Mimicking Nature: How water level management on a large reservoir affects walleye (*Sander vitreus*) spawning habitat

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Jason Travis Papenfuss

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Dedication

I dedicate this thesis to my wife, Kristin S. Vickstrom. You believed in me, and that made all the difference.

Abstract

The Namakan Reservoir, located on the Minnesota-Ontario border, has been successively managed under two water-level management policies ('rule curves') in recent decades. To compare the effects of the rule curves on walleye spawning, I modeled wave energy, ice scour, and habitat availability at 44 spawning locations. Wave energy increased (18% for observed water levels, 6% for modeled water levels) and ice scour decreased 11% (both $P < 0.01$) over spawning habitat during the most recent rule curve. Observed water level data suggested available spawning habitat on Lake Kabetogama increased 95% ($P < 0.01$), but availability on Namakan and Sand Point Lakes was unaffected. However, when controlling for weather events, habitat availability increased significantly (Kabetogama = 179%, Namakan = 72%, Sand Point = 93%, $P < 0.01$) on all three lakes. These findings suggest that the most recent rule curve is likely to improve reproductive success for walleye in the reservoir.

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Chapter 1

General Introduction: Water level management in North American reservoirs and the implications for walleye spawning habitat

Background

The total area of surface water impounded by dams has increased at a semi-log rate since the 1700s, and it was recently estimated that there are over 500,000 individual impoundments on the planet (Downing et al. 2006). Most of these impoundments are relatively small and provide water for livestock, small-scale irrigation, and fish culture (Smith et al. 2002). However, the number of large impoundments (greater than 20 km^3) increased rapidly from 1950 to 1980 in response to global demands for hydropower, large-scale irrigation, and public water supply (Shiklomonav and Rodda 2003). The primary objective of water level management in these large reservoirs is typically to stabilize the amount of stored water, for either electrical power generation, or consumption (Prosser 1986). However, water level management also affects the chemical, physical, and morphological characteristics of reservoirs, and therefore the biota that inhabit them. The amplitude, frequency, and direction of water level fluctuations can significantly alter the structure and composition of reservoirs, especially in littoral zones (Gasith and Gafny 1987, Baxter 1977). Many fish species rely on these littoral zones for habitat and food availability.

Prevalent in many North American reservoirs, walleye (*Sander vitreus*) rely heavily on littoral habitat, particularly in spring during spawning and larval incubation (Niemuth et al. 1959, Johnson 1961, Priegel 1970, Raabe 2006). Walleye are also a culturally and economically important species of freshwater fish throughout both their native and introduced ranges. While their popularity as a game fish has declined slightly in recent decades, walleye remain a highly sought after species. For example, in 2011, over 3 million U.S. anglers targeted walleye and logged an estimated 44 million angling days (USDOI et al. 2011). Walleye are particularly popular in north-central North

America. For example, a 2011 survey of regional anglers in the state of Minnesota revealed that walleye were the most popular sport fish in terms of number of anglers and number of angling days (USDOI et al. 2011). Walleye also generate billions of dollars in the commercial food, retail, and tourism industries (Scott and Crossman 1973). The Minnesota Department of Natural Resources estimated that, in 2011, fishing generated \$2.8 billion in direct annual expenditures in Minnesota and contributed more than \$640 million in tax revenues to the treasuries of the state and federal governments (MNDNR 2011). The majority of these fishing and fishing related expenditures in Minnesota were associated with walleye angling. Similarly, a 2010 survey in Canada revealed more than \$2.5 billion in direct annual expenditures, with walleye being the most frequently harvested species (FAO 2012).

The cultural and economic significance of walleye often contribute to population declines. In Alberta, Canada, for example, heavy angling pressure in the 1990s combined with passive management strategies, late maturity, and slow individual growth rates resulted in the widespread decline and extirpation of some populations (Sullivan 2003). Past responses to failed conservation efforts have included the widespread stocking of walleye into both natural lakes and reservoirs to bolster populations (Anthony and Jorgensen 1977, Schupp and Macins 1977). However, because aquatic ecosystems are complex, the effects of walleye stocking on walleye populations often vary. A meta-analysis of stocking programs across almost 2000 Minnesota lakes and reservoirs concluded that stocking only increased walleye abundance in systems in which walleye were not already reproducing naturally (Li et al. 1996).

The diminishing returns of walleye stocking programs underscore the need for more sustainable and balanced strategies for managing walleye, particularly in reservoirs in which the demand for water often conflicts with the habitat needs of fish. Of specific interest are strategies that might enhance the lacustrine littoral habitats in which walleye spawn, and where the effects of water levels are most significant. The quality and quantity of lacustrine spawning habitat is directly correlated with the survival of naturally spawned walleye eggs and therefore the occurrence of strong year classes (Johnson 1961). Researchers, therefore, have developed strategies that account for relationships between water levels and habitat conditions. For example, Cohen and Radomski (1993) suggested that appropriately managing the amplitude of annual water levels would help to ensure adequate spawning habitat in the Namakan Reservoir. Likewise, Kallemeyn (1987) noted that raising water levels earlier in the year, during spawning seasons, would provide walleye access to more satisfactory spawning habitat on Rainy Lake. The widespread and thoughtful application of strategies like these, in reservoirs where walleye are prevalent, might improve the availability of spawning habitat as well as direct the forces (i.e., waves and ice) that help to maintain it.

