1) from regressions of catch-per-unit-effort versus temperature variables for all lakes. Counts include both trapnet and gillnet regressions. The temperature variable used in each regression, species name, and number of significant positive and negative slopes are shown along with the total number of lakes each species occurred in (N lakes).

Temperature variable	Species	N positive slopes	N negative slopes	N. lakes
Maximum 7-day max				
	Largemouth Bass	6	2	24
	Smallmouth Bass	2	0	14
	Bluegill	4	1	29
	Black Bullhead	3	0	30
	Yellow Bullhead	1	1	22
	Tullibee (Cisco)	0	1	12
	Lake Whitefish	0	1	10
Average annual				
	Largemouth Bass	1	2	24
	Smallmouth Bass	5	0	14
	Bluegill	6	2	29
	Black Bullhead	2	5	30
	Yellow Bullhead	2	2	22
	Tullibee (Cisco)	1	2	12
	Lake Whitefish	2	1	10

Table 4 (continued).

Average summer				
	Largemouth Bass	6	2	24
	Smallmouth Bass	3	1	14
	Bluegill	3	2	29
	Black Bullhead	1	1	30
	Yellow Bullhead	0	1	22
	Tullibee (Cisco)	0	3	12
	Lake Whitefish	1	0	10
Average winter				
	Largemouth Bass	1	4	24
	Smallmouth Bass	1	1	14
	Bluegill	3	1	29
	Black Bullhead	2	2	30
	Yellow Bullhead	1	0	22
	Tullibee (Cisco)	0	0	12
	Lake Whitefish	0	1	10
Degree days above 5 C				
	Largemouth Bass	3	1	24
	Smallmouth Bass	4	0	14
	Bluegill	4	1	29
	Black Bullhead	3	3	30
	Yellow Bullhead	0	1	22
	Tullibee (Cisco)	0	1	12
	Lake Whitefish	1	1	10

Table 5. Best fit (lowest AIC) significant models established from stepwise regressions of the temporal abundance slope versus lake characteristics. Gear type is given if models differed between gillnet (GN) and trapnet (TN) data. The response variable “y” is the slope from regressions of CPUE versus year. XUTM and YUTM are longitude and latitude coordinates respectively in kilometers. MAXD is the maximum depth, and surface area is given as a log-transformed variable “Log(Area)”. R^2 and p-values (*P*) are shown for models.

Model	R^2	*P*
Smallmouth Bass		
y = 0.53 - 0.008Log(Area) - (2.00e-07)XUTM - (6.55e-08)YUTM	0.80	0.007
Bluegill		
y = 4.32 – 0.453Log(Area)	0.15	0.091
Black Bullhead GN		
y = -0.16 + (3.13e-06)YUTM	0.30	0.018
Black Bullhead TN		
y = -0.01 – 0.429log(Area) + (2.30e-05)YUTM	0.46	0.018

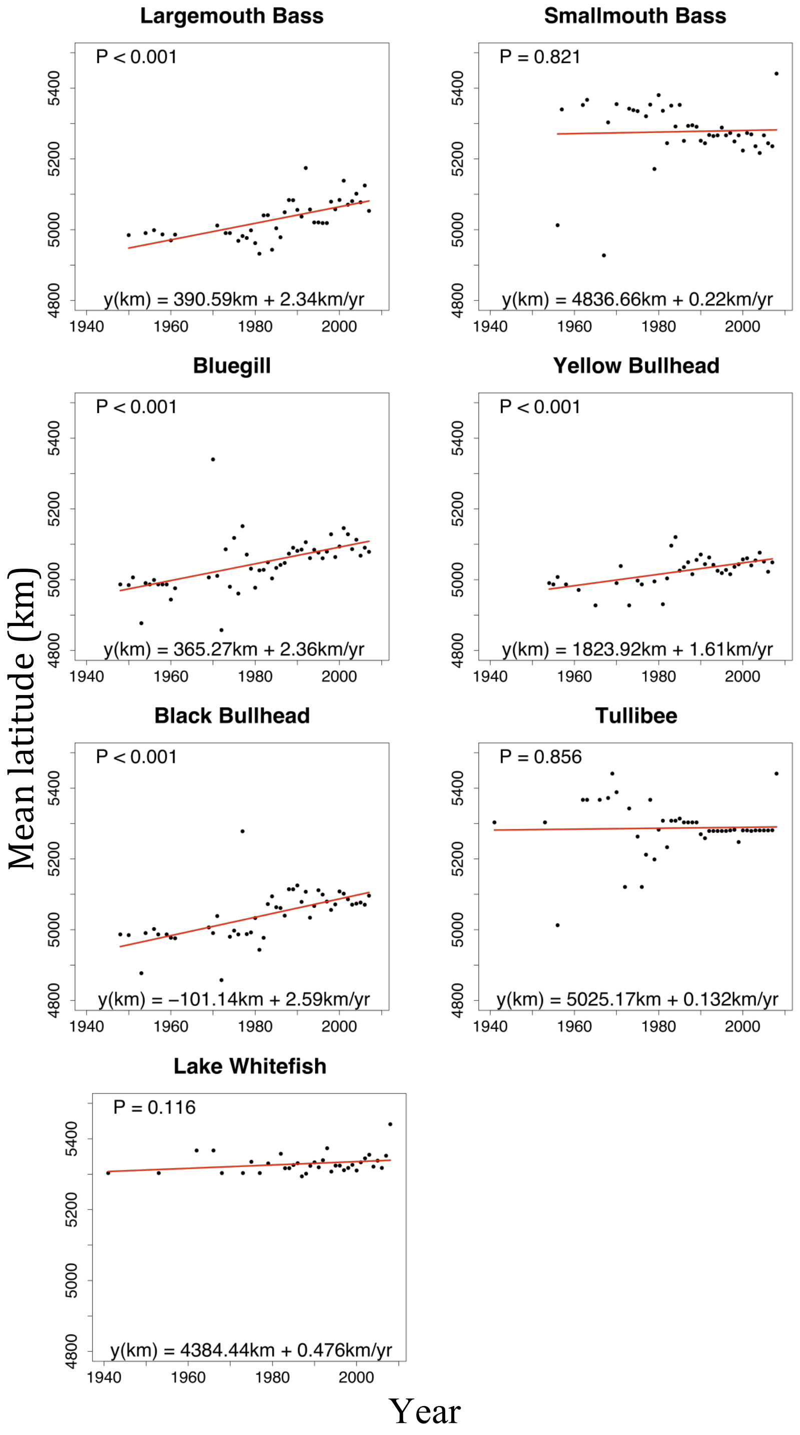

Figure 1. Regressions of mean latitude (km) versus year for 7 species. The red line is the regression line. *P*-values and slopes (km) are shown on plots.

CHAPTER 4

EPILOGUE

As climate change continues to be a topic of growing interest, and changes in species phenology and distributions are observed following predictions from climate change scenarios (Parmesan 2006), concerns arise about the effects of climate change on biological communities. Climate change can affect biological systems directly and indirectly by affecting processes such as migration (Bohlin et al. 1993; Reading 1998), reproduction (Blaustein et al. 2001), and recruitment (Shuter et al. 2002), and by shifting species distributions (Jackson and Mandrak 2002; Perry et al. 2005; Sundby and Nakken 2008). In Minnesota, evidence of climate change such as advanced ice-out dates (Magnuson et al. 2000; Jensen et al. 2007) and increased stream flows (Novotny and Stefan 2007) furthered curiosity about its effects on fish communities. In this thesis I determined if there is evidence of climate change in Minnesota's aquatic communities. I examined walleye spawning records collected by the Minnesota DNR to determine if there have been changes in the timing of spawning runs that are associated with climate change (Chapter 2). I also examined Minnesota ice-out data for changes in ice-out dates and to determine if there is a relationship between the timing of spawning and ice-out (Chapter 2) because there is extensive evidence that the timing of ice-out is sensitive to climate change (Magnuson et al. 1997; Magnuson et al. 2000; Jensen et al. 2007). In Chapter 3, I examined 7 fish species for evidence of changing abundances and shifting distributions associated with climate change. Mean latitude and CPUE were regressed against year to determine if species distributions and abundances were changing respectively, and lake physical and chemical characteristics were examined to determine if variability in trends could be explained by lake surface area, depth, location, or Schupp's (1992) lake classes.

In Chapter 2, I showed that first egg-take was significantly related to the timing of ice-out, and the start of spawning runs and ice-out has advanced at some locations but not all. There was a significant positive relationship between first egg-take and ice-out date at all locations, and even after a Bonferroni correction, 10 of 13 regressions were significant. Walleye spawning runs started 0.5 to 1 day earlier for every day ice-out occurred earlier. Regressions of peak egg-take showed similar results. Walleye spawning is typically reported to occur soon after ice-out (see Scott and Crossman 1973; Wolfert et al. 1975; Becker 1983), but our results indicate that in some cases walleye spawning may begin before ice-out. This may be a result of using first egg-take as an indicator of the start of spawning runs (i.e. individual versus populations response); first egg-take and the first capture of ripe walleye females occurred 20 days before to 27 days after ice-out (average of 3.3. days after ice-out). However, peak egg-take and peak capture of ripe females occurred 0 to 25 days after first egg-take and first capture of ripe females. Photoperiod and prior thermal history are both important determinants of the timing of spawning that likely affected these trends over time (Hokanson 1977; Malison et al. 1994; Malison and Held 1996), but there was still a strong relationship between first egg-take and ice-out dates at all but 3 locations.

