

Water-level change effects on northern pike spawning and nursery habitat and reproductive success in Rainy Lake and Namakan Reservoir, Minnesota

Principal Investigator: Anne Timm (USDA Forest Service)
Principal CO-Investigator: Rod Pierce (Minnesota DNR, retired)

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EXECUTIVE SUMMARY:

Project Background: The 2000 International Joint Commission (IJC) rule curves (RCs) for Rainy Lake and Namakan Reservoir dictated that the dam operators needed to target the mid-point between the upper and lower RCs throughout the year. The 2000 RCs, by providing a summer drawdown, reducing the overwinter drawdown compared to the 1970 RCs, and providing an earlier spring rise were expected to expand the range of elevations covered by emergent aquatic vegetation that would be available as spawning habitat, thus improving spawning and nursery conditions for northern pike (*Esox lucius*).

Study Objectives: The objectives of this study were: 1) To determine if northern pike spawning and nursery habitat and reproductive success have changed due to the 2000 RC; 2) To verify that larval and young-of-the-year (YOY) northern pike are using predicted improved spawning and nursery habitats resulting from the 2000 RC with further larval and YOY sampling; and 3) To assess how well long-term seining data sets represent northern pike reproductive success in Rainy Lake and Namakan Reservoir by comparing catch rate and efficiency of light-trapping and seining methods.

Results

Objective 1

For both Rainy Lake and Namakan Reservoir, mean annual seine catches were significantly higher under the 2000 RC (2000-2012) conditions when compared to the 1970 RC (1986-1999) conditions. Highest mean catch rates for YOY northern pike in seines corresponded to years with the highest monthly mean water levels in May and June for both Rainy Lake and Namakan Reservoir and both RCs. The highest mean catch years were when water levels were above the 1970 and 2000 RC in May and June, specifically 338.1 m for Rainy Lake, and 341.0 m for Kabetogama Lake.

For both Rainy and Kabetogama Lakes, Pearson correlation analysis did not identify a significant positive relationship between daily water level and long-term larval northern pike mean catch data from 2004 to 2013 in Dove Bay, Rainy Lake or Sullivan Bay, Kabetogama

Lake. However, the mean monthly May water level that corresponds to the highest mean larval catches in Rainy Lake, is at or above 337.4 m, which is consistent with the higher larval northern pike catch rates observed at similar water levels in Dove Bay, Rainy Lake, 2004 to 2013. The mean monthly May water level that corresponds to the highest mean larval catches in Kabetogama Lake, is at or above 340.4 m, which is consistent with the higher larval northern pike catch rates observed at similar water levels in Sullivan Bay, Kabetogama Lake, 2004-2012.

Objective 2

Overall findings for the larval and YOY northern pike life stages differ in terms of habitat characteristics related to count. The greatest numbers of sampled larval northern pike were found in habitats with hybrid cattail (*Typha x glauca*), burreed (*Sparganium* spp.), common waterweed (*Elodea canadensis*), and sedges (*Carex* spp.), which is a reflection of the aquatic plant species that are present during the larval stage in sampled bays. The highest mean catch rate (number of larvae per light trap) for all sampled plant species was found in submerged common waterweed.

Finite mixture model analysis to predict larval northern pike count identified water level and the presence of hybrid cattail as the most significant predictive variables, with predicted catch rates (number of larvae per light trap) lower for sites with hybrid cattail present. In addition, Wilcoxon sign-rank tests for non-normal data identified significantly higher larval northern pike catch rates for locations where aquatic vegetation was present when compared to locations where aquatic vegetation was absent.

Finite mixture model analysis to predict YOY northern pike count identified water temperature as a significant variable affecting YOY northern pike count and length, with greater YOY counts associated with water temperatures > 25 °C. The presence of aquatic plant species was significant in relation to year sampled and lake sampled, which is a reflection of the variability of aquatic plant community structure resulting from changes in annual water depth relative to each lake. The presence of coontail (*Ceratophyllum demersum*) was a significant predictive variable for YOY northern pike count in Rainy Lake and the presence of common bladderwort (*Utricularia macrorhiza*) was significant in Kabetogama Lake.

Objective 3

The overall mean catch rate per light-trap was 2.9 times higher than mean catch rate per seine for Rainy Lake and 1.6 times higher for Kabetogama Lake for 2004 to 2013 data. Rainy and Kabetogama Lake light-trap mean catches were higher overall when compared to seine mean catches for 2004 to 2013. However, Rainy and Kabetogama Lake light-trap larval mean catches were not significantly different from seine YOY mean catches for 2004 to 2013. In addition, Pearson correlation analysis did not identify a significant correlation between seine and light-trap mean catch values for 2004 to 2013 for both Rainy and Kabetogama Lakes.

I. INTRODUCTION

Namakan Reservoir was created in 1914 with two constructed dams (Kettle Falls and Squirrel Falls) at the outlet of Namakan Lake and includes Namakan, Kabetogama, Crane, Sand Point, and Little Vermilion Lakes (Miller et al. 2001). There is also a hydropower dam at the outlet of Rainy Lake (Figure 1). The 2000 International Joint Commission (IJC) rule curves (RCs) for Rainy Lake and Namakan Reservoir dictated that the dam operators needed to target the mid-point between the upper and lower RCs throughout the year (Figure 2). In 2001, the IJC issued an Order prescribing the method of regulating the levels of the boundary waters of Rainy Lake and Namakan Reservoir, consolidating and replacing a number of previous orders and supplementary orders (Kallemeyn et al. 2003; Kallemeyn et al. 2009). This “Consolidated Order” was effective on February 28, 2001 and contained the following provision: “This order shall be subject to review 15 years following adoption of the Commission’s Supplementary Order of January 5, 2000, or as otherwise determined by the Commission. The review shall, at a minimum, consider monitoring information collected by natural resource management agencies and others during the interim that may indicate the effect of the changes contained in the Supplementary Order of January 5, 2000.”

In 2007, the IJC formed a Rule Curve Assessment Workgroup to develop a plan of study (POS) in which the Workgroup would prioritize the monitoring and analyses required to review the IJC Order in 2015. Specifically, the POS was written to identify priority studies and describe information/data that remained to be collected, identify what entities might collect the data and perform these studies, and to provide an estimate for the cost to accomplish this work by 2015. The POS for the Evaluation of the IJC 2000 Order for Rainy Lake and Namakan Reservoir and Rainy River was completed in 2009 (Kallemeyn et al. 2009). The 2009 Plan of Study identified priority work on effects of water-level change on northern pike (*Esox lucius*) spawning success as one of the targeted studies. The study would include habitat quantification, aquatic vegetation surveys, light-trapping for larval northern pike, and trap-netting for young-of-the-year (YOY) northern pike.

II. STUDY BACKGROUND

Rule curves (RCs) are implemented by the U.S.-Canadian International Joint Commission (IJC) to regulate water levels in important Minnesota-Ontario border water reservoirs including Rainy Lake and Namakan Reservoir (Cohen and Radomski 1993). Both reservoirs are located on the Canadian glacial shield, which is a geological region of Precambrian rock and thin layers of soil that covers large portions of Canada and extends south into northeastern Minnesota. A result of this geological formation is that lakes in northeastern Minnesota are different than southern and even central Minnesota lakes and can have different water chemistries and flora than lakes farther south and west (Moyle 1956). The RCs for the two

reservoirs are ranges of water levels that vary seasonally, allowing for declining water levels through late fall and winter followed by increasing water levels during spring and early summer. Cohen and Radomski (1993) considered that northern pike might be a species sensitive to the frequency and amplitude of managed water-level fluctuations in these lakes.

Such manipulation of water levels has the potential to affect shallow-water habitats in spring and early summer when northern pike need nursery areas with protective cover and an abundant supply of food (Franklin and Smith 1963; Craig 1996). The 2000 RCs, by providing a summer drawdown, reducing the overwinter drawdown compared to the 1970 RCs, and providing an earlier spring rise were expected to expand the range of elevations covered by emergent aquatic vegetation that would be available as spawning habitat, thus improving spawning conditions for northern pike. This change would also increase the amount of food and nursery habitat, which is also known to be important in determining northern pike production.

Evaluation of the ecological effects of the IJC RCs for managing water levels will require an understanding of how aquatic plants are used as cover by larval and YOY northern pike in their nursery areas and a further understanding of how water-level regulations affect the availability of aquatic plants. Natural patterns of water-level fluctuation have been associated with a more structurally and taxonomically-diverse aquatic plant community (Wilcox and Meeker 1991, 1992). Casselman and Lewis (1996) investigated relationships between northern pike and spring water elevations in Bay of Quinte for 22 years (1971-1992) and found that nursery habitat may be more limiting than spawning habitat, as YOY require wider ranges of depths and related aquatic plant community structural development (Wilcox and Meeker 1992; Minns et al. 1996).

Further research is needed to investigate relationships between water-level change effects on aquatic vegetation community structure and cover and northern pike spawning success. From 2004 to 2011, light traps were used to examine spatial and temporal variation in catches of northern pike larvae in potential nursery areas affected by water-level regulation in Rainy and Kabetogama Lakes (Pierce et al. 2007b; Rod Pierce, personal communication, May 2011). Pierce et al. (2007b) recommended expanding larval and YOY sampling to other areas within Rainy Lake and Namakan Reservoir and to investigate more specific characteristics of vegetation types within northern pike spawning (egg and larvae) and nursery (YOY) locations.

III. LITERATURE REVIEW

Causes of northern pike decline.-Possible causes of northern pike population declines in the Great Lakes region include: shoreline development, water-level changes, changes in temperature, changes in nearshore habitat and aquatic macrophyte cover, and siltation (Jude and Pappas 1992; Casselman and Lewis 1996). These factors that have led to declines in northern pike populations are linked to losses of historic spawning habitat (Brynildson 1958; Reid 1990).

General habitat characteristics.-Northern pike are considered cool-water fish, best adapted to < 12 m, productive, mesotrophic-eutrophic well-oxygenated (> 3mg/L) lakes. Important factors in quality northern pike habitat include vegetative cover, temperature, oxygen, and water transparency (Casselman and Lewis 1996). Headrick and Carline (1993) showed that northern pike preferred habitats 20° C or less. Lethal high temperatures in the lab were 29.4°, and northern pike can tolerate temperatures as low as 0.1° C. Oxygen levels are lethal to northern pike at 0.5-1.5 mg/L, and feeding behavior lapses at 2 mg/L (Casselman 1978). Water transparency has been positively related to northern pike's ability to feed, with northern pike weight being positively related to increases in Secchi depth (Craig and Babaluk 1989).

Spawning habitat.-Northern pike spawn in Northern Minnesota after ice out, in April or early May. Female northern pike have lay their eggs in vegetation at water depths ranging from 20 cm to 5.8 meters (Casselman and Lewis 1996; Pierce et al. 2007a). Northern pike eggs are laid in floating vegetation that suspends them above anoxic substrates in nearshore or wetland habitats that are approximately 8-12° C. Vegetative criteria for quality northern pike spawning habitat include hummocks of grasses and sedges and moderately dense vegetative cover (2-4 hummocks per m²) (Casselman and Lewis 1996). Previous research has documented relationships between aquatic vegetation diversity and spatial extent of vegetative cover to northern pike spawning and the presence of aquatic vegetation is a key component for northern pike spawning success (Brynildson 1958; Reid 1990; Jude and Pappas 1992; Casselman and Lewis 1996).

Nursery habitat.-Northern pike YOY grow and leave spawning areas in relation to water depth, availability of prey, and density of aquatic vegetation. Previous research has correlated water depth to age and size of YOY (Casselman and Lewis 1996), and optimal temperatures for YOY growth are 19 °C (Bevelhimer et al. 1985). Optimal vegetative cover for northern pike YOY feeding efficiency is 40-80% (Anderson 1993).

Nursery habitats for YOY northern pike are much less thoroughly studied than spawning habitats even though the larval stage may be a critical period for survival (Franklin and Smith 1963; Casselman and Lewis 1996). Forney (1968) concluded that maintenance of northern pike populations in many lakes may depend primarily on production of juvenile fish in their nursery habitat. One of the reasons nursery habitats are less thoroughly studied is that these areas are difficult to sample due to the presence of shallow water and high percentages of submerged and emergent vegetation (Bry 1996; Casselman and Lewis 1996).

Aquatic vegetation preferences.-Previous research documented northern pike preference for a variety of aquatic plant species, which may vary by size and age of individuals (Inskip 1982; Anderson 1993). Pierce (2004) and Pierce et al. (2007a) documented radio-tracked spawning females expelling eggs into water bulrush (*Scirpus subterminalis*), sedges (*Carex* sp.),

muskgrass (*Chara* spp.) and stonewort (*Nitella* sp.). Studies in Ontario showed that YOY northern pike preferred milfoil (*Myriophyllum* sp.) and pondweed (*Potamogeton* sp.) (Anderson 1993). A study in Colorado showed that YOY northern pike preferred coontail (*Ceratophyllum demersum*), common waterweed (*Elodea canadensis*), pondweed spp., and muskgrass (Cook and Bergersen 1988).

Effects of water-level change on northern pike and their spawning habitat.-Northern pike are a useful indicator species for water-level regulation because spring flooding triggers spawning, and water levels during and following spawning will determine larval survival, successful recruitment, and year-class strength (Dumont and Fortin 1977; Casselman and Lewis 1996). Previous research showed that higher water levels were associated with higher productivity, increased prey availability, and larger areas of accessible habitat (Bodaly and Lysack 1984).

Mingelbier et al. (2008) developed a model to predict spawning habitat for northern pike in the St. Lawrence River system based on water velocity, wetland type, and water temperature data. This model focused on areas for egg deposition and potential embryonic-larval mortality due to low water levels within spawning and nursery habitats and identified potential habitat surfaces that existed between 1960 and 2000. Results of this study suggest that spawning sites are ideal in terms of vegetation, water temperature, and velocity when the upper part of the floodplain of a system is submerged due to high discharge.

Mingelbier et al. (2008) showed that shortening the spring flood by three weeks, as a result of regulation in the St. Lawrence system, had a large impact on spawning habitats and resulting year-class strength. The authors recommended providing high water levels for 35-40 days to ensure egg and larval survival and to allow natural flow regimes as part of a water regulation plan for the Lake Ontario-St. Lawrence system (Mingelbier et al. 2008).

Effectiveness of sampling methods.-Quantitative, representative sampling of larval and YOY fish in floodplains is problematic due to increasing mobility as the larval stage grows into the larger YOY stage, lack of accessibility to spawning and nursery habitats as a result of debris and dense vegetation, and the patchiness of larval and YOY fish populations (Mann 1971; Copp and Penaz 1988).

Lighted quatrefoil plexiglass traps can be used for larval northern pike sampling in vegetation because northern pike larvae are positively phototactic and drawn into the four columns of the traps by artificial light during nocturnal sampling (Kelso and Rutherford 1996; Pierce et al. 2007b). Light traps offer the advantage of minimally disrupting fish nursery habitat compared to other sampling techniques such as seining. Two previous studies evaluated the potential of light traps for sampling larval northern pike. Zigler and Dewey (1995) used a series of raceway and pond experiments to test for phototaxis in larval and juvenile northern pike.