Effects of water levels on walleye spawning habitat

One way to improve the availability of walleye spawning habitat is to control water levels in the spring such that walleye have access to preferred substrates during spawning, and fertilized eggs are not too shallow or too deep during incubation. Water levels dictate the spatial arrangement of available substrates and the depth of potential incubation in a reservoir. Optimizing the availability of this habitat requires the coordination of water level fluctuations in spring with the timing and duration of walleye spawning. Optimal spawning habitat for walleye consists of clean (i.e., low embeddedness), wind-swept gravel, cobble, and rubble (16 to 256 mm diameter) at water depths ranging approximately from 5 to 125 cm (Niemuth et al. 1959, Johnson 1961, Priegel 1970, Raabe 2006). Spawning over this substrate increased the survival rate of eggs in a boreal lake in northern Minnesota (Johnson 1961). The high specificity toward, and presumed benefit of, relatively coarse substrates with low embeddedness is the provision of interstitial spaces that allow eggs to develop in an oxygen-rich environment that also provides protection from siltation, transport, abrasion, and predation (Bozek et al. 2011b). Dissolved oxygen is critical to the survival and development of walleye eggs and varies with depth (i.e., water levels). Dissolved oxygen concentrations > 5-6 mg/L are optimal for walleye egg incubation (Oseid and Smith 1976), and dissolved oxygen concentrations < 3 mg/L result in high egg mortality (Auer and Auer 1990). Therefore, walleye production in a reservoir is under the direct influence of water levels during the spawning season because walleye require access to preferred substrates at optimal depths and oxygen concentrations.

The way in which water levels are managed in reservoirs can also have indirect consequences for spawning habitats. For example, wave energy along shorelines can affect the suspension and redistribution of periphyton and fine sediment (Osborne and Greenwood 1993, Bailey and Hamilton 1996). These particulates are associated with low concentrations of dissolved oxygen in littoral areas (Cooley and Franzin 2008). Therefore, wave energy at proper elevations exposes spawning habitats to shear stresses that assist in removing periphyton and fine sediment. However, the timing of the reservoir drawdown should be of critical importance because strong wind events during incubation periods can transport shallow eggs from the spawning site either onto dry land (e.g., Johnson 1961) or into pelagic zones (e.g., Roseman et al. 2001). In one study, water velocities produced from nearshore wind-wave energy were high enough to move walleye eggs in a spawning area 19% of the time that eggs were incubating there (Raabe 2006).

A second and less studied way in which water levels can indirectly affect walleye spawning habitat is through ice scour. Ice forms in the late fall when reservoir levels are typically dropping. The downward movement of the ice during this drawdown can impart significant forces to the benthos and surrounding substrates. The upward movement of ice sheets in the spring before and during ice-out periods may have a similar effect. These forces are moderately studied in coastal and intertidal marine environments, where the periodic buildup of ice due to wind, waves, and current can cause disturbance to benthic communities (Barnes 1999, Gutt 2001, Scrosati and Heaven 2004) and displace sediments (Rearic et al. 1990, Woodworth-Lynas et al. 1991). However, this mechanism of habitat disturbance has not been studied on inland freshwater systems where scouring forces upon substrates are likely to have an analogous cleaning effect. If ice scour is spatially coincident with areas of optimal walleye spawning habitat in reservoirs, the potential effect of removing or cleaning fine sediments from those substrates will have an indirect positive effect on egg survival during the incubation season.

Overview of study

My hypothesis is that variations in water level management practices can help to improve the quantity and quality of spawning habitat for walleye in many North American reservoir systems. Testing this hypothesis requires the retrospective analysis of a reservoir system that has been managed under multiple water level policies (henceforth 'rule curves'). The Namakan Reservoir (Figure 1.1) is one such waterbody that is located on the border between Minnesota, USA, and Ontario, Canada. Because the reservoir is an international waterway, management jurisdiction falls under the bilateral International Joint Commission (IJC). Water levels in the reservoir were managed under one rule curve from 1970 to1999 (henceforth '1970 rule curve') (Figure 1.2). In 2000, the IJC implemented an updated rule curve (henceforth '2000 rule curve') (Kimmett et al. 1999). There are several differences in the timing and ranges of fluctuations in water levels between the two policies. For example, water levels under the 2000 rule curve reach higher elevations in the spring when walleye spawn due to a higher minimum level in winter. The 2000 rule curve also imposes a drawdown of approximately 0.6 m during the summer. The IJC intended these changes, in part, to improve spawning conditions for walleye by giving spawning fish access to more suitable habitat, and by improving wave and ice energy over suitable habitats.