Biological constraints that determine the duration of spawning could also affect relationships between the timing of walleye spawning runs and ice-out. With later ice-outs most fish may have mature gametes and be ready to spawn, but with earlier ice-outs we might expect to observe extended spawning runs. However, there was no indication that run duration was generally increasing in Minnesota. Hokanson (1977) suggested that environmental conditions have only a limited effect on the duration of stages of gonad maturity in adult percids, and therefore, instead of changes in spawning duration in response to temperature changes, there would be a shift in spawning temperatures and a change in the timing of spawning. Similarly, in a study of walleye from upper Midwestern lakes and rivers, Malison et al. (1994) suggested that it may be possible to induce earlier spawning in walleye via environmental manipulations because gonadal maturation was more or less completed several months before spawning (about mid-winter). Although, the timing of walleye spawning runs was affected by changes in temperature, spawning duration essentially remain unchanged.

Regressions of walleye spawning and ice-out dates over time showed mostly negative trends. Regressions of start of walleye spawning versus year indicated that walleye spawning is getting significantly earlier at some locations in Minnesota, but not all. If we applied a Bonferroni correction, only 1 (Lake Koronis) of 16 regressions would be significant. However, the probability of getting 14 negative slopes out of 16 regressions was very low (0.0018). For the timing of ice-out versus year, 25 of 26 regressions were negative, and although a Bonferroni correction would result in no significant regressions, the probability of getting 25 negative slopes out of 26 regressions was very low (<0.0001). The results for ice-out are consistent with previous studies that documented earlier ice-out over time (Schindler et al. 1990; Robertson et al. 1992; Magnuson et al. 2000; Johnson and Stefan 2006), and in general, results suggest that the timing of ice-out and walleye spawning runs were getting earlier. The lack of significance at each location could indicate either that there is, in fact, no relationship or that the power to detect a significant relationship is low for any particular location (discussed in more detail later). Moreover, statewide distribution of trends may be more relevant than local site trends when studying regional effects of climate change (see Urquhart et al. 1998).

Changes in the timing of walleye spawning runs are of interest because earlier (or later) spawning may have negative impacts on walleye populations. Earlier spawning could cause a temporal mismatch in the timing of peak zooplankton blooms and peak larval walleye abundance that would negatively affect growth and survival of walleye if prey populations do not respond to climate change by hatching earlier. Studies have documented negative impacts on species such as Atlantic cod (Gadus morhua) and Daphnia resulting from a temporal mismatch of this kind (Gotceitas et al. 1996, Winder and Schindler 2004). Additionally, because there is strong evidence that discharge events affect larval walleye survival (Becker 1983; Mion et al. 1998; Jones et al. 2006), walleye recruitment may suffer if there is a temporal mismatch in the timing of peak larval emergence and optimal discharge events.

Because ice-out date is sensitive to climate change (e.g. Magnuson et al. 1997; Magnuson et al. 2000) and because of the significant relationship between egg-take and ice-out dates, I suggested that the timing of walleye spawning would be a useful biological indicator of climate change. My work suggests that at least a strategic set of walleye egg-take sites should continue to be monitored. Aside from a biological indicator, it would also provide insight about effects of climate change on walleye populations that could have important implications for management and fisheries policies.

In Chapter 3, I examined Minnesota historical lake survey data for changes in abundances and distributions of 7 fish species that appeared to be indicators (largemouth bass, smallmouth bass, bluegill, yellow and black bullhead, tullibee (cisco), and lake whitefish). Centrarchid abundance was increasing in lakes, black bullhead abundance was decreasing, and other species were increasing in some lakes and decreasing in others. All species' ranges were significantly advancing northward except smallmouth bass and whitefish. Changes in species abundances and distributions were associated with local climate variables, and lake characteristics may have influenced these responses.

My results indicate that centrarchids and possibly bullhead may be good indicators of climate change. My recommendation for centrarchids as indicators is further supported by previous work that studied climate-driven changes in centrarchid populations (Meisner et al. 1987; Chu et al. 2005) and the effects of centrarchid invasions on native populations (Findlay et al. 2000; Jackson 2002; Jackson and Mandrak 2002). However, research on bullhead populations has focused mostly on temperature preferences and effects of temperature on the biology of these species instead of the use of bullheads as indicators of climate change (e.g. Black 1953; Cvancara et al. 1977; Kayes 1977; Reynolds and Casterlin 1978; Carveth et al. 2006). Yellow bullhead typically responded negatively to warmer temperatures, and black bullhead responses were variable, however, both species, which are known to prefer warm temperatures (Cvancara et al. 1977; Kayes 1977; Reynolds and Casterlin 1978; Carveth et al. 2006), were advancing northward in Minnesota. Further research on the response of bullheads to climate change is warranted. Analyses of whitefish populations mostly lacked trends, but temperature analyses showed that tullibee and whitefish typically responded negatively to warmer temperatures.

Observations of significant relationships between CPUE and air temperature are important because of growing concerns about climate change, but I acknowledge that temperature alone does not drive changes in biological communities; i.e. photoperiod, land use, eutrophication, etc., may be important. It would have been difficult to determine all sources of variation in fish community responses to climate, so we instead chose to analyze only a few lake physical and chemical characteristics that were readily available for all lakes. My results indicated that lake characteristics and lake class (or groups) explained variability in trends for some species. For future research and management plans, I recommend the use of sampling designs that help eliminate variability due to lake physical and chemical characteristics or analyses that incorporate lake characteristics into predictive models.

It's important to understand and identify changes in fish abundances and distributions associated with climate change because of potential implications for native fish populations, anglers, and aquatic resource management agencies. Most notable may be the expansion of ranges and increases in abundance of centrarchid populations. These changes could alter trophic interactions and community structure in lakes; numerous studies have shown that introduced centrarchids, such as smallmouth bass and bluegill, negatively impact fish communities by decreasing species richness and by decreasing abundance of fishes such as cyprinids (Jackson and Harvey 1989; Marchetti 1999; Findlay et al. 2000; Jackson and Mandrak 2002). Jackson (2002) showed that lakes with bass had significantly fewer species than lakes without bass. As centrarchids invade, fish communities may shift so that managers need to manage for bass and sunfish instead of walleye, and sport fisheries may become dominated by bass. Management agencies and biologists can use my results to make predictions that aid in future management plans for Minnesota's aquatic resources. Therefore, I recommend the continuation of lake surveys and further investigation of lake characteristics' influence on fish community responses to climate change.

From results for both chapters 2 and 3, it may be too obvious to say that significant trend detection and sampling design/methods are important aspects of this project that need further consideration. Small sample sizes and relatively short time spans likely limited the power to detect significant trends in individual lakes and for certain species. From Russ Lenth's power analysis (2006-09) I computed that the power to detect significant trends in egg-take data was only 48% (detectable beta = 02; Median sample size = 35, Error SD = 0.6), and the power to detect significant trends in ice-out data was only about 30% (detectable beta = 0.2; Median sample size = 38; Error SD = 0.9 and 0.8). Larson et al. (2001) showed that the probability of detecting a 2% per year trend with no interannual variation could be about 90% after 10 years with 100 sites, but if components of variability are influencing trends, it could take 15 to 25 years of data to reach a power of 80% with 100 sites. Similarily, Stockwell and Peterson (2002) reported that for linear regression to achieve 65% accuracy, about 50 data points were needed reaching maximum accuracy at 100 data points. My datasets for each lake or river were typically much smaller; walleye spawning and ice-out data ranged from 8 to 89 years, and lake survey data ranged from 15 to 43 years. Because my work suggests the timing of walleye spawning and some fish (centrarchids and ictalurids) distributions and abundances may be good indicators of climate change, I recommend that egg-take sites and lake surveys, or at least of subset of these, should continue to be monitored over time to increase samples sizes, timespans, and the power to detect significant trends.