They compared catches in lighted (using chemical light sticks) versus unlighted quatrefoil traps, and their results showed that catches of northern pike were 3-35 times greater in lighted traps. Pierce et al. (2006) reported that light-trap catch rates discriminated between different densities of larval northern pike stocked into hatchery raceways and that light traps were capable of detecting patchy fish distributions. This study also illustrated growth rates and differential survival among managed wetlands. Light trapping can effectively sample larval northern pike from the time their mouths form, and they begin exogenous feeding (10-12 mm) through the sizes when they complete the larval stage and attain the general form of the adults (about 35-40 mm; Franklin and Smith 1960; Pierce et al. 2006).

For northern pike YOY sampling, previous research has documented significant differences ($P < 0.01$) in relative abundance and species composition sampled by fyke nets and seines in littoral zones of lakes, with fyke net samples having more individuals and species (Clark et al. 2007). Seines are known to be especially inefficient in areas with a lot of debris and dense aquatic vegetation (Pierce et al. 2001; Clark et al. 2007). In areas without debris, capture efficiency for bag seines of YOY northern pike in shallow water (up to 1.5 meter depth) can be 72.3% (unpublished data, Farrell 2001).

IV. GOALS AND OBJECTIVES

Study goals.-The goals of this study were to investigate effects of water level on specific types of aquatic plants present in spawning and nursery habitats and to identify characteristics of aquatic plant community structure that result in greater production of larval and YOY northern pike. Another goal of this study was to quantify effectiveness of sampling methods for larval and YOY northern pike that have been applied in Rainy, Kabetogama, and Namakan Lakes.

Study objectives.-The objectives of this study were: 1) To determine if northern pike spawning and nursery habitat and reproductive success have changed due to the 2000 RC; 2) To verify that larval and YOY northern pike are using predicted improved spawning and nursery habitats resulting from the 2000 RC with further larval and YOY sampling; and 3) To assess how well long-term seining data sets represent northern pike reproductive success in Rainy Lake and Namakan Reservoir by comparing catch rate and efficiency of light-trapping and seining methods.

V. METHODS

Study area.- Rainy, Kabetogama, and Namakan Lakes are located on or near the border between Minnesota and Ontario and are the three lakes investigated as a part of this study. Rainy Lake has a surface area of 92,110 ha, Kabetogama Lake has a surface area of 10,425 ha, and Namakan Lake has a surface area of 10,170 (Kallemeyn et al. 2003) (Figure 1). Larval northern pike sampling was conducted in Rainy and Kabetogama Lakes, which were also sampled

historically since 2004, and YOY northern pike sampling was conducted in Rainy, Kabetogama, and Namakan Lakes to expand the number of sample sites.

Site selection and sample strategy.-Site selection was based on previously-known northern pike spawning areas within Rainy Lake and Namakan Reservoir (Figure 3) (Pierce et al. 2007b) and areas with preferred vegetation types documented in the literature: water bulrush, sedges, muskgrass, stonewort, milfoil sp., pondweed sp., coontail, and common waterweed (Cook and Bergersen 1988; Anderson 1993; Pierce 2004; Pierce et al. 2007a). In addition, we chose our sampling sites based on proximity to spawning areas as an important quality of YOY northern pike nursery habitat, along with the presence of relatively dense submergent and emergent aquatic plants (Casselman and Lewis 1996). Water levels affecting spring habitat for fish, particularly in the shallow waters we sampled, are regulated by IJC RCs and controlled by dams at outlets from each of the reservoir systems.

We sampled eleven sites per year for larval northern pike among six locations in Rainy Lake and seven locations in Kabetogama Lake (Figure 4), with Bowman and Cranberry Bays only sampled in 2012 and Kraus and Tilson Bays only sampled in 2013. Our sampling was stratified randomly throughout depths where aquatic macrophytes were available for spawning and nursery habitat. Depths in spawning habitat ranged from 0.15 to 1.0 meter, and depths in nursery habitat ranged from 0.6 to 2.0 meters. We sampled twelve sites for YOY northern pike in Rainy Lake, nine sites in Kabetogama Lake, and four sites in Namakan Lake (Figure 5).

Larval sampling.-Sampling for northern pike larvae was conducted in the spring directly after ice-out on Rainy Lake and Kabetogama Lake using light traps. From historic and recent sampling of larval northern pike in Rainy Lake and Kabetogama Lake, 2004 to 2013, the earliest date in which larval northern pike were sampled was April 26, 2010, and the latest sample was collected on June 11, 2013.

The quatrefoil light traps featured a 6-mm entrance slot and light-emitting diodes (LED lights) powered by dry-cell batteries. This light-trap design was modified from the Killgore (1991) design to a 6-mm entrance width, which was larger than the 5-mm entrance used by Zigler and Dewey (1995) in testing for phototaxis of larval northern pike. The LED lights were chosen over chemical light sticks because they emit a very consistent light intensity for the duration of each sampling period.

A night of larval northern pike sampling in each sample bay consisted of setting 18-20 light traps within representative dominant vegetation for two hours beginning at sunset. Light traps were floated from 1.2-m-long fiberglass stakes driven into bottom substrates in water 0.3 to 1.0 meters deep. We applied a stratified random sampling approach by setting light traps randomly throughout a variety of depths where aquatic macrophytes were available for northern pike spawning. Samples were stratified by depths where aquatic plant growth occurred because we

were investigating characteristics of the aquatic macrophyte community that related to larval northern pike production.

During April to May 2012, aquatic vegetation was accessible at depths up to 65 cm. During May to June 2013, aquatic vegetation was accessible at depths up to 1.0 meter. The light trap was suspended above the bottom to sample larval northern pike effectively, so 0.15 meter was the minimum for keeping the light trap above the sediment. Vegetation types at each light trap were classified according to the most abundant one or two species within 0.5 m of the light trap. Water temperature was recorded for each sampled bay, and water depth was recorded at each light-trap location. Northern pike larvae total counts and lengths (mm) for each light trap were recorded and compiled for each sampled bay (Pierce et al. 2007b). Electronic temperature loggers were set in Dove Bay, Rainy Lake and Sullivan Bay, Kabetogama Lake to record water temperatures throughout the northern pike spawning season from April to July.

YOY sampling.-Sampling for YOY northern pike using trap nets was conducted approximately one month after the last larval northern pike was sampled in Rainy, Kabetogama, and Namakan Lakes. From sampling of YOY northern pike in Rainy and Kabetogama Lakes, 2011 to 2013, the earliest date in which YOY northern pike were sampled was June 18, 2012, and the latest sample was collected on August 8, 2013.

Nursery habitat for northern pike is difficult to sample because of the shallow water and submerged vegetation (Bry 1996; Casselman and Lewis 1996). This study applied trap-netting methods to investigate YOY northern pike catch rate and to identify nursery areas. We applied a stratified random sampling approach by setting trap nets perpendicular to the shoreline, distributed randomly where aquatic macrophytes, regardless of species, were available for northern pike spawning. Samples were stratified by depths where aquatic plant growth occurred because we were investigating characteristics of the aquatic macrophyte community that related to larval northern pike production. The number of trap nets set (1-6) depended on the area of each vegetation type present. Trap nets were set late morning or afternoon and retrieved as close to 24 hours later as possible (Clark et al. 2007).

Sampling efficiency comparison for seining and light-trapping methods. – Minnesota DNR Fisheries, the United States Geological Survey, and Voyageurs National Park collected YOY northern pike seining data for Rainy Lake and Kabetogama Lake from 2004-2013. These data were compared to larval northern pike light trap data from Rod Pierce, 2004-2011, plus 2012-2013 field data to compare sampling efficiency for seining and light trapping methods. These datasets were also compared to identify years with higher reproductive success. This comparison needs to take into account natural high annual variation in larval northern pike counts, which has been observed in Dove Bay, an indicator bay of Rainy Lake and Sullivan Bay, an indicator bay of Kabetogama Lake (Figure 6 and 7).

I. STATISTICAL ANALYSIS AND MODELING

Hydrological model and reproductive success for 1970 and 2000 rule curves.-Aaron Thompson developed a hydrological model to show water-level conditions under the 1970 and 2000 RCs up to 2012, accounting for annual variation and outflows from the Rainy River, Squirrel Falls, and Kettle Falls dams. Modeled water-level quarterly values for April to August under the 1970 and 2000 RCs were compared to 1986-2012 annual YOY seine mean catch rates from the Minnesota DNR long-term seining dataset and 2004-2012 larval light trap mean catch rates to identify correlations between annual mean catch rates and monthly water level conditions. Hydrographs for April to August water levels were plotted with mean catches for YOY seine data, 1986-2012, and larval light trap data, 2000-2012, to identify relationships between water level conditions and mean catch. This analysis was done separately for Rainy Lake RC conditions and Namakan Reservoir RC conditions (Kabetogama and Namakan Lakes).

We applied nonparametric one-way ANOVA, Wilcoxon two-sample tests, and Kruskal-Wallis tests to identify differences in YOY northern pike mean catches for years when 1970 RC conditions were in effect (1986-1999) to mean catches for years when 2000 RC conditions were in effect (2000-2012). We also applied Peterson correlation analysis techniques to identify relationships between mean catch and mean water levels in April, May, June, July, and August for each year under the 1970 and 2000 RC conditions. Historic larval pike sample data from 2004 to 2012 were compared to modeled monthly water-level conditions to identify potential correlations between water level and mean catch rates as well.

Mixed effects model and aquatic vegetation effects on northern pike larval count.-We developed a mixed effects multivariate regression model of larval northern pike count data among the eleven bays sampled during the 2012 field season. For the 2013 larval northern pike count data in each of the eleven bays, we conducted a non-parametric one-way ANOVA, comparing counts from light traps set in aquatic vegetation (122 light traps) to the light traps set in no vegetation (106 light traps). Wilcoxon sign-rank tests for non-normalized data were used to look for significant differences in catch rates between locations where aquatic vegetation was present and locations where aquatic vegetation was not present.

Patchy fish distribution data, such as our counts of larval and YOY fish abundance, often have large proportions of zeros that cause skewed distributions that are non-normal and do not fit standard models such as the Poisson distribution for count data (Heilbron 1994; Martin et al. 2005). Alternatively, models such as the zero-inflated Poisson (ZIP), negative binomial Poisson, zero-inflated negative binomial (ZINB), and the negative binomial hurdle model have been developed to accommodate datasets with large proportions of zeros (Hall 2000; Martin et al. 2005; Warton 2005; Miller 2007). All of these models can accommodate both random and fixed effects, and negative binomial distributions are probability based, with zero-inflation referring to

the probability of generating a zero (Hall 2000). Mullahy (1986) and King (1989) developed the hurdle probability model where a certain probability of a non-zero count allows the “hurdle” to be crossed (Cameron and Trivedi 1998). Zero-inflated poisson distributions are best for datasets with lower proportions of zeros (0.10 to 0.25); negative binomial poisson models can be used for datasets where variance is greater than the mean and the proportion of zeros is 0.50 to 0.75; and negative binomial hurdle models work best for datasets where variance is greater than the mean and where the proportion of zeros is between 0.75 and 0.90 (Hall 2000; Miller 2007).

Our study fit negative binomial Poisson, zero-inflated Poisson (ZIP), zero-inflated negative binomial (ZINB), and negative binomial hurdle models using the FMM procedure for Finite Mixture Models in SAS 9.3 (SAS Institute Inc. 2011) to determine significant variables related to larval northern pike counts. Model selection was determined using Akaike’s information criterion (AIC) for each model run (Burnham and Anderson 2002). The following variables were included in models for the 2012 larval pike data set: water temperature, water elevation, bay, presence of hybrid cattail (*Typha x glauca*), presence of sedge, presence of wild rice (*Zizania palustris*), and presence of burreed. *Typha x glauca* is a combination of hybrids between *Typha latifolia* and *Typha angustifolia*, and previous research in Voyageurs National Park documents the hybrid as the dominant species at sites in Rainy and Kabetogama Lakes (Travis et al. 2010). Therefore, for the purpose of this study, we will refer to the hybrid cattail throughout. These four plant classifications were the most abundant among light-trap sampling locations. In these models, the vegetation variables (presence of hybrid cattail, presence of sedge, presence of wild rice, and presence of burreed) were considered fixed effects, and water elevation was considered a covariate.

Statistical analysis and mixed effects models of northern pike YOY count and length.-Our study also fit negative binomial Poisson, zero-inflated Poisson (ZIP), zero-inflated negative binomial (ZINB), and negative binomial hurdle models using the FMM procedure for Finite Mixture Models in SAS 9.3 (SAS Institute Inc. 2011) to determine significant variables related to YOY northern pike counts for the 2012 and 2013 field seasons. The following variables were included in the YOY models: aquatic plant species, water depth, and water temperature.

Based on frequency analysis of the most abundant aquatic plant species in 2012, presence for the following aquatic plant species was included in preliminary mixed effects models to identify significant variables related to YOY northern pike count data: hybrid cattail, pondweed spp., wild rice, coontail, water lily (*Nymphaea* spp.), arrowhead (*Sagittaria* spp.), sedge spp., common bladderwort (*Utricularia macrorhiza*), and northern water milfoil (*Myriophyllum sibiricum*). Based on frequency analysis of the most abundant aquatic plant species in 2013, presence for the following aquatic plant species was included in preliminary mixed effects models for analysis of 2013 data: hybrid cattail, pondweed spp., coontail, arrowhead spp.,

common waterweed, water marigold (*Bidens beckii*), water celery (*Vallisneria americana*), floating-leaf burreed (*Sparganium fluctuans*), water lily spp., and northern water milfoil. Once significant aquatic plant presence variables were determined, final models were developed for all count and plant presence data for all years, for 2012 data only, for 2013 data only, and separated for Kabetogama Lake and Rainy Lake due to differences in the presence of aquatic plant species in the littoral community. For example, floating-leaf burreed, common burreed (*Sparganium eurycarpum*), and wild rice were most frequent in the aquatic plant community in Rainy Lake but were not among the most frequent in the aquatic plant community in Kabetogama Lake. Mixed effects models were also developed for 2012 and 2013 counts of YOY northern pike in relation percentages of emergent, submerged, and floating aquatic plant species in the littoral zone aquatic plant community.

Finite mixture model analysis was used to identify relationships among YOY northern pike count, temperature, depth, percent cover, and stem density. Because YOY northern pike length could be used as an indicator of growth over time, we also developed mixed effects models of temperature, depth, percent cover, and stem density related to minimum, maximum, and mean length of captured YOY northern pike. To identify specific temperatures and depths related to YOY northern pike counts, we applied mixed model analysis and the Tukey adjusted LS-Means procedure to analyze differences in count according to various ranges of temperatures and depths. We used Pearson correlation analysis to identify correlations between temperature, depth, percent cover, and stem density to identify the most significant relationships to include in mixed models. We also developed mixed effects models that included temperature, depth, and aquatic plant presence to identify aquatic plant species that may only be present in specific temperature or depth categories. These model results could be used to try to separate significant relationships between YOY northern pike count and temperature/depth from aquatic plant species presence.

Sampling efficiency comparison for seining and light-trapping methods.-Sampling efficiency comparisons are most useful when comparing long-term datasets for the same years that can accommodate natural variation in counts that result from annual variation in populations outside of catchability of present individuals (Pierce et al 2006; Pierce et al. 2007b). Long-term larval northern pike datasets were available for Rainy Lake and Kabetogama Lake, 2004-2011 (Rod Pierce, personal communication, May 2011), in addition to 2012-2013 field season data, which included water level, number of days after ice-out, light-trap catch numbers, water temperature, and vegetation type. In addition, Minnesota DNR long-term seining data for YOY northern pike were available for 2004-2013.