Variability due to sampling designs also likely affected my ability to detect significant trends. Walleye spawning records collected by the Minnesota DNR contained information on egg-take and individual fish counts obtained from twelve walleye egg collection operations conducted by various Minnesota hatcheries from 1938 to 2007. From 1987 to 2007, the data recorded included number of walleye captured by sex and reproductive state of females (green, ripe, or spent), along with egg-take on each date. Prior to 1987, data on individual walleyes were generally not recorded and only data on egg-take were available. Sampling protocols have also varied over time for lake surveys in Minnesota. Lake survey data from the Minnesota DNR was collected for 4,145 lakes with data ranging from 1940 to 2007. Surveys were used to collect information about fish communities (i.e. species present, number of individuals…etc.) and general lake characteristics such as water temperature and secchi depth. Data were collected from several types of surveys: initial, re-survey, populations assessments, and special assessments. Special assessments were all surveys not considered to be standard, so these were excluded in our analyses. There were 61 different types of sampling stations that used gear such as standard gillnets, standard trapnets, ice fishing, seining, and trotlines. We narrowed the dataset down to 21 lakes with 18 or more years of gillnet data and 21 lakes with 15 or more years of trapnet data. There were 35 individual lakes within this subset because some lakes had both gillnet and trapnet data. All years were not sampled, and sampling effort varied within and across lakes over time. I chose to work with a subset of the data to eliminate locations with the shortest timespans and because of time constraints on this project. The broader dataset is available and could be used for further investigations.

Some components of variation that likely affected my ability to detect significant trends were (see Urquhart et al. 1998; Larson et al. 2001): index variance such as crew variance, measurement variance, gear variance, etc.; interaction variance from year-to-year changes in each lake unrelated to changes in other lakes; and site-to-site differences occurring within (i.e. variance due to sampling at different locations within a lake or river each year) and across locations. Year-to-year variation was not a concern for egg-take versus ice-out regressions because there was no evidence of autocorrelation, nor was it a concern for time series data because when investigating climate signals or climate-driven changes over time, you are essentially looking for annual variation that is explained by climate variables. Because sampling design has an effect on the ability to detect trends, I recommend that agencies develop sampling designs that consider components of variation such as those discussed by Urquhart et al. (1998). Discontinuity in variables measured, failure to record dates, or procedural changes such as variability in gear type or sampling effort are counterproductive for trend detection. Although technology allows for new methods of sampling such as electrofishing that are more efficient and effective than previous methods, my work suggests that these should be incorporated with older methods (gillnets and trapnets) instead of replacing them to avoid losing the ability to assess trends. Finally, for future research and management studies, I suggest analyzing regional trends in data instead of local trends to help reduce variability and to increase the ability to detect significant trends.

In summary, I’ve presented evidence that the timing of walleye spawning runs, fish abundances, and fish distributions in Minnesota are changing, and these changes, consistent with predicted effects (e.g. Magnuson et al. 1990; Meisner 1990; Magnuson et al. 1997; Stefan et al. 2001; Chu et al. 2005; Jensen et al. 2007), may be associated with climate change. Information from this and other studies about climate-driven changes in fish phenology and distributions will benefit state and local agencies as they develop future management plans for Minnesota’s aquatic resources. I recommend continued monitoring of the timing of walleye spawning runs in Minnesota because it may be a good biological indicator that can also be used to document climate-driven changes in walleye populations. While there is nothing comparable to ice-out in warmer regions, fish species responses may be similar across regions and thus, may be a more universal indicator than ice-out. Spawning records for other populations or species may be good indicators in other regions. Furthermore, I recommend continued monitoring of centrarchids and perhaps bullhead in lake surveys as these species may also be good indicators of climate change. Finally, it’s important for management agencies and biologists to consider the influence of lake characteristics on fish responses to climate change; my work suggests that location, lake size, and lake class may be important covariates to consider. The ability to define these relationships will become even more important if we continue to observe trends of warming temperatures.

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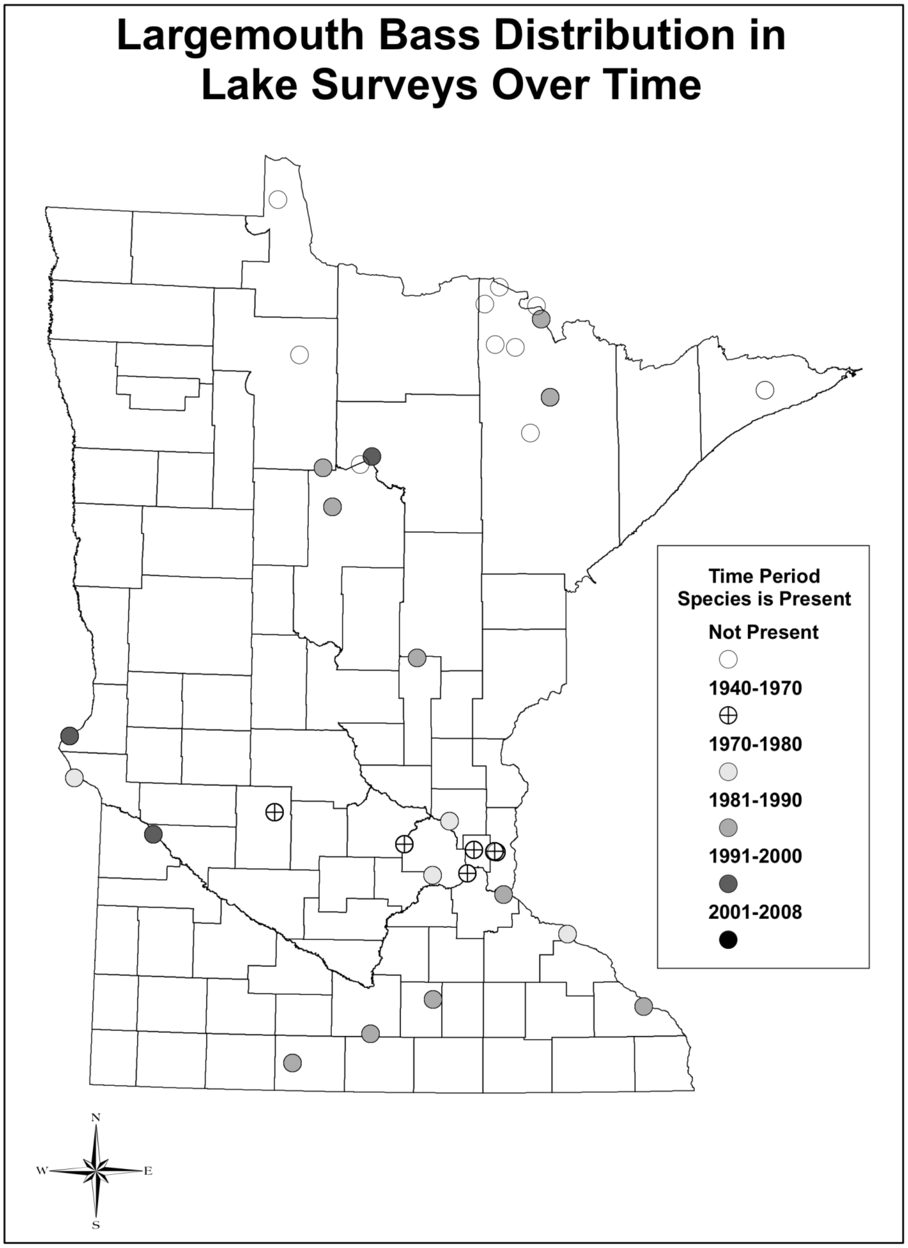
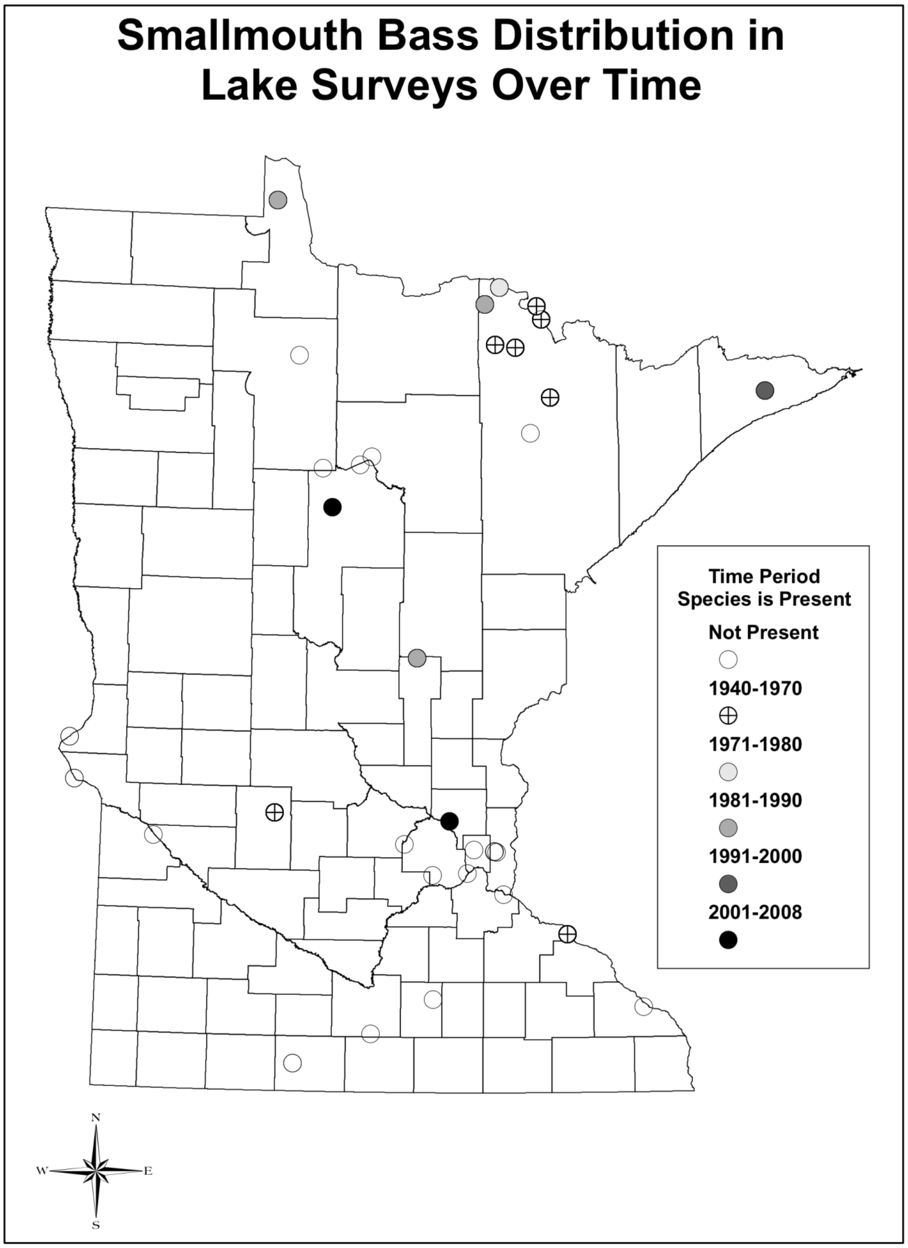
Appendix A: Maps of species distributions over time in Minnesota lake surveys.

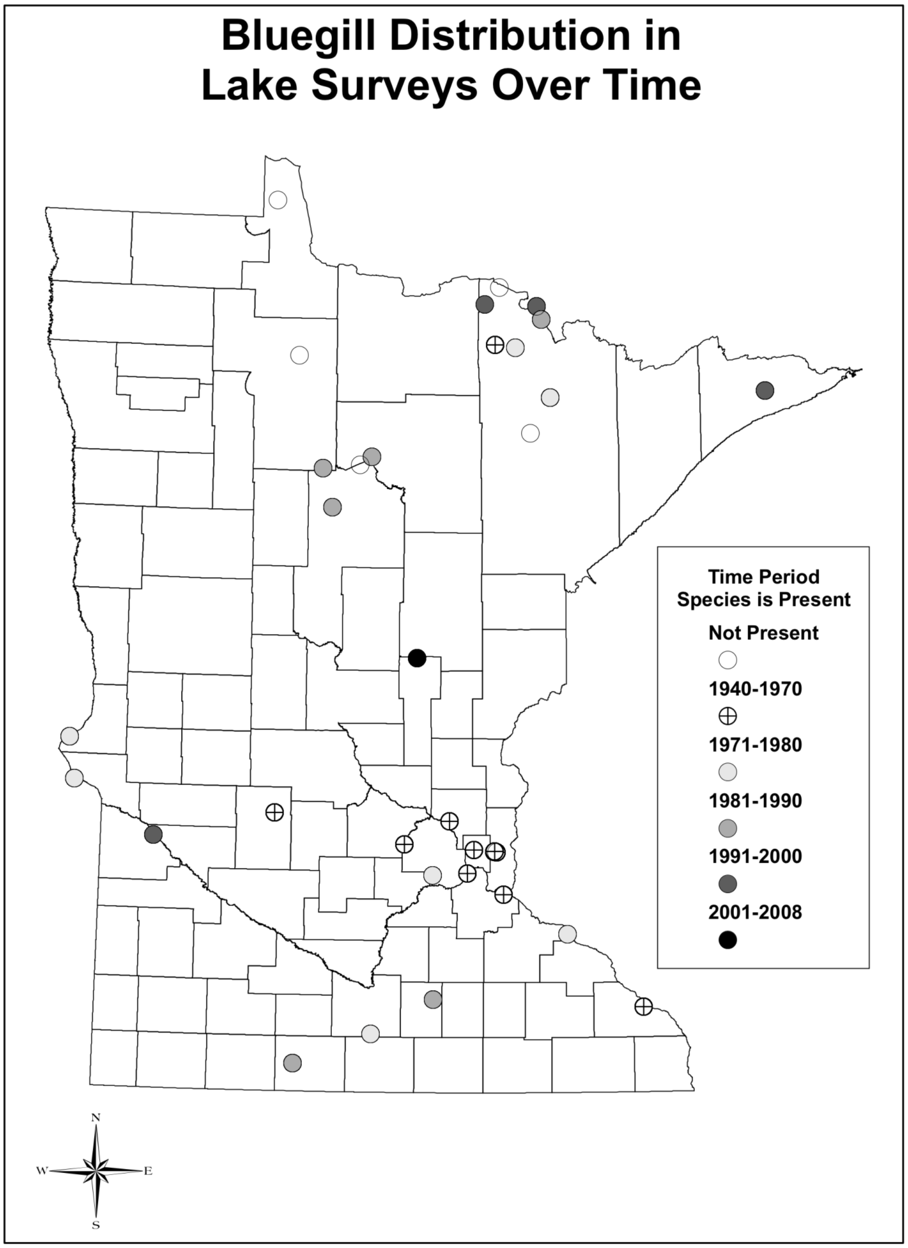
Appendix A1: Map of largemouth bass distributions



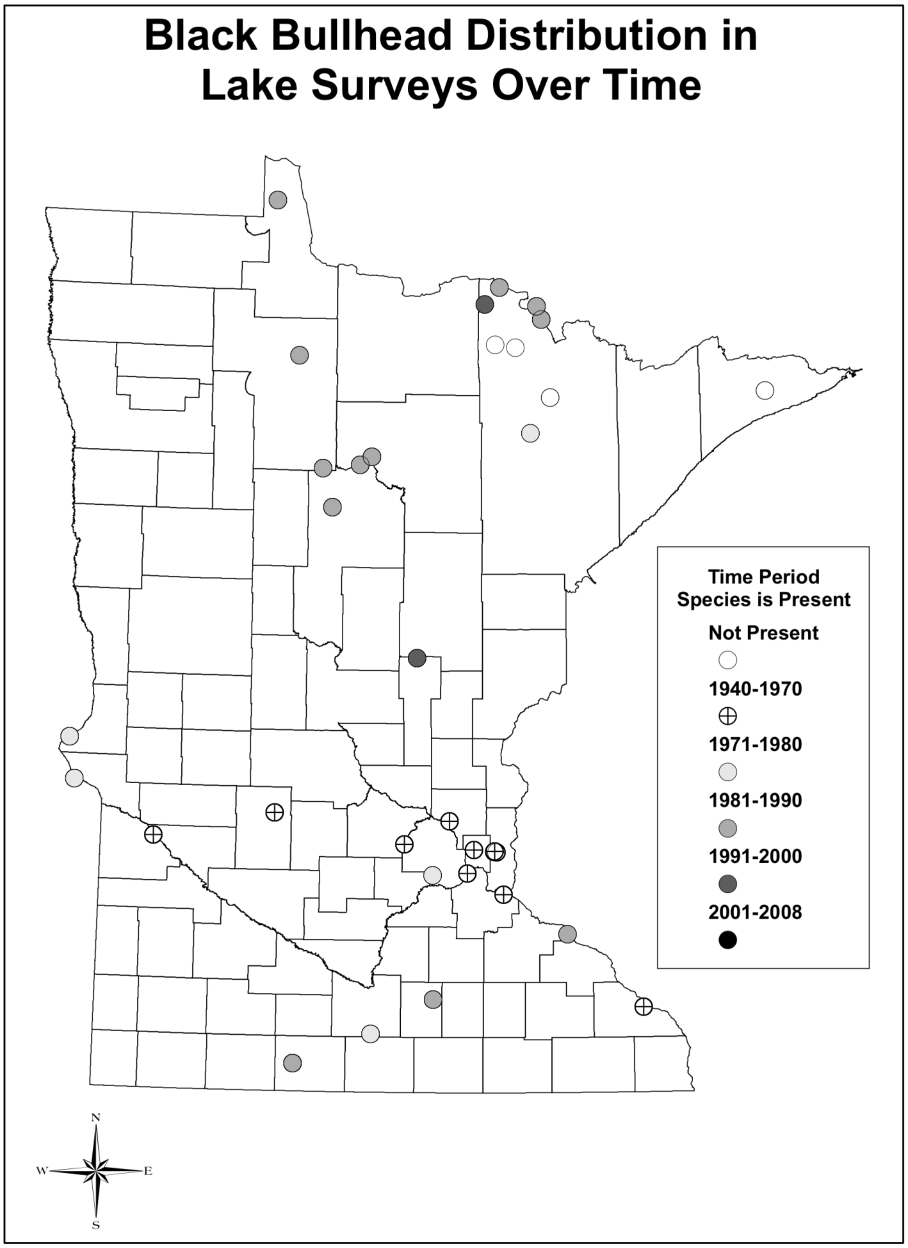
Appendix A2: Map of smallmouth bass distributions