To test for differences in catch rates among sample methods, light-trapping and seining mean catch rate datasets for 2004-2013 were compared by using a non-parametric one-way

ANOVA for non-normal data distributions (Pierce et al. 2007b). This comparison of data collected using different methods was used to investigate how indicative the long-term YOY seining method in non-vegetated areas was in comparison to larval light-trap in aquatic vegetation over time. Robust sample sizes over many years, comparisons between light trap and seine catches by year, and the presence of YOY northern pike in seines may indicate reproductive success over time.

VII. RESULTS

Objective 1: To determine if northern pike spawning and nursery habitat and reproductive success have changed due to the 2000 Rule Curve.

Kabetogama Lake.-Under 1970 RC conditions for Kabetogama Lake, the highest mean catch rate, 0.41 YOY northern pike per seine haul, corresponds to the highest monthly mean water levels in May and June in 1996, for all years, 1986 to 1999 (Figure 8), when the water level was above the 1970 RC from the end of April to the beginning of June (Figure 9). Under the 2000 RC conditions in Kabetogama Lake, the high mean catch rates of 0.63 in 2001 and 0.72 in 2008 correspond to the highest monthly mean water levels in May and June (Figure 10). The highest mean catch value for 2000-2012 was 0.72, when water levels were above the 2000 RC throughout May and into June (Figure 11).

Kabetogama Lake seine YOY mean annual catches were significantly higher under the 2000 RC conditions when compared to the 1970 RC conditions (Wilcoxon rank sum, normal approximation, $Z = 3.73$, $P < 0.0001$; Kruskal-Wallis test, $P > 0.0002$). Pearson correlation analysis identified significant positive correlations between annual mean catch and May water levels ($r = 0.51$, $P > 0.04$) and June water levels ($r = 0.52$, $P > 0.030$) under 1970 RC conditions in Kabetogama Lake. Pearson correlation analysis also identified significant positive correlations between annual mean catch and May water levels ($r = 0.69$, $P > 0.01$) and June water levels ($r = 0.72$, $P > 0.01$) under 2000 RC conditions in Kabetogama Lake.

Rainy Lake.-Under the 1970 RC conditions for Rainy Lake, the highest mean catch rate, 0.38 YOY northern pike per seine haul, corresponds to the highest monthly mean water levels in May and June in 1996, for all years, 1986 to 1999 (Figure 12), when the water level was above the 1970 RC throughout May and into the beginning of June (Figure 13). Under the 2000 RC conditions in Rainy Lake, the high mean catch rates of 0.28 in 2001 correspond to the highest monthly mean water levels in May and June (Figure 14), when the water level was above the 2000 RC throughout May and June (Figure 15).

Rainy Lake seine YOY mean annual catches were significantly higher under the 2000 RC conditions when compared to the 1970 RC conditions (Wilcoxon rank sum, normal approximation, $Z = 1.69$, $P < 0.05$). Pearson correlation analysis identified no significant correlations between annual mean catch and April to August monthly mean water levels under

1970 RC conditions in Rainy Lake. Pearson correlation analysis did identify significant positive correlations between annual mean catch and April mean monthly water levels ($r = 0.61$, $P > 0.03$) and May mean monthly water levels ($r = 0.59$, $P > 0.03$) under 2000 RC conditions in Rainy Lake.

Pearson correlation analysis did not identify a significant positive relationship between daily water level and mean light-trap catch for larval northern pike mean catch data from 2004 to 2013 in Dove Bay, Rainy Lake or Sullivan Bay, Kabetogama Lake. Despite no significant relationship and annual variation in mean catches, there appears to be higher larval northern pike catch rates in Dove Bay, a representative bay for Rainy Lake, at water levels ≥ 337.4 m (Figure 6) and in Sullivan Bay, a representative bay for Kabetogama Lake, at water levels ≥ 340.4 m (Figure 7) (Rodney Pierce, personal communication, November 16, 2011).

Plots of Rainy Lake mean larval northern pike catch and monthly mean water levels for 2000 Rule Curve years, 2000-2012, show that the highest mean catch rate for 2000-2012 data was 0.55 per light trap in 2008, which corresponds to the highest monthly mean water levels for May and June (Figure 16). The mean monthly May water level that corresponds to the highest mean larval catches in Rainy Lake, 2000 to 2012, is at or above 337.4 m, which is consistent with the higher larval northern pike catch rates observed at similar water levels in Dove Bay, Rainy Lake (Figure 6).

Plots of Kabetogama Lake mean larval northern pike catch and monthly mean water levels for 2000 Rule Curve years, 2000-2012, show that the highest mean catch rate for 2000-2012 data was 1.10 per light trap in 2011, which corresponds to high monthly mean water levels for May and June. The second highest mean catch rate was 1.07 per light trap in 2008, which corresponds to the highest monthly mean water level for May and June for all years (Figure 17). The mean monthly May water level that corresponds to the highest mean larval catches in Kabetogama Lake, 2000 to 2012, is at or above 340.4 m, which is consistent with the higher larval northern pike catch rates at similar water levels observed in Sullivan Bay, Kabetogama Lake (Figure 7).

Objective 2: To verify that larval and YOY northern pike are using predicted improved spawning and nursery habitats resulting from the 2000 rule curve with further larval and YOY sampling.

Field data results

Trap-net YOY data from 2011 field season.-Trap-net data were collected from July 26-28, 2011 and compiled into a database for one bay in Rainy Lake, four bays in Kabetogama Lake, and one bay in Namakan Lake. The total count of sampled YOY northern pike in 2011 was 75 from 30 trap-net samples for an overall mean catch of 2.5 YOY northern pike per trap net. Mean

number per trap net ranged from 1 to 6 and lengths of YOY northern pike ranged from 99 to 173 mm (Table 1).

Light-trap larval data from 2012 field season.-Due to a warm spring and early ice-out, light-trap sampling began on April 23, but larval northern pike were not caught until May 8-16, 2012. Light-trap data were collected for four bays in Rainy Lake and seven bays in Kabetogama Lake (Figure 4). Data collected included number of larval northern pike, lengths of larval northern pike, GPS location, water depth, water temperature, and aquatic vegetation from 18-20 trap nets for each bay. The total count of sampled larval northern pike in 2012 was 164 from 210 light-trap samples for an overall mean catch of 0.78 larval northern pike per light trap.

In 2012, aquatic plants present most often were hybrid cattail (83 light traps); floating-leaf burreed and common burreed (37 light traps); sedge spp. (19 light traps); and wild rice (12 light traps) (Table 2). Other important aquatic plant habitat for larval northern pike included common waterweed in Blind Ash Bay, Kabetogama Lake and northern water milfoil (*Myriophyllum sibiricum*) in Jackfish Bay, Rainy Lake. Light traps with the greatest numbers of sampled larval northern pike were found in microhabitats with hybrid cattail (48%), burreed spp. (16%), burreed/hybrid cattail (11%), common waterweed (11%), sedge (4%), and cattail/common waterweed (4%). The other category included plant categories with less than 3 light-trap samples: common bladderwort, common bladderwort/northern water milfoil, common waterweed/northern water milfoil, horsetail (*Equisetum* sp.), northern water milfoil/sedge, and sedge/wild rice (Table 2).

During April and May, these plant types were available in different growth stages, although most were in the form of newly emerging green shoots such as those of burreed, wild rice, and sedges. In contrast to newly emerging plant materials, hybrid cattails were available mainly as dried-up stalks from the previous summer, and wild rice was also often evident as remnants from the previous year. Of interest was the observation that while emergent forms of vegetation had the highest overall counts of larval northern pike (hybrid cattail, 79; burreed, 26; and burreed/hybrid cattail, 18), the highest mean catch rate (count/# light traps per plant category) was found in submerged common waterweed (mean catch rate of 6 per light trap; Table 2).

Catches of zero larval northern pike were common for light trapping in the various plant categories. Frequent occurrences of catch rates of zero indicate patchy distributions of the larval northern pike and illustrate the difficulty of sampling larval fish that were only 10-35 mm total length in such large aquatic systems. More zero values in one year compared to other years may also indicate lower recruitment of larval northern pike in that year. The percentage of zero catches of larval northern pike for all eleven bays sampled in 2012 was 68% (143 out of 210

records). The percentage of zero catches for the top four aquatic plant categories were 63% for hybrid cattail, 68% for burreed spp., 68% for sedge spp., and 75% for wild rice (Table 3).

Trap-net YOY data from 2012 field season.-Trap-net data were collected from June 11-August 10, 2012 and compiled into a database for eight bays in Rainy Lake, six bays in Kabetogama Lake, and two bays in Namakan Lake, for a total of 16 bays and 155 trap-net samples (Figure 5). Data collected at each trap-net location included GPS, water depth, water temperature, aquatic macrophyte species presence, YOY counts and lengths, and other fish and crayfish species and numbers.

The total count of sampled YOY northern pike in 2012 was 52 from 155 trap-net samples for an overall mean catch of 0.34 YOY northern pike per trap net. Overall sizes of YOY northern pike ranged from 71.1 to 183 mm. The top ten most frequently occurring aquatic plant species in 16 bays where trap-net data were collected included hybrid cattail, submerged pondweeds, wild rice, coontail, water celery, water lily spp., arrowhead spp., floating-leaf burreed, floating-leaf pondweed, and common burreed (Table 4). Aquatic plant stem density data were collected for seven bays total, for a total of 25 sample sites where trap-net data were collected. The number of sample sites was too small to make statistically-valid comparisons between Rainy and Kabetogama Lakes, with only three bays in Rainy Lake and four bays in Kabetogama Lake. Therefore, mean aquatic plant stem density overall for the 25 sample sites was 29 stems / meter and mean aquatic plant percent cover was 26% or moderate cover.

Light-trap larval data from 2013 field season.-Light-trap data were collected May 28-June 11, 2013 and compiled into a database for 11 bays, including five bays in Rainy Lake and six bays in Kabetogama Lake (Figure 4). Data collected included number of larval northern pike, lengths of larval northern pike, GPS location, water depth, water temperature, and aquatic vegetation from 18-20 trap nets for each bay. The total count of sampled larval northern pike in 2013 was 22 from 228 light-trap samples for an overall mean catch of 0.10 larval northern pike per light trap.

Trap-net YOY data from 2013 field season.-Trap-net data were collected from June 19-August 7, 2013 and compiled into a database for the nine bays in Rainy Lake, nine bays in Kabetogama Lake, and three bays in Namakan Lake with a total of 137 trap-net samples (Figure 5). Data collected at each trap-net site included GPS location, water depth, temperature, conductivity, aquatic macrophyte species presence, percent cover, and stem density. Also collected were fish species counts, lengths and weights of northern pike, lengths of yellow perch (*Perca flavescens*), sunfish species (*Lepomis* spp.), and black crappie (*Pomoxis nigromaculatus*), as well as crayfish species and numbers.

The total count of sampled YOY northern pike in 2013 was 62 from 137 trap-net samples for an overall mean catch of 0.45 YOY northern pike per trap net. Overall sizes of YOY

northern pike ranged from 76 to 161 mm. The top ten most frequently occurring aquatic plant species in the 21 bays where trap-net data were collected in 2013 included hybrid cattail, submerged pondweeds, coontail, arrowhead, common waterweed, water marigold, water celery, floating-leaf pondweed, water lily spp., and northern water milfoil (Table 4). The overall mean stem density of aquatic plants in all 21 sampled bays, with a total of 137 trap-net sites was 34 stems per meter, and the overall mean percent cover of aquatic plants in all bays was 52%.

Comparing results across years for Rainy, Kabetogama, and Namakan Lakes.- For the 2012 and 2013 field seasons, total larval northern pike count, mean number per bay, and mean number per light trap were all greater in Kabetogama Lake in comparison to Rainy Lake (Table 5). YOY northern pike count, mean number per bay, and mean number per trap net were all greater in 2012 when compared to 2013. In addition, YOY northern pike count, mean number per bay, and mean number per trap net were all greater in Rainy Lake when compared to Kabetogama Lake in 2012, with these values being very similar in 2013 (Table 6). Counts of YOY northern pike were low in Namakan Lake for both 2012 and 2013.

In 2013, aquatic plant percent cover and stem density data were collected at each trap-net location at nine bays in Rainy Lake, nine bays in Kabetogama Lake, and three bays in Namakan Lake. For the 78 sample locations in Kabetogama and Namakan Lakes, the mean stem density was 34 stems per meter, and the mean percent cover was 50%. For the 59 sample locations in Rainy Lake, the mean stem density was 31 stems per meter, and the mean percent cover was 56%.

Statistics and modeling

Mixed model results for 2012 and 2013 larval northern pike data.- Preliminary analysis of the 2012 larval northern pike dataset using the FMM procedure for Finite Mixture Models in SAS 9.3 (SAS Institute Inc. 2011) eliminated bay, lake, and water temperature as significant variables. Across all of the eleven 2012 sample sites, water level and the presence of hybrid cattail seemed to have important influences on catches of larval northern pike. Final models for the compiled 2012 dataset (with all eleven bays) included the following parameters: water level, presence of hybrid cattail, presence of sedge, presence of wild rice, and presence of burreed. The model with the lowest AIC was the negative binomial with water level and hybrid cattail as significant variables, (Table 7) and estimated model parameters were:

Catch rate, hybrid cattail present = $-88.1260 + 0.2602 \text{ water level} - 0.6350 \text{ hybrid cattail}$

Catch rate, hybrid cattail absent = $-88.1260 + 0.2602 \text{ water level} + 0 \text{ hybrid cattail}$

We applied known water elevations for our light trap sample sites to the estimated model and produced predicted catch rate results. Predicted catch rates (number of fish per light trap) from the above models were higher for all combined sample sites with hybrid cattail absent (mean catch rate of 0.97) when compared to sample sites with hybrid cattail present (mean catch

rate of 0.60). Higher predicted catch rates were also higher where hybrid cattail was absent when analysis was separated for Kabetogama and Rainy Lakes (Figure 18). In addition, Wilcoxon sign-rank tests for non-normal data identified a significant difference in 2013 larval northern pike catch rates between locations where aquatic vegetation was present (mean catch rate: 0.13 ± 0.03 SE) and locations where aquatic vegetation was absent (mean catch rate: 0.06 ± 0.03) (Wilcoxon rank sum, $P < 0.003$).

Mixed effects model results for YOY northern pike count and length data.-Finite mixture model analysis to predict YOY northern pike count for all lakes included water depth, water temperature, and presence of aquatic plants as variables in the model. Analysis for 2012 data (155 samples) identified water temperature ($P > 0.0001$), presence of water lily spp. ($P > 0.003$), and presence of arrowhead spp. ($P > 0.0003$; AIC=306.3) as the most predictive variables. The best fit finite mixture model for 2013 YOY northern pike count data (159 samples) from all lakes included water temperature ($P > 0.05$), presence of water celery ($P > 0.008$), and presence of common bladderwort ($P > 0.0002$; AIC=231.7). Finite mixture model analysis to predict YOY northern pike count for sites where aquatic plant percent cover and stem density data were collected included water depth, water temperature, percent cover, and stem density as variables. Best fit finite mixture models (AIC = 273.2) included stem density ($P > 0.02$) and percent cover ($P < 0.0001$) as significant variables related to YOY northern pike count.