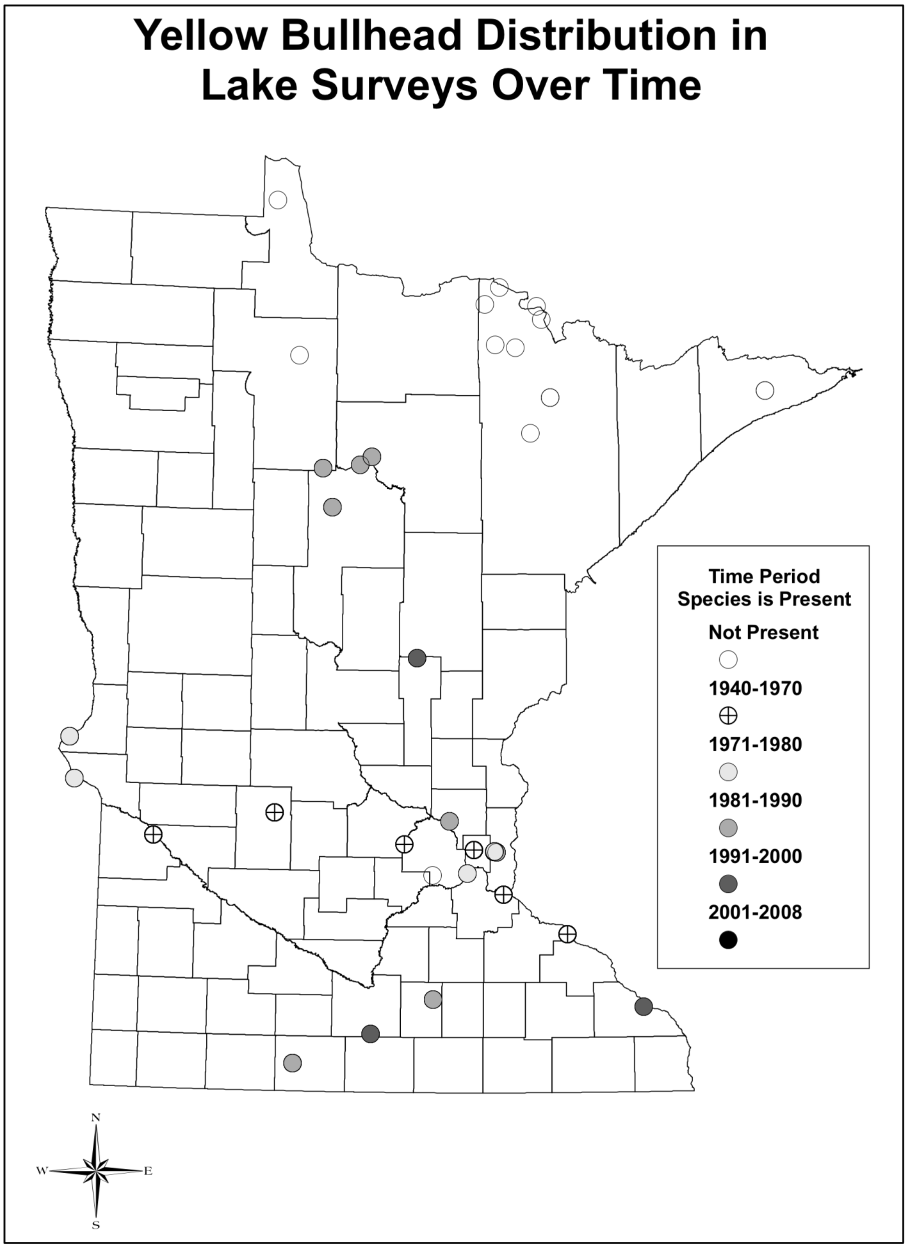
Appendix A3: Map of bluegill distributions



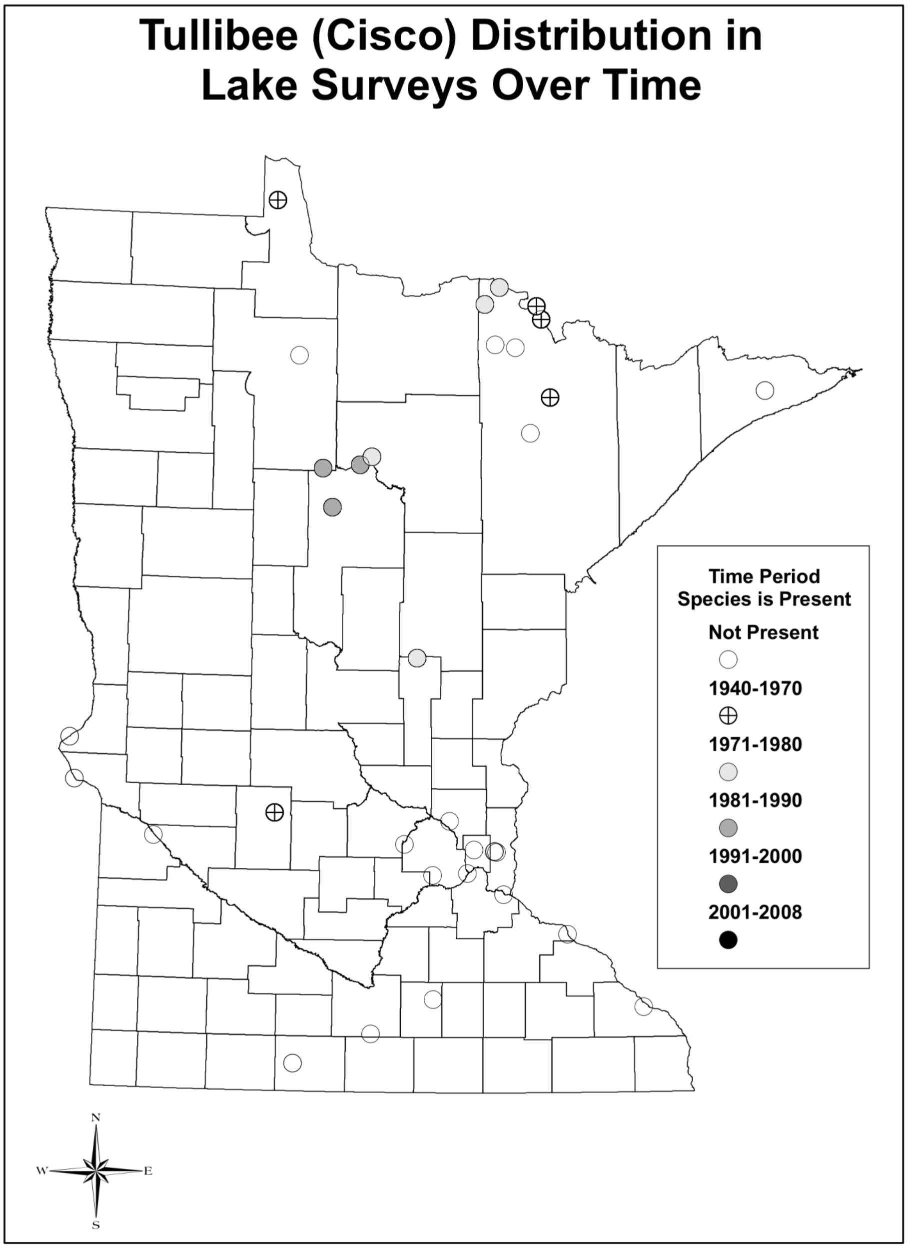
Appendix A4: Map of black bullhead distributions



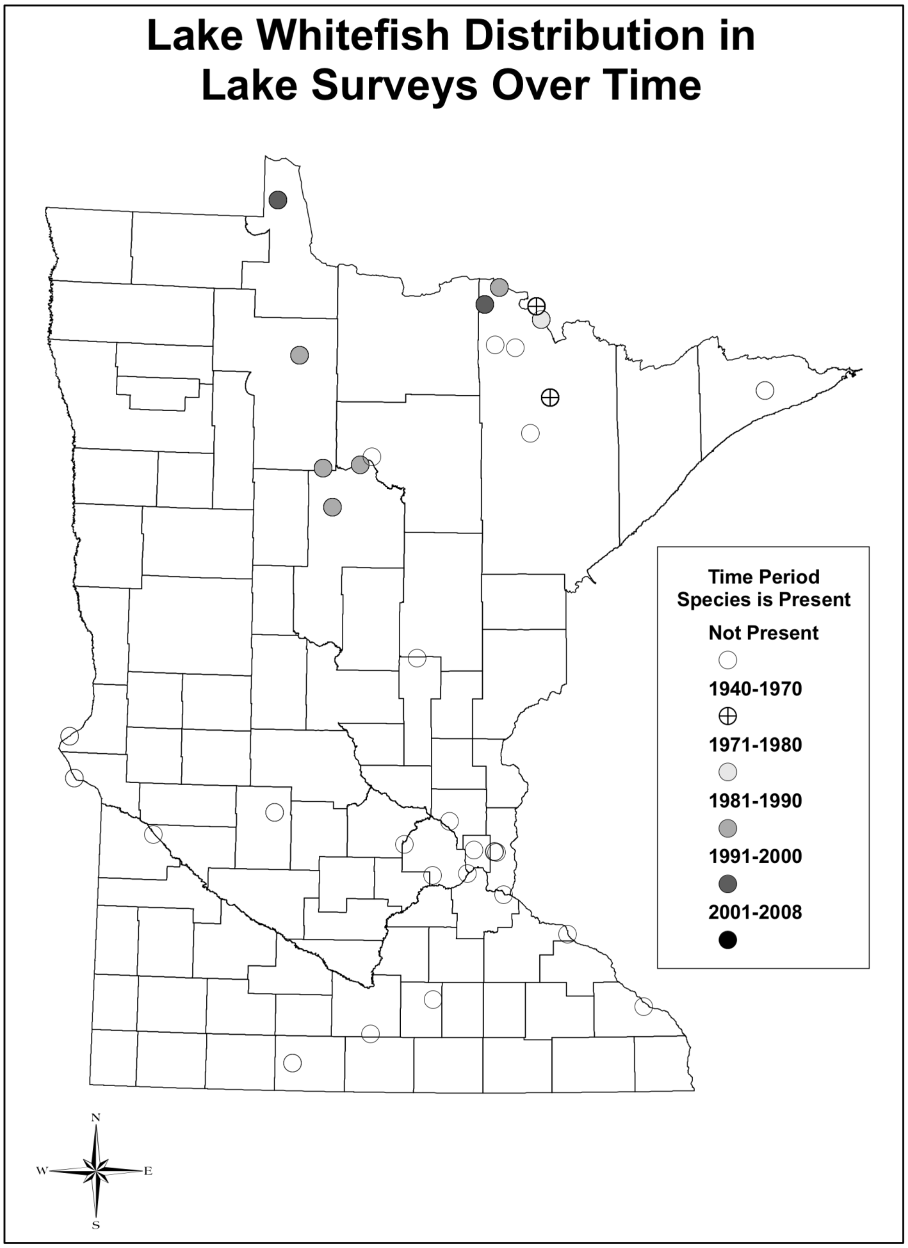
Appendix A5: Map of yellow bullhead distributions