When finite mixture model analysis to predict YOY northern pike count was separated according to lake, the best fit finite mixture model (AIC = 163.4) for 2012 YOY northern pike count data in Rainy Lake (74 samples) included water temperature ($P < 0.0001$) and presence of coontail ($P > 0.01$). The best fit finite mixture model (AIC = 111.0) for 2013 YOY northern pike count data in Rainy Lake (59 samples) only included temperature ($P > 0.01$) and no aquatic plants. The best fit finite mixture model (AIC = 148.3) for 2012 YOY northern pike count data in Kabetogama and Namakan Lakes (75 samples) included water temperature ($P > 0.001$), presence of water lily spp. ($P > 0.02$), presence of arrowhead spp. ($P > 0.02$), and presence of common bladderwort ($P > 0.009$). The best fit model (AIC=118.9) for 2013 YOY count data in Kabetogama and Namakan Lakes (78 trap-net samples) included depth ($P > 0.002$), presence of common waterweed ($P > 0.016$), presence of water celery ($P > 0.002$), and presence of common bladderwort ($P > 0.015$).

Finite mixture model analysis using the 2013 YOY trap-net sample data for 44 YOY northern pike from both Rainy and Kabetogama Lakes identified water temperature as a significant variable related to minimum length ($P > 0.002$), maximum length ($P > 0.002$), and mean length ($P < 0.0001$). Given this significant relationship between YOY northern pike length and water temperature, we determined three temperature categories for 2012 and four

temperature categories for 2013 based on the overall range of temperatures recorded during field sampling to analyze relationships between specific temperatures and YOY northern pike count.

Best fit finite mixture model analysis identified a significant relationship between YOY northern pike count and temperature for 2012 data ($P > 0.016$) and 2013 data ($P > 0.05$). In addition, LS means analysis identified a significant difference in YOY northern pike count between temperature category 1 (≥ 16.0 and ≤ 21.0 °C) and 3 (≥ 25.1 and ≤ 30.0 °C) ($P > 0.01$) for 2012 data, between temperature category 1 (≥ 18.0 and ≤ 20.0 °C) and 4 (≥ 24.6 and ≤ 29.0 °C) ($P > 0.01$) for 2013 data, and between 2 (≥ 20.1 and ≤ 22.0 °C) and 4 (≥ 24.6 and ≤ 29.0 °C) ($P > 0.03$) for 2013 data. For each of these significant differences, higher YOY northern pike count was associated with the higher temperature category.

Objective 3: To assess how well long-term seining data sets represent northern pike reproductive success in Rainy Lake and Namakan Reservoir by comparing catch rates of light-trapping and seining methods.

Sampling efficiency comparison for seining and light-trapping methods. – In Rainy Lake, 2004 to 2013, mean light-trap catch rates varied from 0.00 in 2007 to 0.55 in 2008, and mean seine catch rates ranged from 0.00 in 2007 and 2008 to 0.19 in 2004. The overall mean catch rate for Rainy Lake light-trap data was 0.23 ± 0.07 , and the overall mean catch rate for Rainy Lake seine data was 0.08 ± 0.02 (Figure 19). In Kabetogama Lake, 2004 to 2013, mean light-trap catch rates varied from 0.01 in 2006 to 1.10 in 2011, and mean seine catch rates ranged from 0.03 in 2007 to 0.72 in 2008. The overall mean catch rate for Kabetogama Lake light-trap data was 0.42 ± 0.15 , and the overall mean catch rate for Kabetogama Lake seine data was 0.26 ± 0.07 (Figure 20).

Rainy Lake light-trap mean catches were higher overall when compared to seine mean catches from 2004 to 2013 (Figure 19). However, Rainy Lake light-trap larval mean catches were not significantly different from seine YOY mean catches for 2004 to 2013 (Wilcoxon rank sum, normal approximation, $Z = 0.69$, $P < 0.25$). In addition, Pearson correlation analysis did not identify a significant correlation between seine and light-trap mean catch values for 2004 to 2013 ($r = 0.31$, $P > 0.18$). Kabetogama Lake light-trap mean catches were higher overall when compared to seine mean catches from 2004 to 2013 (Figure 20). However, Kabetogama Lake light-trap larval catches were also not significantly different from seine YOY mean catches for 2004 to 2013 (Wilcoxon rank sum, normal approximation, $Z = 0.19$, $P < 0.43$). In addition, Pearson correlation analysis did not identify a significant correlation between seine and light-trap mean catch values for 2004 to 2013 ($r = 0.22$, $P > 0.35$).

VIII. DISCUSSION

Northern pike spawning success in relation to water level.-The first objective of this study was to determine if northern pike spawning and nursery habitat and reproductive success have changed due to the 2000 RC. Mean water levels increased approximately 1 meter under the 2000 RC conditions in comparison to 1970 RC conditions in Kabetogama Lake. As a result, long-term Minnesota DNR YOY northern pike seining data were significantly higher for mean catches under 2000 RC conditions in comparison to mean catches under the 1970 RC conditions. Mean water levels did not increase under the 2000 RC conditions in Rainy Lake compared to the 1970 RC conditions to a similar degree as Kabetogama Lake. As a result, significant differences in mean catches under 2000 RC conditions were not as significant in comparison to mean catches under the 1970 RC conditions. Highest mean catch rates for YOY northern pike in seines corresponded to years with the highest monthly mean water levels in May and June under both 1970 RC and 2000 RC conditions for all sampled lakes. These high mean catches were years when water levels were out of the RC in May and June, specifically above 341.0 m in Kabetogama Lake and 338.0 m in Rainy Lake.

Daily water level was identified as a significant predictive variable for larval pike count according to our finite mixture model analysis. Water-level changes have caused increases in percent coverage of cattail over time, as documented by the 155-241% increase of cattail in a study conducted in the St. Lawrence River (Cooper et al. 2008). Our predictive model results showed a reduced catch rate of larval pike where hybrid cattail was present. Water-level regulations may have their greatest influence on larval northern pike through the quality of vegetation available in shallow water during nursery periods. Despite results from our predictive larval northern pike model, correlation analysis did not identify a significant positive relationship between daily water level and larval mean catch rate from 2004-2013 long-term light-trap sampling data. Data from targeted larval sampling and plots of monthly mean water levels in relation to larval catch suggest higher mean catches when water levels are ≥ 337.4 m in Dove Bay, Rainy Lake and ≥ 340.4 m in Sullivan Bay, Kabetogama Lake.

Larval habitat and aquatic vegetation in Rainy, Kabetogama, and Namakan Lakes.-The second objective of this study was to verify that larval and YOY northern pike were using currently available spawning and nursery habitats resulting from improved habitat conditions under 2000 RCs conditions for all sampled lakes. The presence of larval northern pike was documented in 13 bays throughout Rainy and Kabetogama Lakes as a result of this study. This study contributes to the limited amount of information available on types of aquatic vegetation used as spawning and nursery habitat in natural systems by larval northern pike. One of the few other studies to sample larval northern pike in natural and constructed wetlands was conducted by Morrow et al. (1997) in Conesus Lake, New York. In this study, larval northern pike used

cattails, willows (*Salix* spp.), buttonbush (*Cephalanthus occidentalis*), and reed canary grass (*Phalaris arundinacea*). Franklin and Smith (1963) identified vegetation used by larval northern pike adjacent to Lake George, Minnesota, including cattails, sedges, reed canary grass, smartweed (*Persicaria hydropiper*), arrowhead, and spikerush (*Eleocharis ovate*).

Results from this study showed that larval northern pike used habitat associated with several different aquatic plant forms, including hybrid cattail stands, sedges, burreed spp., and wild rice. Results also showed a significantly higher catch rate of larval northern pike from light-trap locations where aquatic vegetation was present compared to light-trap locations where aquatic vegetation was absent. Larval northern pike catch numbers were the highest for hybrid cattail in both Rainy and Kabetogama Lakes, as a reflection of the dominance of hybrid cattail as available spawning habitat. This hybrid cattail dominance is most likely why it was a significant explanatory variable for modeling larval catches. However, hybrid cattail did not have the highest mean catch rate overall in comparison to submerged aquatic plant species, and the predictive models with hybrid cattail present had lower counts overall.

Our results contradicted previous research by Franklin and Smith (1963) that documented northern pike avoidance of cattail for spawning. It also contradicted research by Farrell (2001) that documented a decrease in northern pike spawning success as a result of less access to submerged aquatic macrophytes as a result of an increase in the presence of cattail. In our study, the cattail dominated the habitat and reduced available areas for other submerged macrophytes to grow, but the cattail was exposed to water and was accessible for spawning throughout the system. The submerged macrophytes grew in the same depths as the cattail inside the outer ring of cattail that was the outer boundary of the littoral zone in our case, which was not the case in the Farrell (2001) and Cooper et al. (2008) studies.

Our sampling with light traps was directed toward aquatic plant species that were available in late April and May when larval northern pike are developing and when most aquatic plant species are only beginning to sprout or emerge. The aquatic plant species and structural forms encountered by larval northern pike suggest that they use nearly any vegetated cover available in early spring. Ultimately, the species of vegetation may not be as important as the physical quality or form of the vegetation in supplying feeding and hiding cover for larval northern pike.

YOY habitat and aquatic vegetation in Rainy, Kabetogama, and Namakan Lakes.-The presence of YOY northern pike was documented in 25 bays throughout the Rainy, Kabetogama, and Namakan Lakes as a result of our field sampling 2011-2013. The presence of aquatic vegetation was significant in relation to YOY northern pike count, with variation between year, lake, and bay for significant relationships between count and specific aquatic plant species. According to previous research by Meeker and Harris (2009), Namakan Reservoir had less

emergent and floating leaf vegetation, and changes in vegetative cover under 2000 RC conditions included increases in wild celery, burreed (*Sparganium* spp.), and variable pondweed (*Potamogeton gramineus*). According to results from this study, the presence of coontail was significant predictive variable for YOY northern pike count in Rainy Lake, whereas common waterweed, water celery, and common bladderwort were significant in Kabetogama Lake.

In relation to water temperature and water depth, this study documented significantly higher YOY northern pike counts and temperatures ≥ 25.1 and $\leq 30.0^{\circ}\text{C}$ in comparison to lower temperatures. This study also documented significantly higher YOY northern pike counts in relation to depths ≥ 0.50 and ≤ 0.90 meters compared to deeper water depths. Water temperature was the only significant variable related to YOY northern pike length when water depth, aquatic plant stem density, and aquatic plant percent cover were included in the analysis. These results are consistent with previous research that found that water depths occupied by northern pike throughout their first summer were highly correlated with the age and size of the fish, with the smallest fish found in the shallowest habitats (Casselman & Lewis 1996).

Sampling efficiency and value of long-term larval and YOY data sets.-The third objective of this study was to assess how well long-term seining data sets represent northern pike reproductive success in Rainy Lake and Namakan Reservoir by comparing catch rates of light-trapping and seining methods. Rainy and Kabetogama Lake light-trap mean catches were higher overall when compared to seine mean catches for data from 2004 to 2013; however, this relationship was not statistically significant. Years identified with higher mean catches for both light-trap and seining included 2004, 2009, and 2011 in Rainy Lake and 2004, 2008, 2011, and 2012 in Kabetogama Lake. Despite these consistently higher mean catches for both sample methods, no significantly positive correlation was identified between light-trap mean catches and seine mean catches for the 2004 to 2013 data. Comparisons of larval and YOY northern pike mean catch to mean monthly water levels from the Aaron Thompson model for 2000-2012 both showed that years where May and June water levels were high resulted in higher catches. Further analysis of duration and consistency of high water levels throughout May and June may reveal differences in effect for the larval and YOY northern pike stage, depending on timing of spawning after ice out and extent of aquatic plant community structure.

Principal challenges for larval and YOY northern pike sampling include natural annual variations in weather and environmental conditions that affect survival and catch for both sampling methods. Year-to-year annual variation in water level affects the nearshore aquatic macrophyte habitat available for larval and YOY northern pike. Spring weather patterns also affect ice-out dates and subsequent water temperatures that, in turn, seem to influence survival and growth of northern pike eggs and fry, which is directly related to survival and growth of YOY (Pierce et al. 2007b; Pierce 2012). The lack of significant correlation between larval and

YOY northern pike mean catches is likely a result of effects of this annual variation, in addition to a lack of consistent comparison between light-trap and seine methods. Seining is known to be less effective in aquatic vegetation where YOY northern pike are present, as seen by significant relationships between aquatic vegetation and YOY northern pike count in our study (Pierce et al. 2001). The long-term seining data used as part of the analysis for this study were collected from non-vegetated sites as a part of the MN DNR long-term seining data protocol, which may have resulted in underestimates of YOY northern pike counts.

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TABLES

Table 1. Young-of-the-year northern pike count, mean number per trap net, and size range (mm) per bay for 2011.

Sample location	Count	Mean # / trap net	Size range (mm)
Alder Creek Bay, Rainy Lake	36	6	99-133
Blind Ash Bay, Kabetogama Lake	15	3	117-170
Daley Bay, Kabetogama Lake	4	1	124-137
Long Slough, Kabetogama Lake	8	1	107-173
Johnson Bay, Namakan Lake	12	2	130-163

Table 2. Number of light-traps, total larval count, mean light-trap catch rate, and overall mean catch rate for all 15 plant categories, with samples in Rainy and Kabetogama Lakes combined. The total count of light traps was 210 and the total count of northern pike larvae was 164.

Plant category	# light traps	Count	Mean catch rate
<i>Typha x glauca</i>	83	79	0.95 ± 1.61
<i>Sparganium</i> spp.	37	26	0.70 ± 1.22
<i>Carex</i> spp.	19	6	0.32 ± 0.48
<i>Zizania palustris</i>	12	3	0.25 ± 0.45
<i>Sparganium</i> spp./ <i>Typha x glauca</i>	9	18	2.00 ± 3.28
<i>Myriophyllum sibiricum</i>	9	1	0.11 ± 0.33
<i>Potamogeton</i> sp.	7	0	0.00 ± 0.00
<i>Sparganium</i> spp./ <i>Carex</i> spp.	4	1	0.25 ± 0.50
<i>Typha x glauca</i> / <i>Carex</i> spp.	4	3	0.75 ± 1.50
<i>Schoenoplectus</i> spp.	3	0	0.00 ± 0.00
<i>Sparganium</i> spp./ <i>Myriophyllum sibiricum</i>	3	1	0.33 ± 0.58
<i>Sparganium</i> spp./ <i>Zizania palustris</i>	3	1	0.33 ± 0.58
<i>Typha x glauca</i> / <i>Elodea canadensis</i>	3	6	2.00 ± 1.00
<i>Elodea canadensis</i>	3	18	6.00 ± 4.36
Other (plant categories < 3 light traps)	11	1	0.09 ± 0.30
Mean ± SD:	14 ± 21	11 ± 21	0.94 ± 1.54

Table 3. Frequency (and percentage) of northern pike larvae present or absent among four of the most frequently sampled plant types, with samples in Rainy and Kabetogama Lakes combined. The frequency of larva present/absent represents the number of times out of the total samples for each aquatic plant that a larva is present or absent. The percentage of larva present/absent represents the percentage of times that a larva was present or absent.

Aquatic plant	Total samples	Frequency larva present	Frequency larva absent
<i>Typha x glauca</i>	83	31 (37%)	52 (63%)
<i>Sparganium</i> spp.	37	12 (32%)	25 (68%)
<i>Carex</i> spp.	19	6 (32%)	13 (68%)
<i>Zizania palustris</i>	12	3 (27%)	9 (75%)
Mean ±SD:	38±32	13±13	25±19

Table 4. The ten most common aquatic plants species sampled in 2012 and 2013, expressed as the frequency of occurrence for 155 aquatic plant survey locations in 2012 and frequency of occurrence for 159 aquatic plant survey locations in 2013.

Aquatic plant species	2012 Frequency	2013 Frequency
hybrid cattail (<i>Typha x glauca</i>)	0.85	0.80
submerged pondweeds (<i>Potamogeton</i> spp.)	0.61	0.64
wild rice (<i>Zizania palustris</i>)	0.52	0.32
coontail (<i>Ceratophyllum demersum</i>)	0.45	0.55
water celery (<i>Vallisneria americana</i>)	0.43	0.49
water lily (<i>Nymphaea</i> spp.)	0.32	0.38
arrowhead (<i>Sagittaria</i> spp.)	0.26	0.53
floating-leaf burreed (<i>Sparganium fluctuans</i>)	0.21	0.39
floating-leaf pondweed (<i>Potamogeton natans</i>)	0.18	0.03
common burreed (<i>Sparganium eurycarpum</i>)	0.17	0.01
common waterweed (<i>Elodea canadensis</i>)	0.13	0.50
water marigold (<i>Bidens beckii</i>)	0.02	0.50
northern water milfoil (<i>Myriophyllum sibiricum</i>)	0.15	0.37

Table 5. Light-trap results for 2012 and 2013, including count, mean number per bay, mean number per light trap, and size (mm) of larvae.

Year	Lake	# bays	Count	Mean #/ bay	Mean # / light trap	Size (mm)
2012	Rainy	4	20	5	0.26	12.7-18.9
2013	Rainy	5	6	1	0.06	14.0-29.7
2012	Kabetogama	7	144	21	1.1	10.3-22.8
2013	Kabetogama	6	16	2	0.12	13.8-36.3

Table 6. Young-of-the-year northern pike count, mean number per bay, mean number per trap net, and size (mm) per bay for 2012 and 2013.

Year	Lake	# bays	Count	Mean #/ bay	Mean # / trap net	Size (mm)
2012	Rainy	8	63	5.73	0.82	71.1-195.6
2013	Rainy	9	30	3.00	0.50	76-149
2012	Kabetogama	6	43	3.91	0.65	83.8-172.0
2013	Kabetogama	9	32	3.20	0.53	83-161
2012	Namakan	2	1	0.50	0.08	183.0
2013	Namakan	3	0	0	0	N/A

Table 7. Model comparisons for all 2012 sampled bays. Modeled parameters were water elevation, hybrid cattail, sedge, wild rice, and burreed.

Model	AIC	Significant parameters
Zero-inflated poisson	598.1	water elevation ($z = 3.74$, $P = 0.0002$) hybrid cattail ($z = -3.40$, $P = 0.0007$)
Negative binomial	484.0	water elevation ($z = 2.19$, $P = 0.0284$) hybrid cattail ($z = -2.06$, $P = 0.0398$)
Zero-inflated negative binomial	485.2	sedge ($z = 3.24$, $P = 0.0012$) wild rice ($z = 2.66$, $P = 0.0077$)
Negative binomial hurdle	486.3	none

FIGURES

Figure 1. The study area along the United States-Canada border with IJC regulated Kettle Falls, Squirrel Falls, and Rainy River Dams. Rainy Lake has a surface area of 92,110 hectares, Kabetogama Lake has a surface area of 10,425 hectares, and Namakan Lake has a surface area of 10,170 hectares.

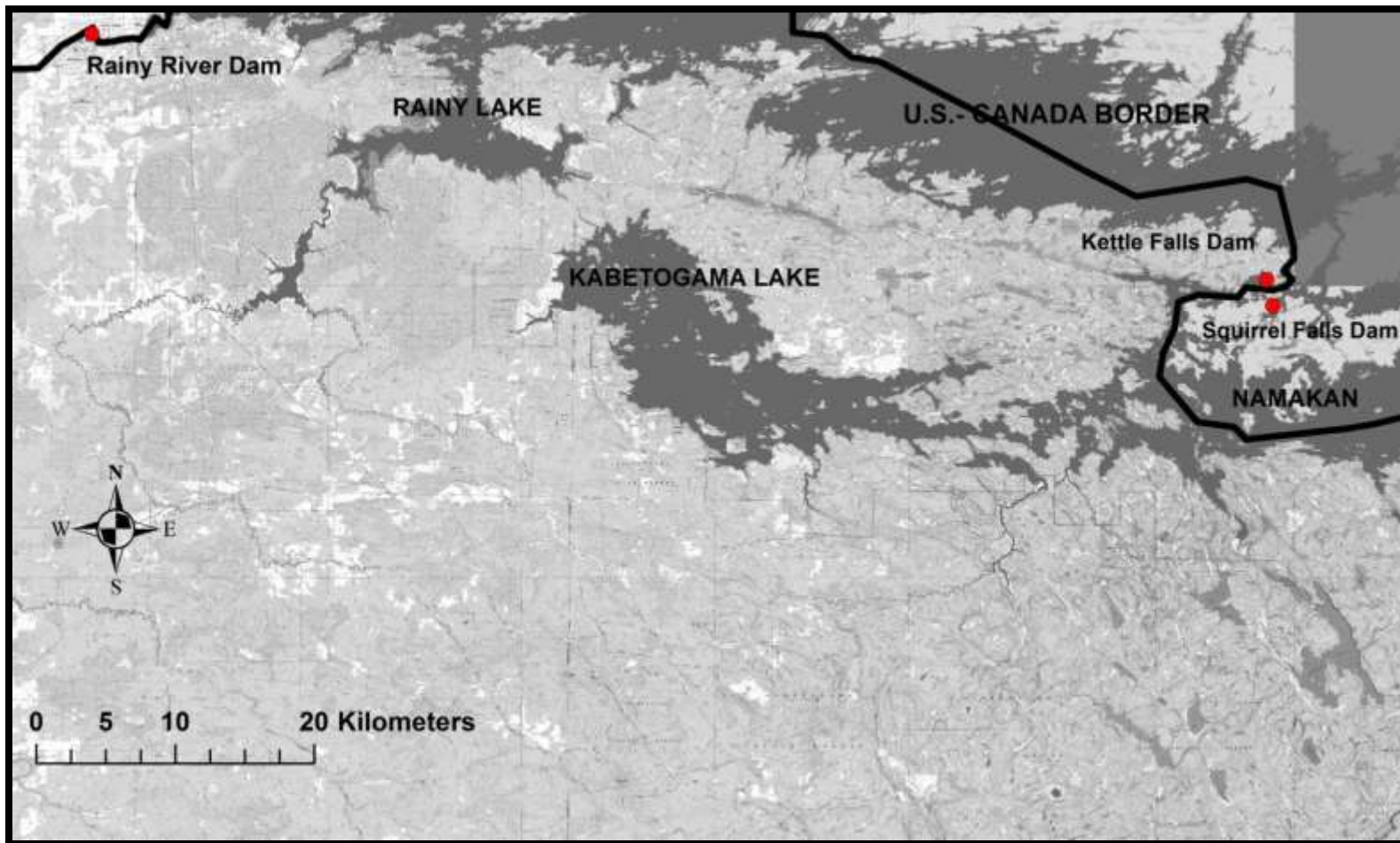


Figure 2. International Joint Commission 1970 and 2000 rule curves for Namakan and Rainy Lakes (Kallemeyn et al. 2003; Kallemeyn et al. 2009).

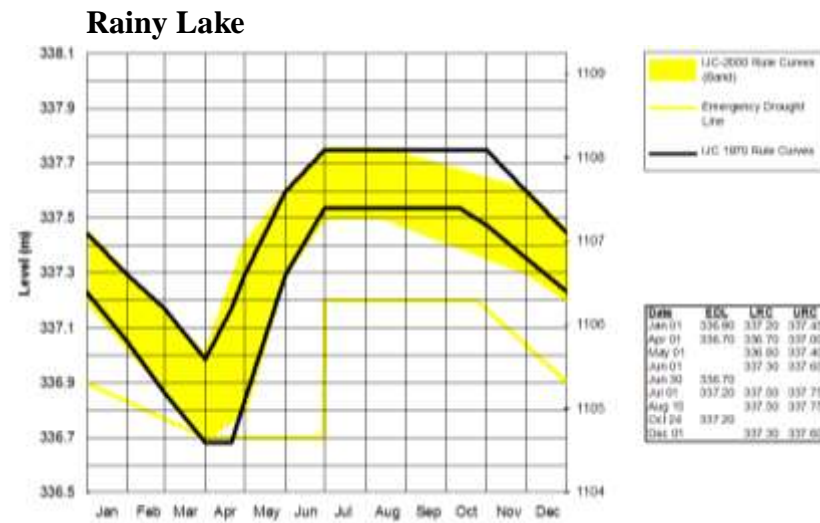
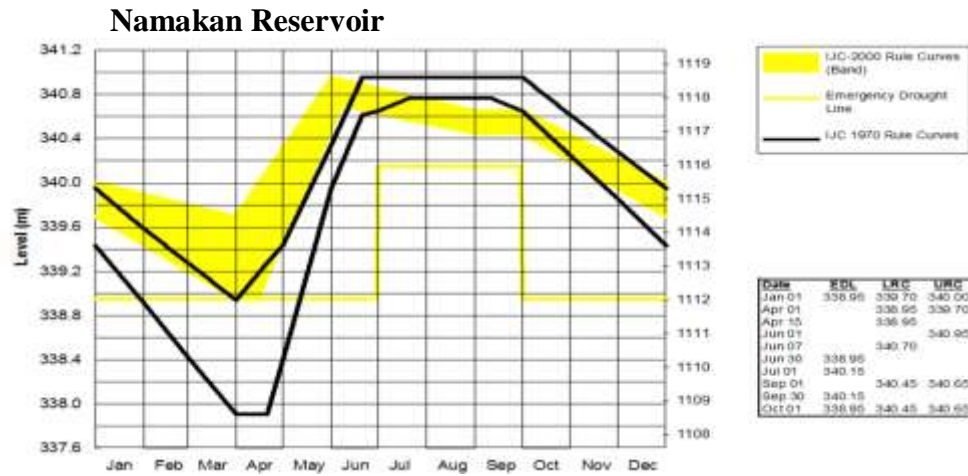


Figure 3. Predicted northern pike spawning habitat in Rainy Lake and Namakan Reservoir.

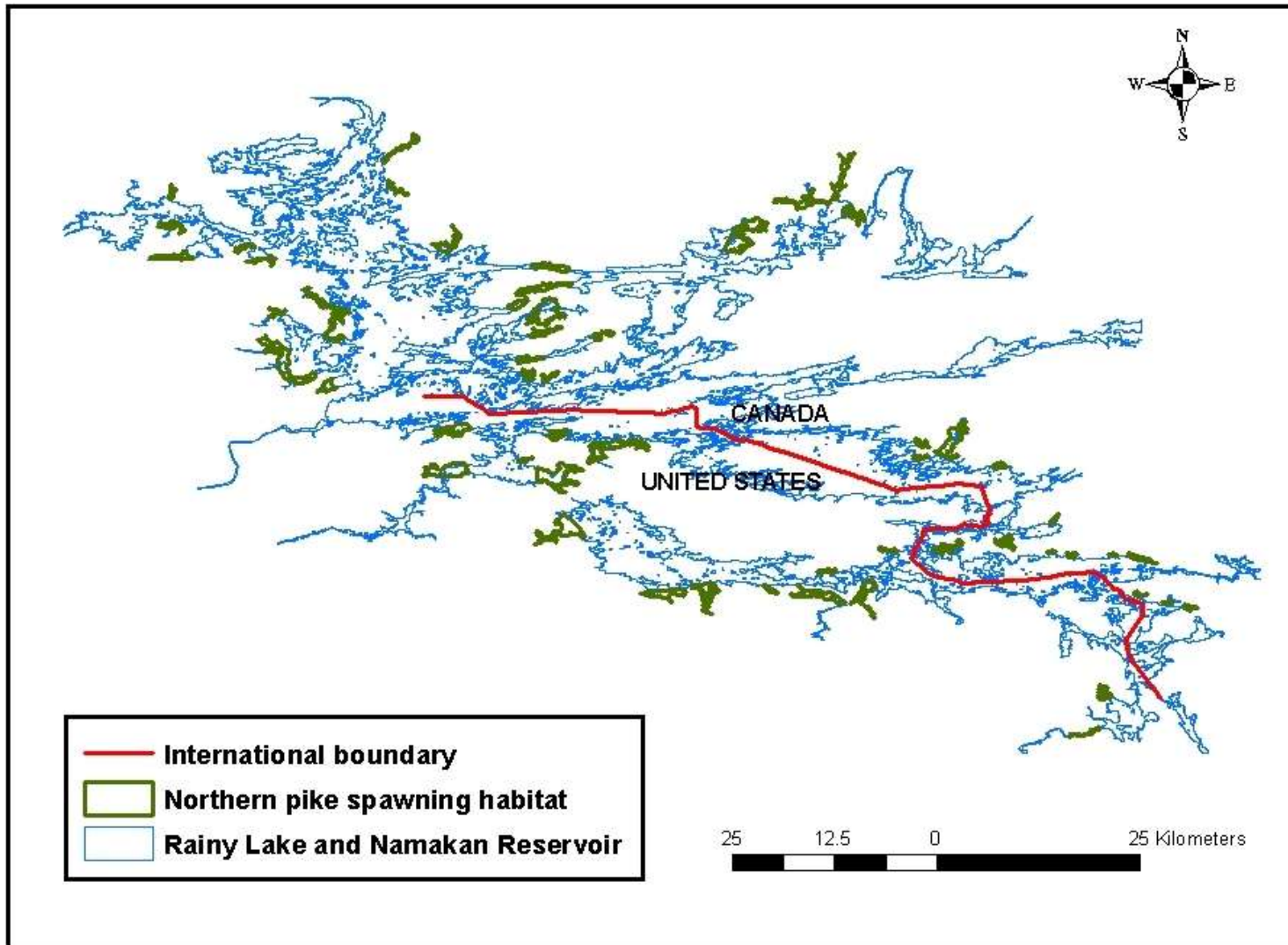


Figure 4. Thirteen larval northern pike sample bays in Rainy and Kabetogama Lakes.