Appendix A6: Map of tullibee distributions

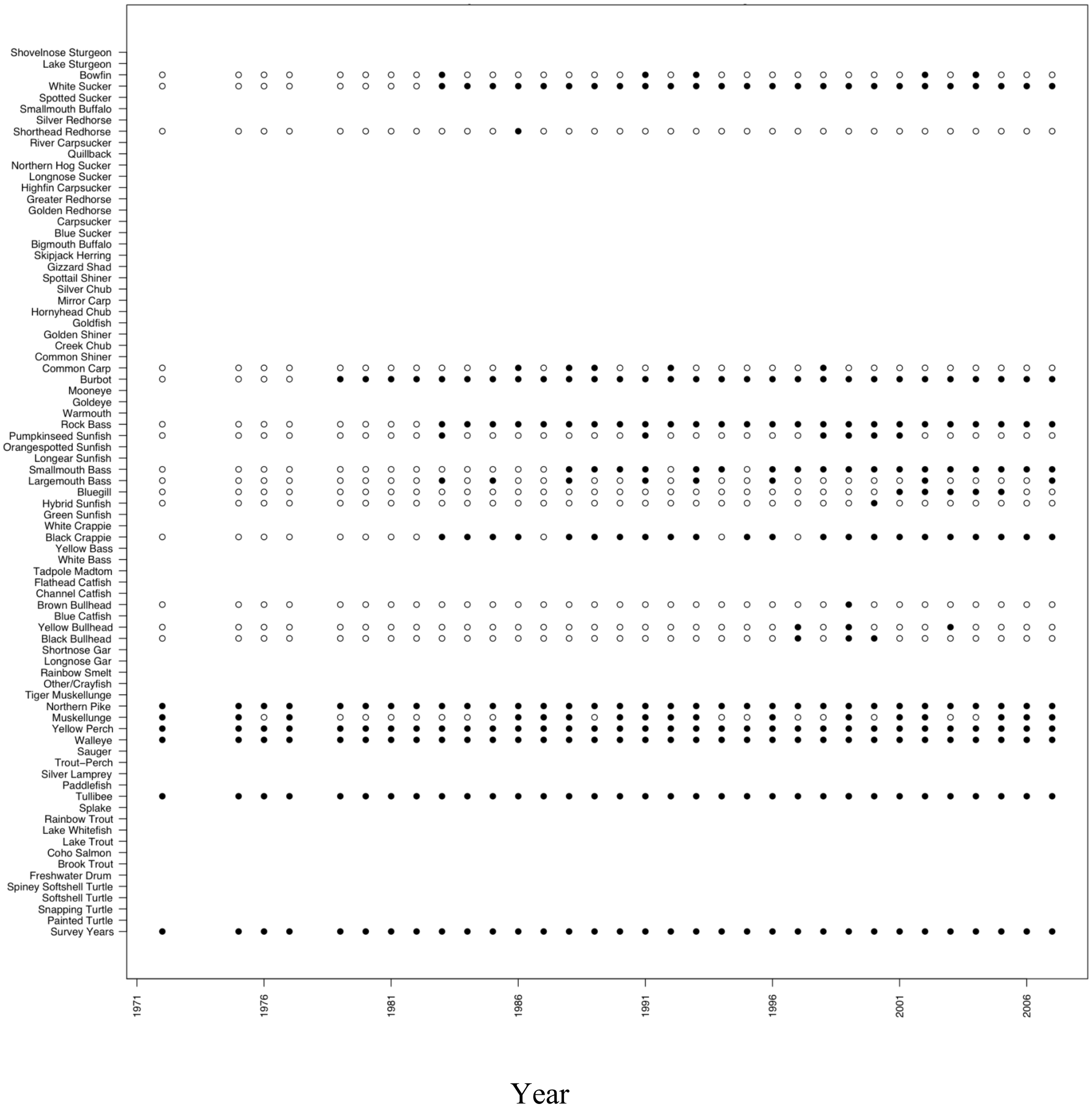


Appendix A7: Map of lake whitefish distributions

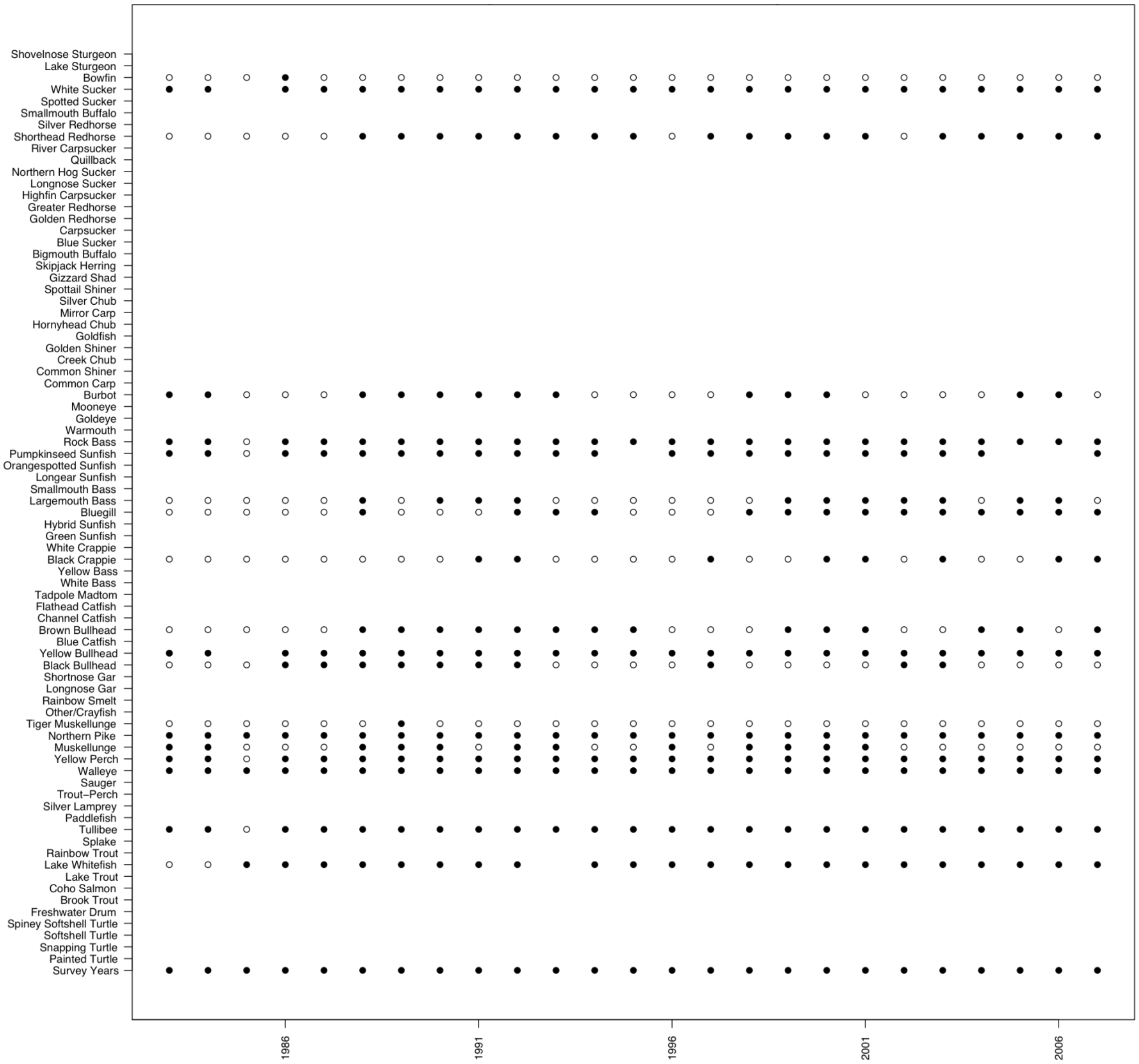


Appendix B: Example plots of species occurrence over time in Minnesota lake surveys for gillnets and for trapnets. Common names of species are listed on the y-axis. Circles represent years sampled, and solid circles indicate species presence.