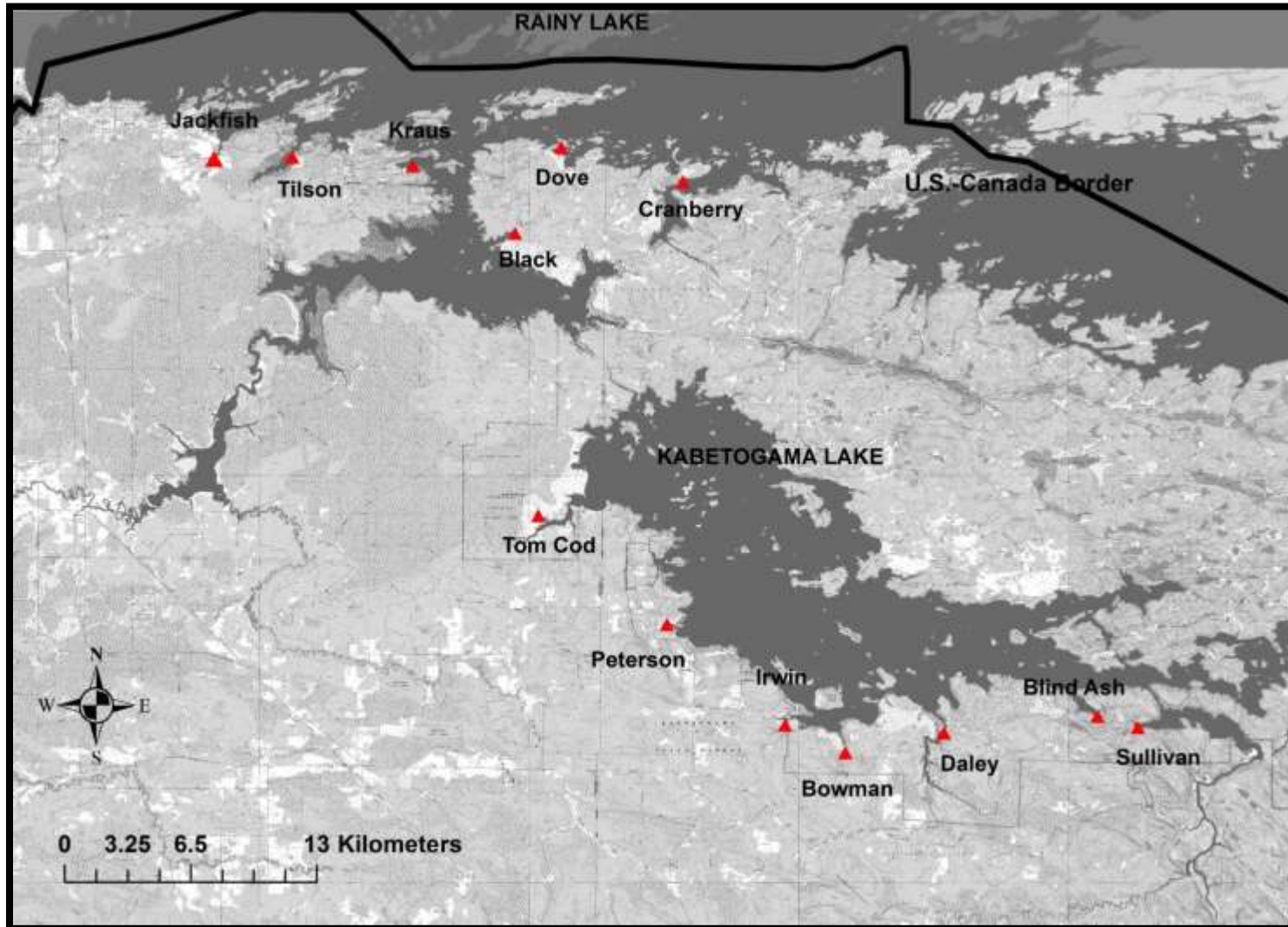


Figure 5. Twenty-four YOY northern pike sample bays in Rainy, Kabetogama, and Namakan Lakes.

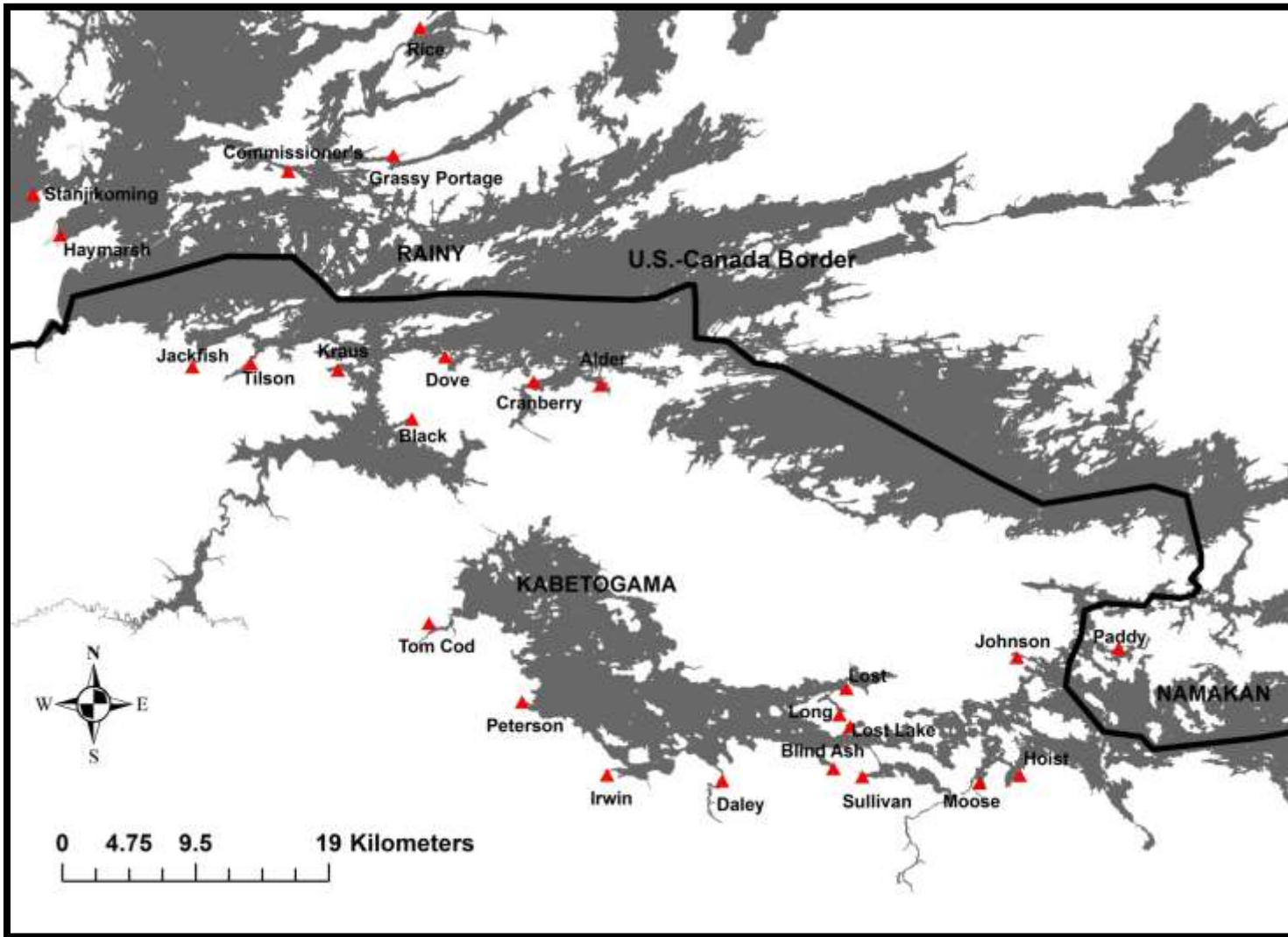


Figure 6. Dove Bay, Rainy Lake light-trap catch rates, 2004-2013, in relation to water level (m). Higher larval northern pike catch rates in Dove Bay correspond with water levels ≥ 337.4 m, as shown by the red line.

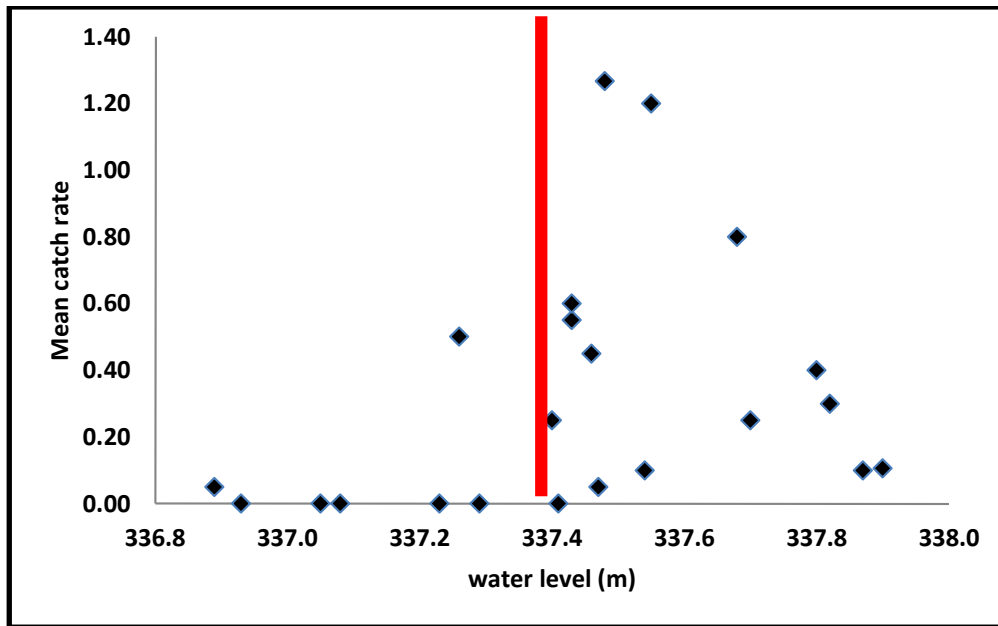


Figure 7. Sullivan Bay, Kabetogama Lake light-trap catch rate, 2004-2013, in relation to water level (m). Higher larval northern pike catch rates in Sullivan Bay correspond with water levels ≥ 340.4 m, as shown by the red line.

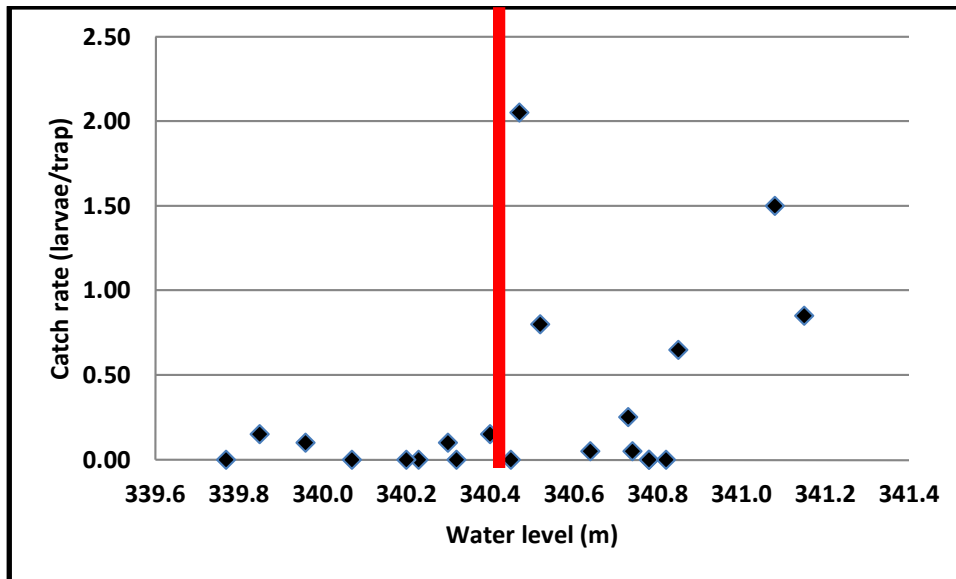


Figure 8. Kabetogama Lake mean catch and monthly mean water levels for April to August for the 1970 Rule Curve. Mean catch per year is represented by the black line with the y axis on the right side. Mean water level per month is represented by the colored lines with the y axis on the left side. The highest mean catch rate in 1996 corresponds to the year with the highest monthly mean water levels in May and June.

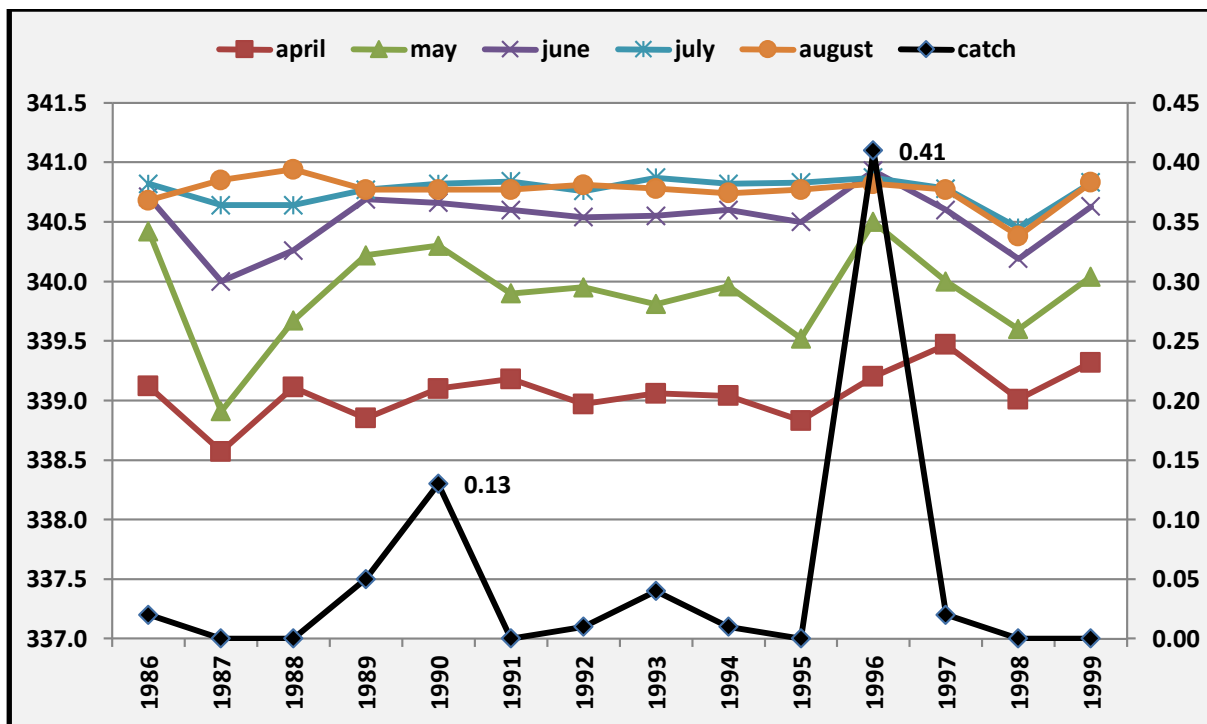


Figure 9. Modeled quarterly water levels from the Aaron Thompson model for April to August for 1989, 1990, and 1996 for years when YOY northern pike seine mean catches were highest. The colored lines are the quarterly water levels and the black lines are the Kabetogama 1970 Rule Curve (RC) minimum and RC maximum. The highest seine mean catch value for all Kabetogama Lake 1970 RC years, 1986 to 1999 was 1996 when the water level was above the rule curve from the end of April to the beginning of June.

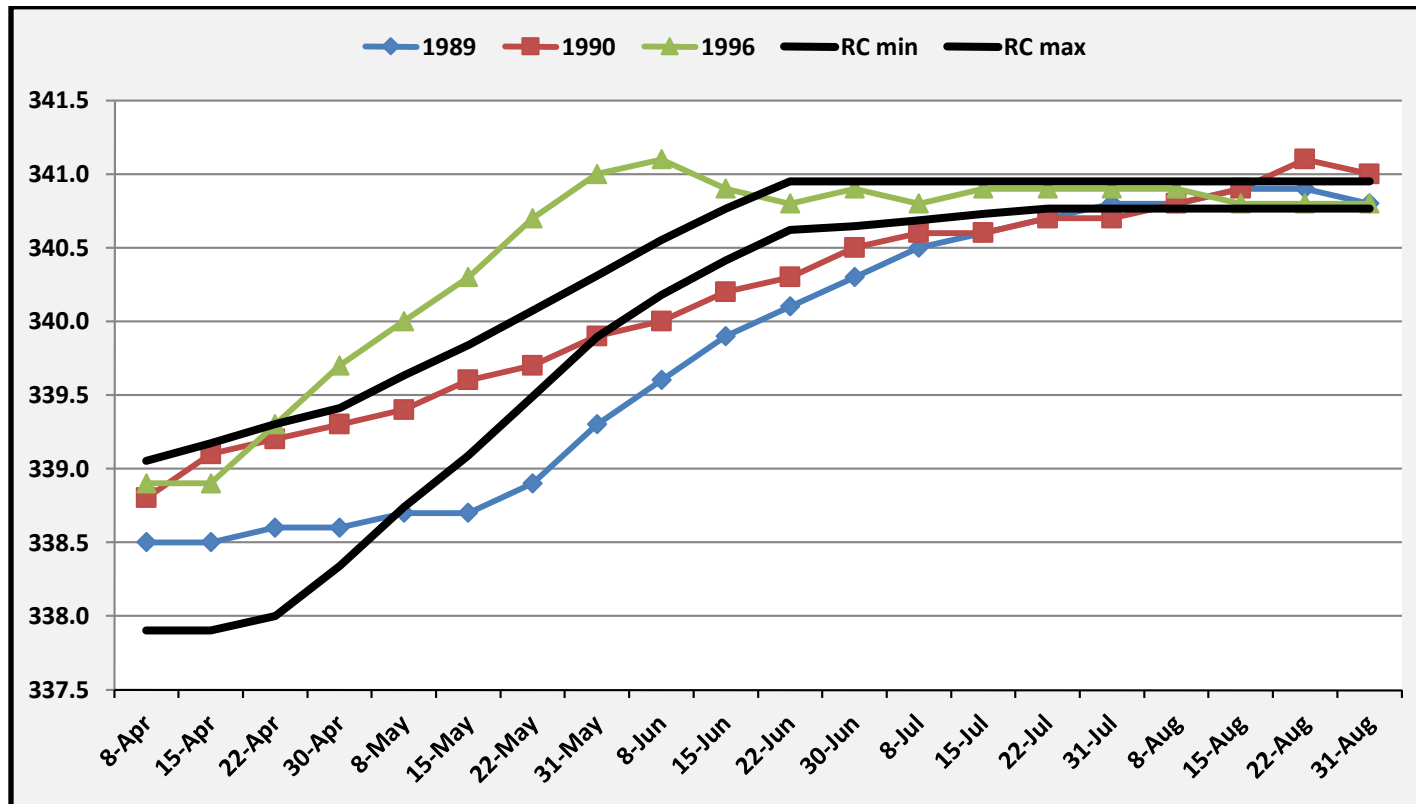


Figure 10. Kabetogama Lake mean catch and monthly mean water levels for the 2000 Rule Curve. Mean catch per year is represented by the black line with the y axis on the right side. Mean water level per month is represented by the colored lines with the y axis on the left side. The high mean catch rates in 2001 and 2008 correspond to the highest monthly mean water levels in May and June for all years, 2000 to 2012.

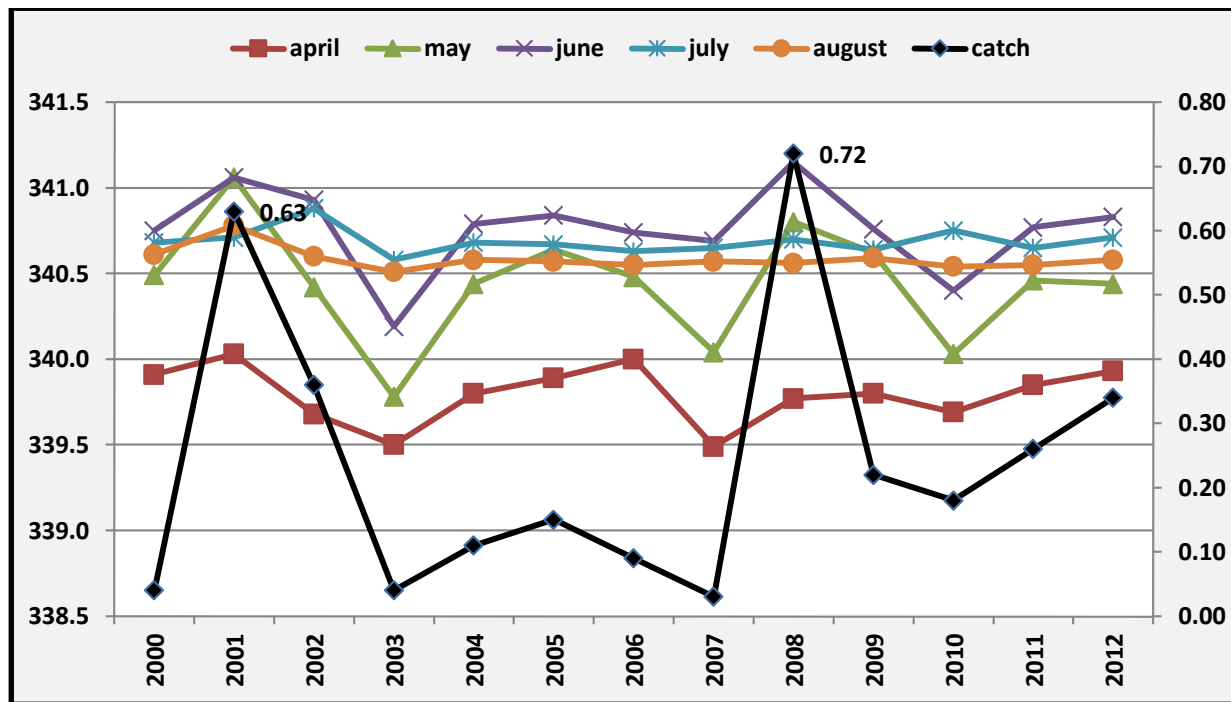


Figure 11. Kabetogama Lake modeled quarterly water levels from the Aaron Thompson model for April to August for 2001, 2002, and 2008 for years when YOY northern pike seine mean catches were highest. The colored lines are the quarterly water levels and the black lines are the Kabetogama 2000 Rule Curve (RC) minimum and maximum. The highest seine mean catch value for all Kabetogama Lake 2000 RC years, 2008, corresponds to a year when the water level was above the rule curve throughout May and into the beginning of June.

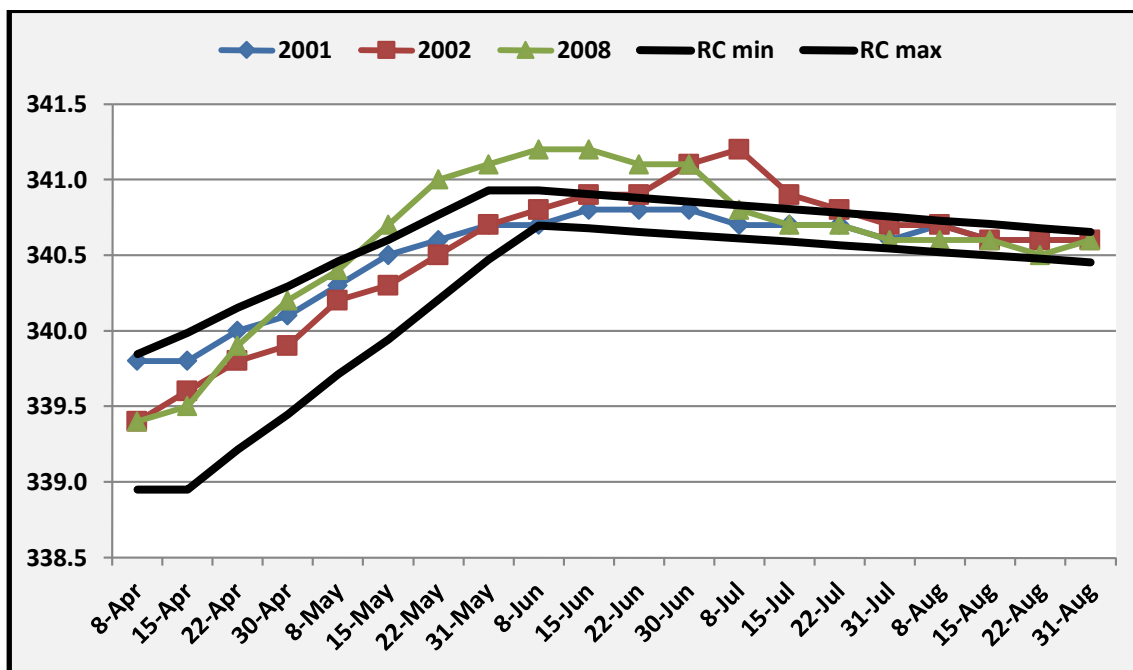


Figure 12. Rainy Lake mean catch and monthly mean water levels for the 1970 Rule Curve. Mean catch per year is represented by the black line with the y axis on the right side. Mean water level per month is represented by the colored lines with the y axis on the left side. The highest mean catch rates in 1996 correspond to the highest monthly mean water levels in May and June for all years 1986 to 1999.

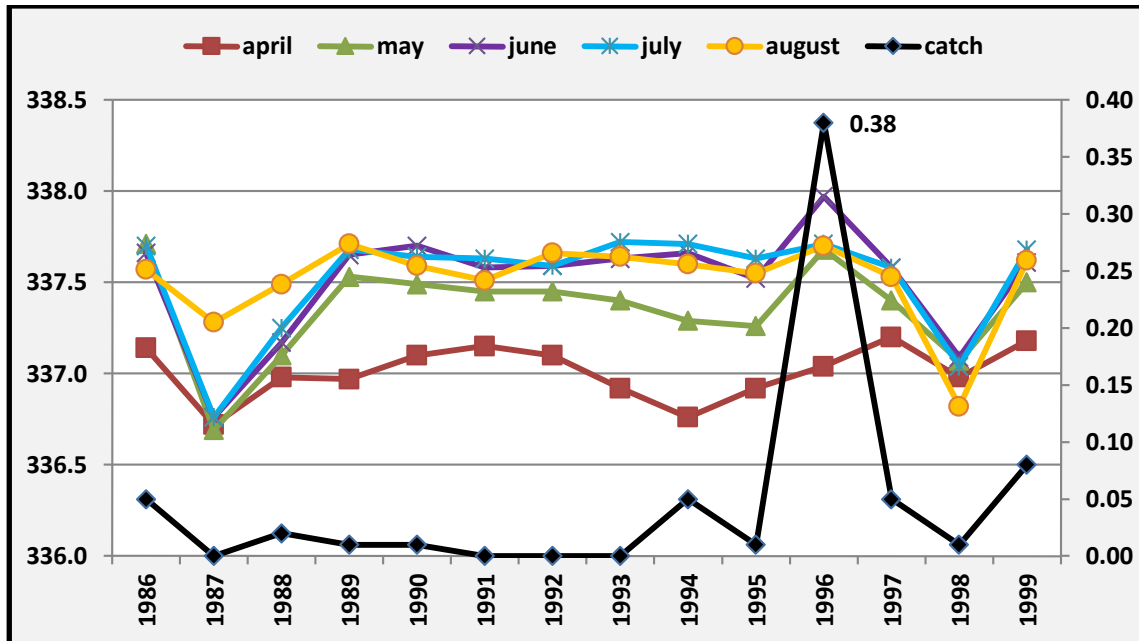


Figure 13. Rainy Lake modeled quarterly water levels from the Aaron Thompson model for April to August for 1994, 1996, and 1999 for years when YOY northern pike seine mean catches were highest. The colored lines are the quarterly water levels and the black lines are the Rainy Lake 1970 Rule Curve (RC) minimum and maximum. The highest seine mean catch value for all Rainy Lake 1970 RC years, 1996, corresponds to a year when the water level was above the rule curve throughout May and into the beginning of June.

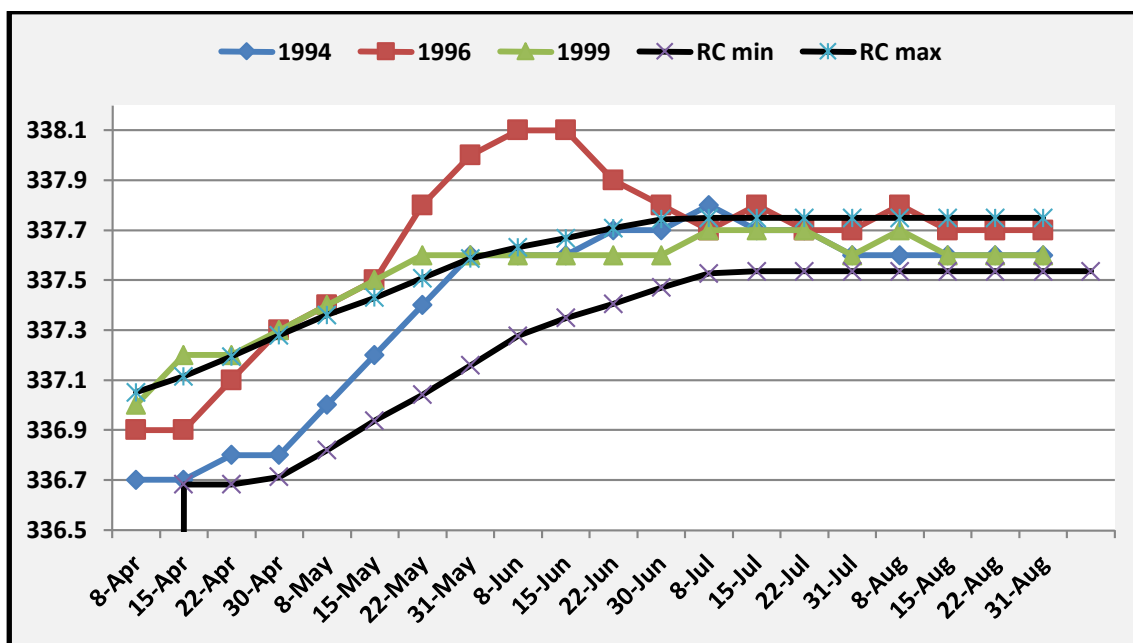


Figure 14. Rainy Lake mean catch and monthly mean water levels for the 2000 Rule Curve. Mean catch per year is represented by the black line with the y axis on the right side. Mean water level per month is represented by the colored lines with the y axis on the left side. The highest mean catch rates in 2001 correspond to the highest monthly mean water level for May and June for all years, 2000 to 2012.