Appendix B1: Species occurrence in Mille Lacs gillnets

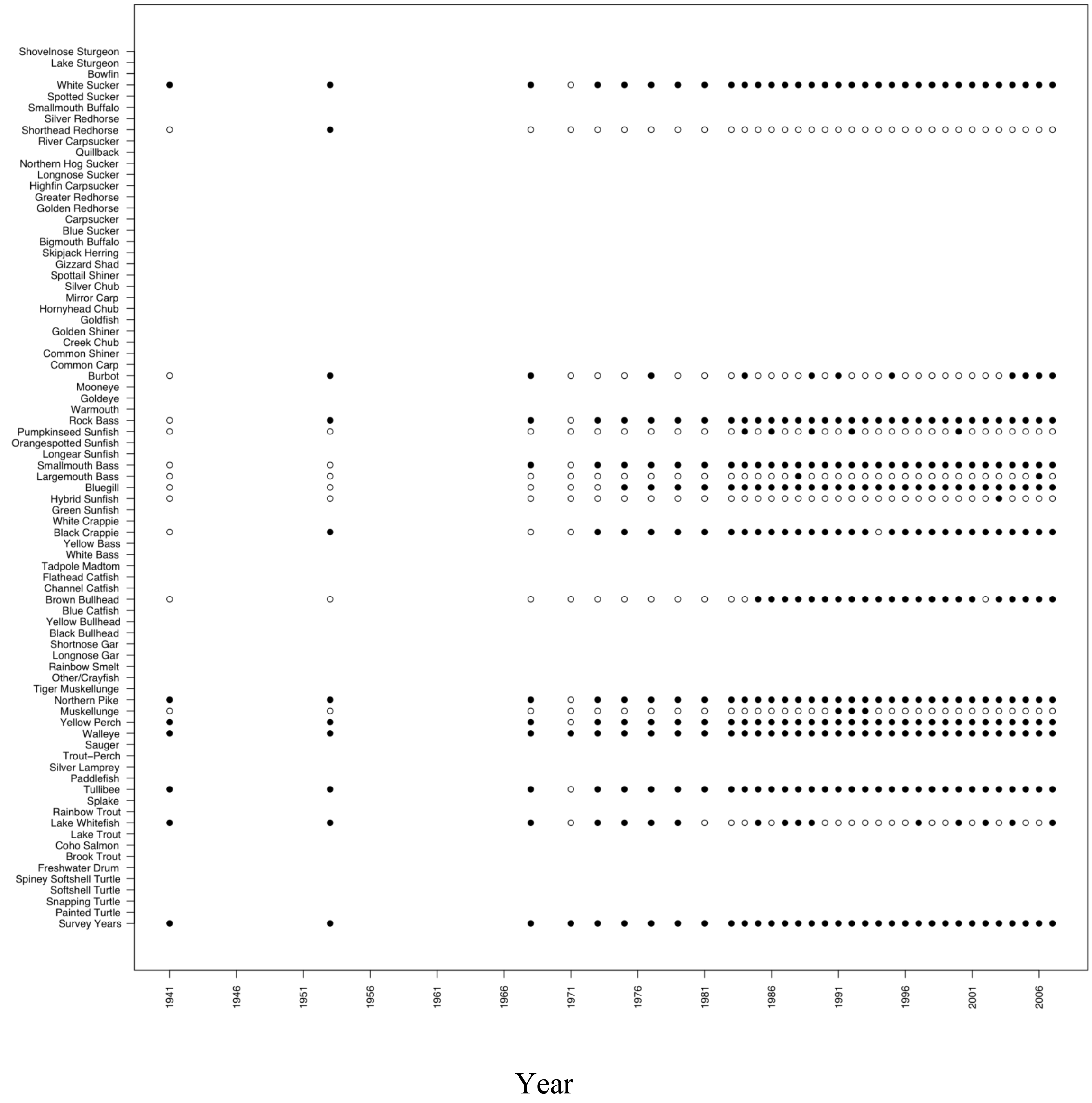


Appendix B2: Species occurrence in Cass gillnets

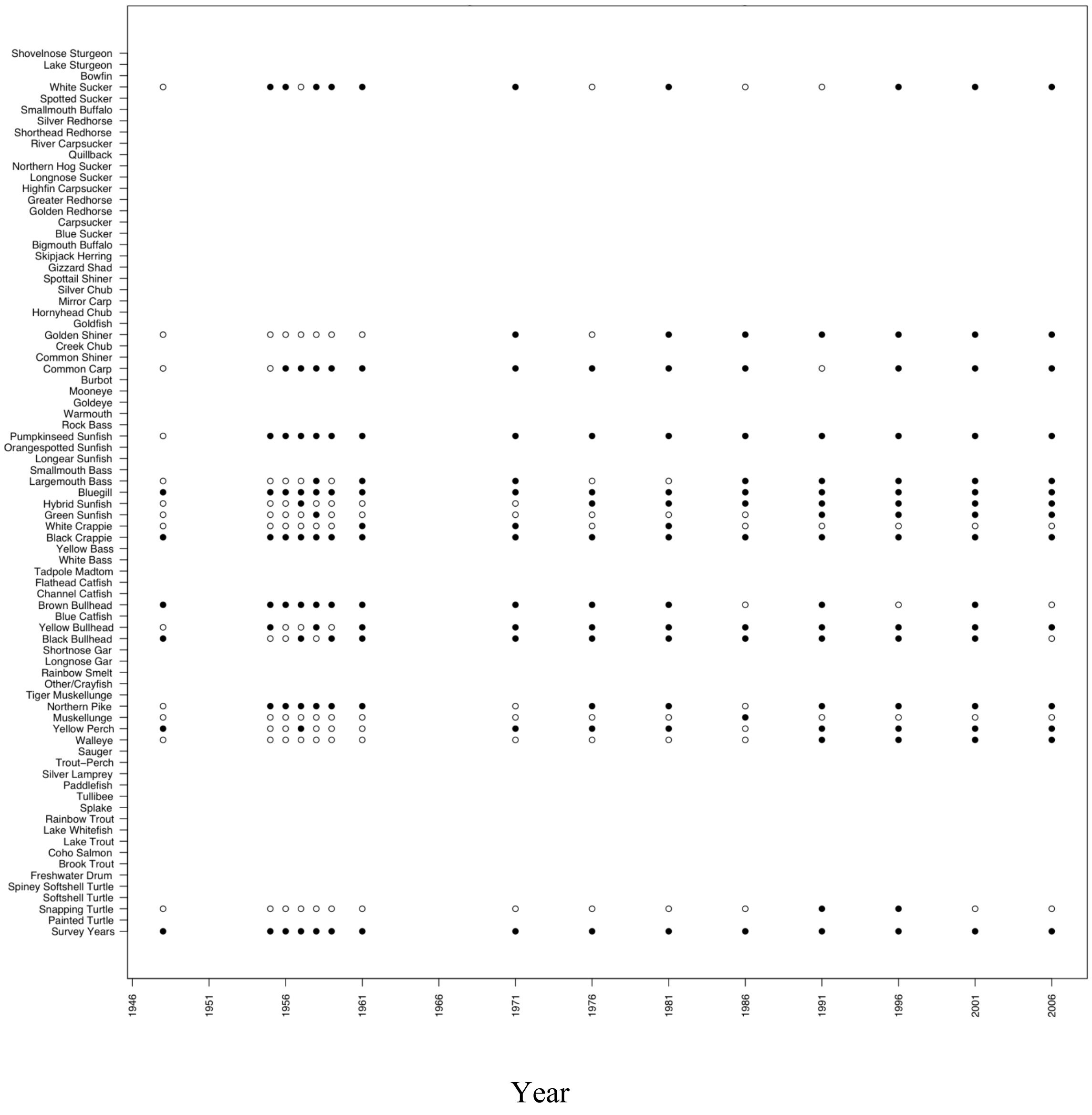


Year

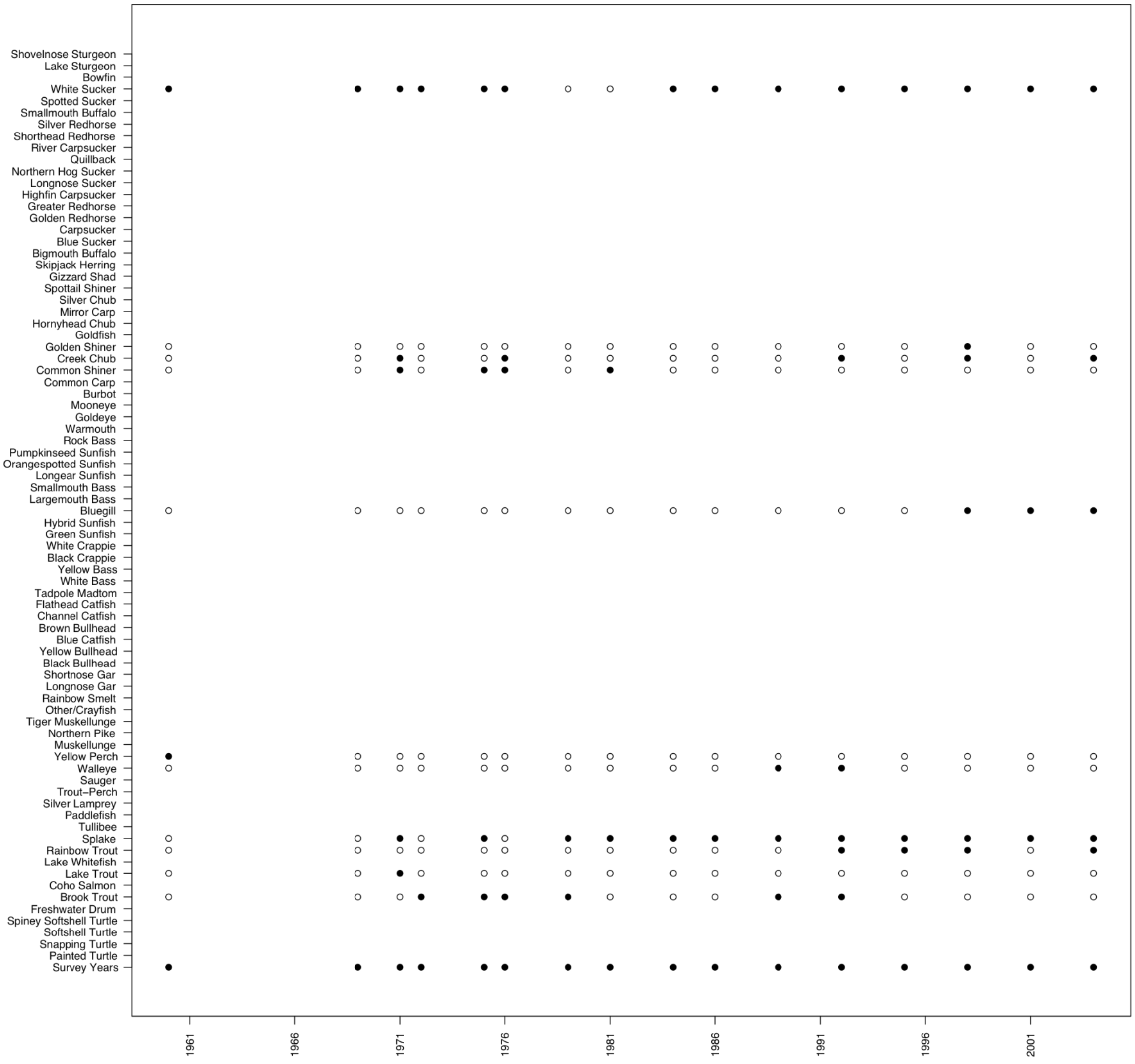
Appendix B3: Species occurrence in Vermilion gillnets



Appendix B4: Species occurrence in Owasso trapnets

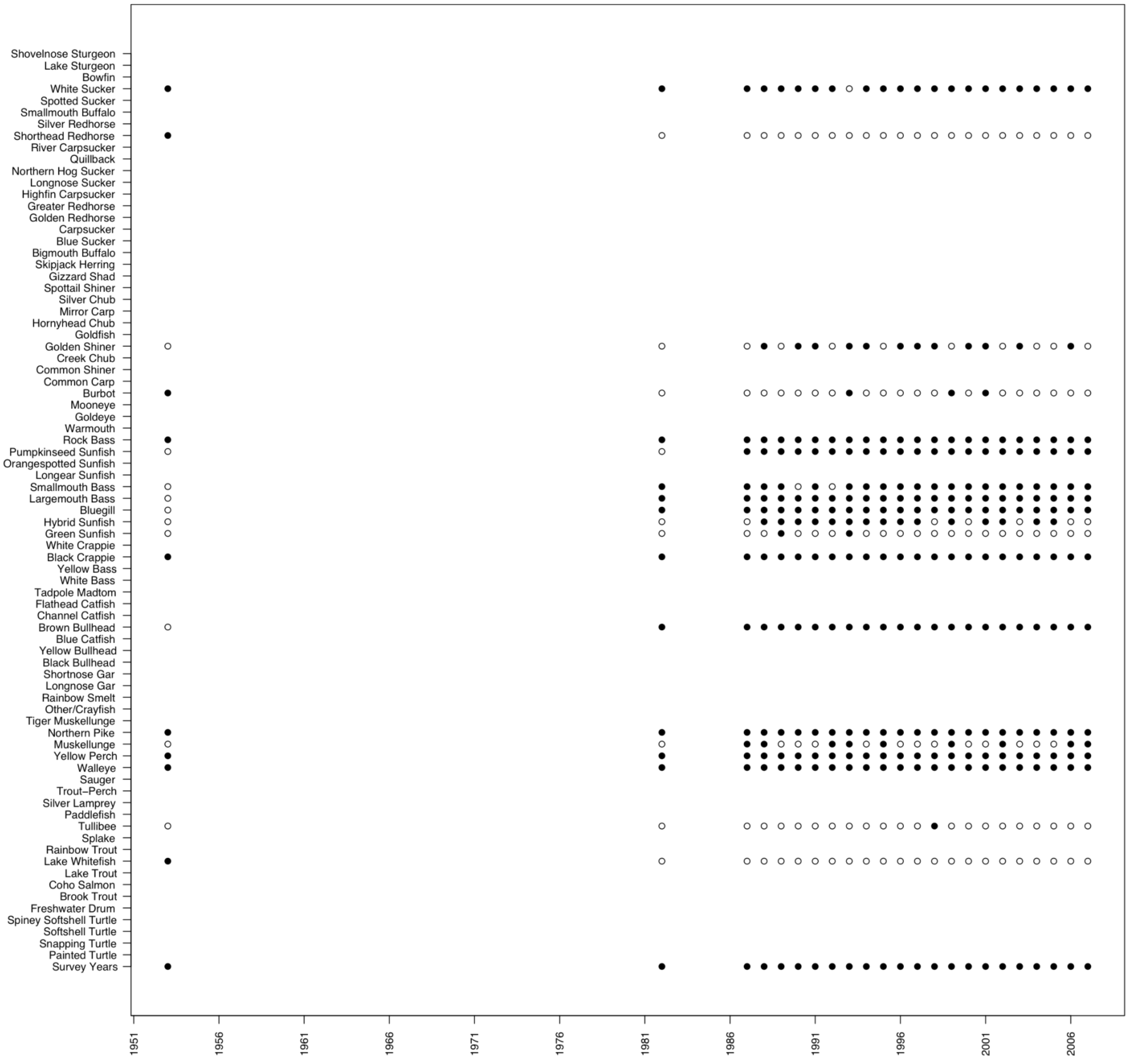


Appendix B5: Species occurrence in Pine River trapnets



Year

Appendix B6: Species occurrence in Vermilion trapnets.



Year

Appendix C: Regression of mean latitude (km) of lakes surveyed (gillnet and trapnet) versus year. The solid line is the regression line. Each point represents one year.