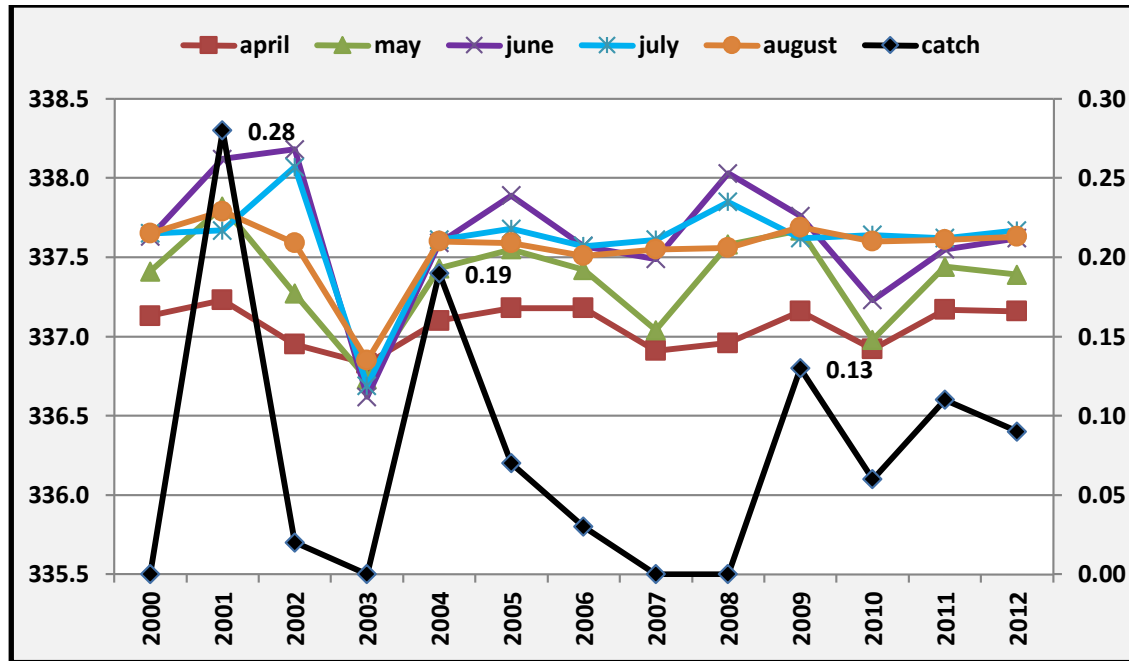


Figure 15. Rainy Lake modeled quarterly water levels from the Aaron Thompson model for April to August for 2001, 2004, 2009, and 2011, for years when YOY northern pike seine mean catches were highest. The colored lines are the quarterly water levels and the black lines are the Rainy Lake Rule Curve (RC) minimum and maximum. The highest seine mean catch value for all Rainy Lake 2000 RC years, 2001, corresponds to a year when the water level was above the rule curve throughout May and June.

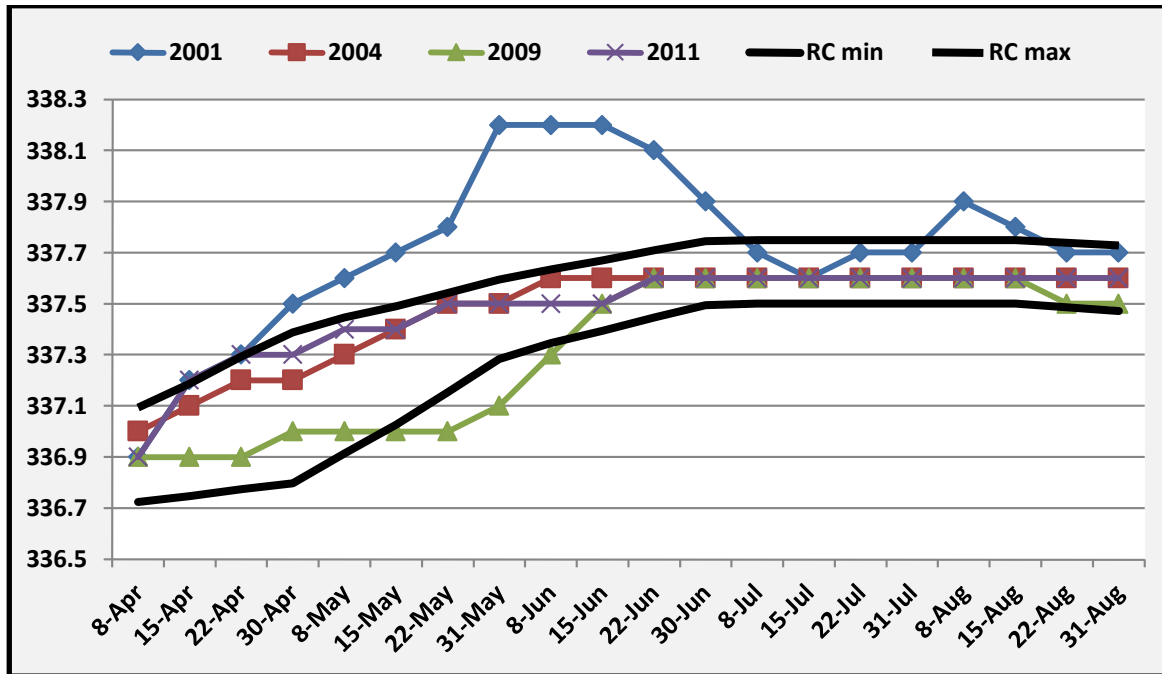


Figure 16. Rainy Lake mean larval northern pike catch and monthly mean water levels for 2000 Rule Curve years, 2000-2012. Mean catch per year is represented by the black line with the y axis on the right side. Mean water level per month is represented by the colored lines with the y axis on the left side. The highest mean catch rate for 2000-2012 data was 0.55 per light trap in 2008, which corresponds to the highest monthly mean water levels for May and June.

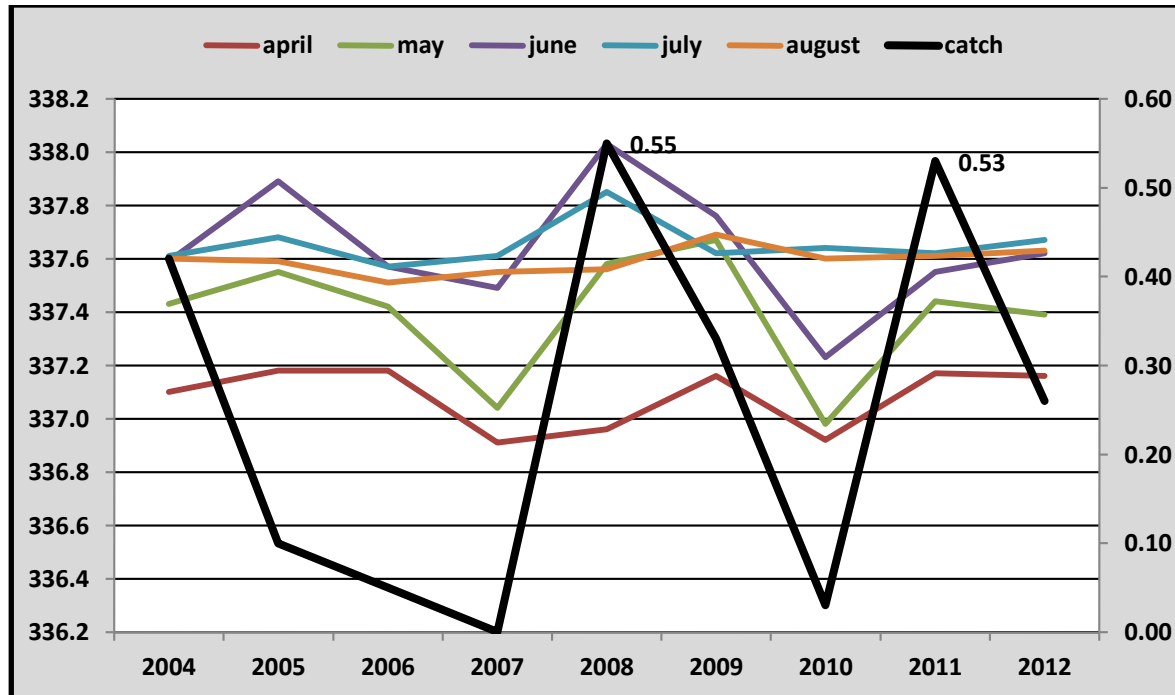


Figure 17. Kabetogama Lake mean larval northern pike catch and monthly mean water levels for 2000 Rule Curve years, 2000-2012. Mean catch per year is represented by the black line with the y axis on the right side. Mean water level per month is represented by the colored lines with the y axis on the left side. The highest mean catch rate for 2000-2012 data was 1.10 per light trap in 2011, which corresponds to the high monthly mean water levels for May and June.

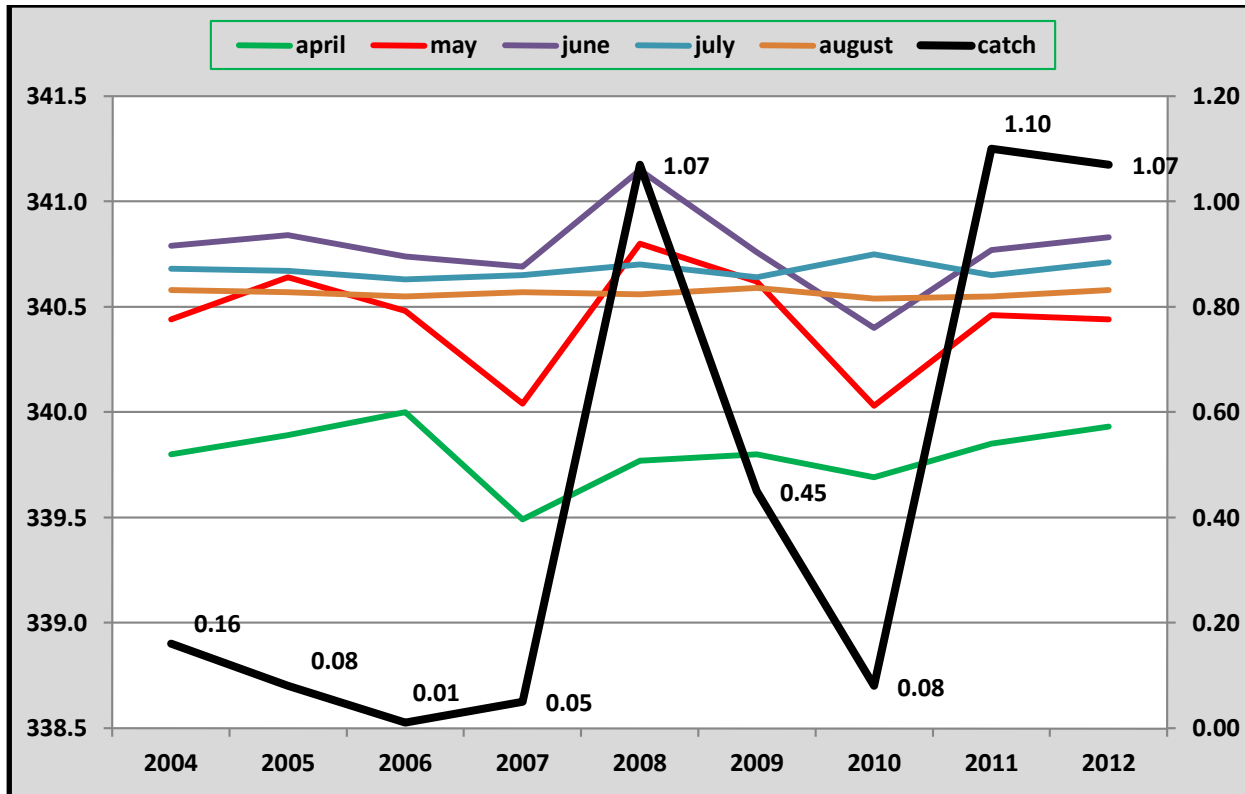


Figure 18. Predicted mean larval pike catch rates for light traps in Rainy and Kabetogama Lakes with hybrid cattail absent and hybrid cattail present. The mean larval pike catch rates (number of fish per light trap) presented here are based on the predictive negative binominal model that we applied using known water elevations for our light-trap sample sites.

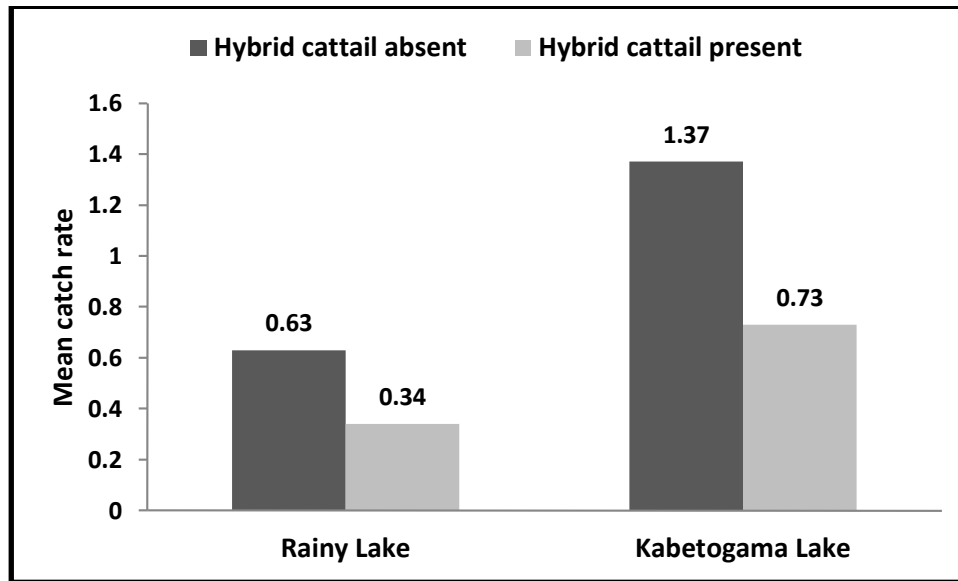


Figure 19. Rainy Lake mean catch rates for light trap and seine data, 2004-2013.

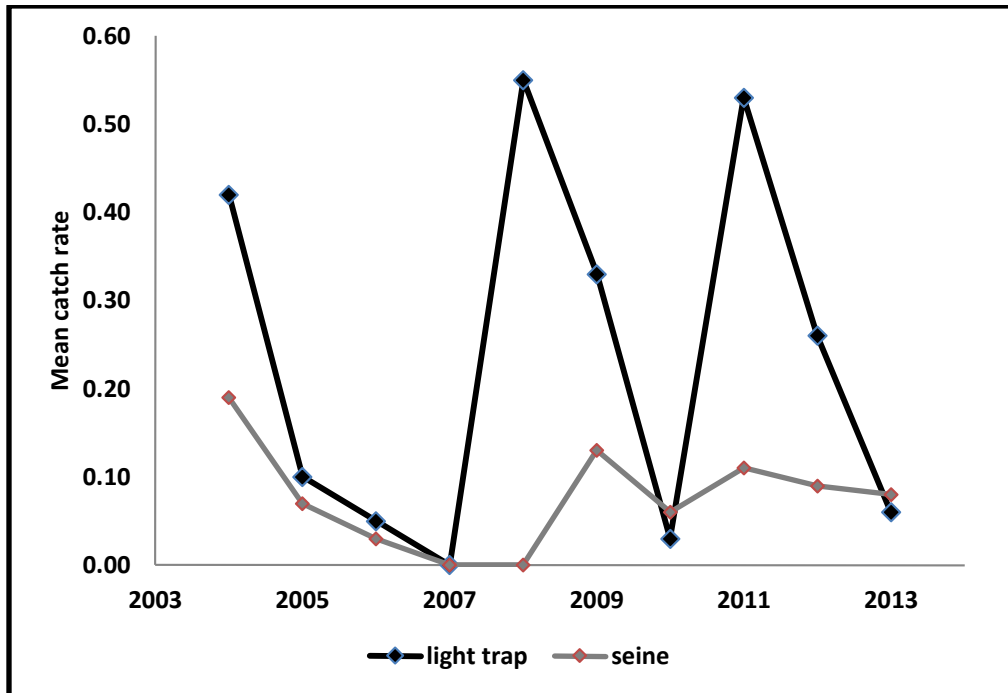


Figure 20. Kabetogama Lake mean catch rates for light trap and seine data, 2004-2013.