My thesis is a retrospective evaluation of the effects of the rule curves on walleye spawning habitat in the Namakan Reservoir. Chapter 2 focuses on the effects of those forces that maintain habitat by quantifying the cleaning of substrates by wind generated wave energy and ice scour. Chapter 3 examines the effects of the rule curves on the availability of spawning habitat during spawning seasons. Both of these chapters have been prepared as manuscripts for publication.

This study will contribute to the management of reservoirs in which walleye are prevalent by assessing how the quantity and quality of available spawning habitat might be optimized. Specific recommendations for managing the Namakan reservoir and the implications for managing agencies are presented in Chapter 4. These recommendations are intended to contribute to the revision and improvement of existing water level management policies in order to continue to provide benefits to both human and non-human inhabitants of North American boreal reservoir systems.

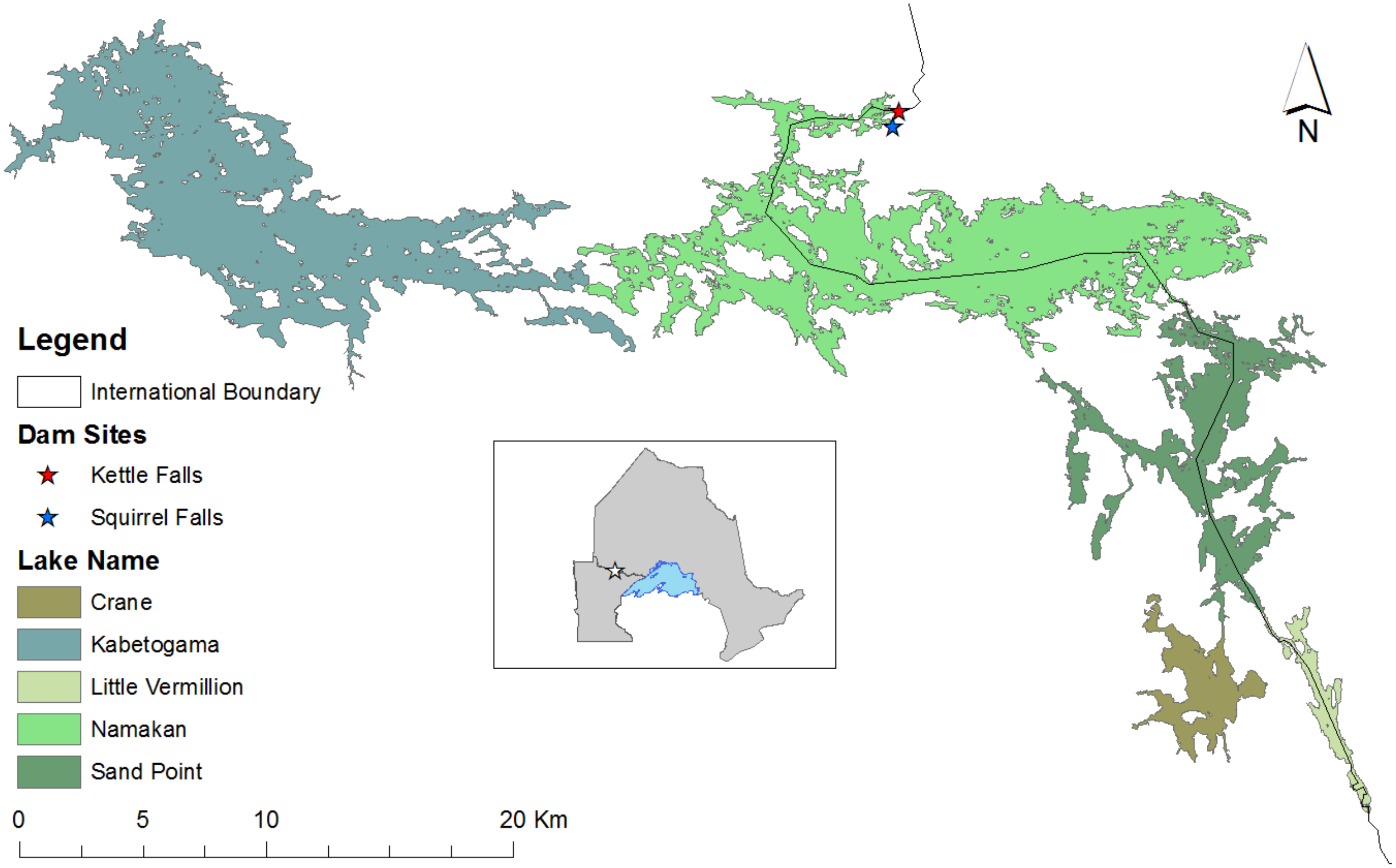

Figure 1.1. The Namakan Reservoir is located on the border between Minnesota, USA, and Ontario, Canada (see inset). The system comprises five lakes totalling approximately 25,000 ha and receives the majority of its influx from the Namakan and Vermillion rivers. Outflow occurs at the two dam sites on Namakan Lake, Squirrel Falls and Kettle Falls.

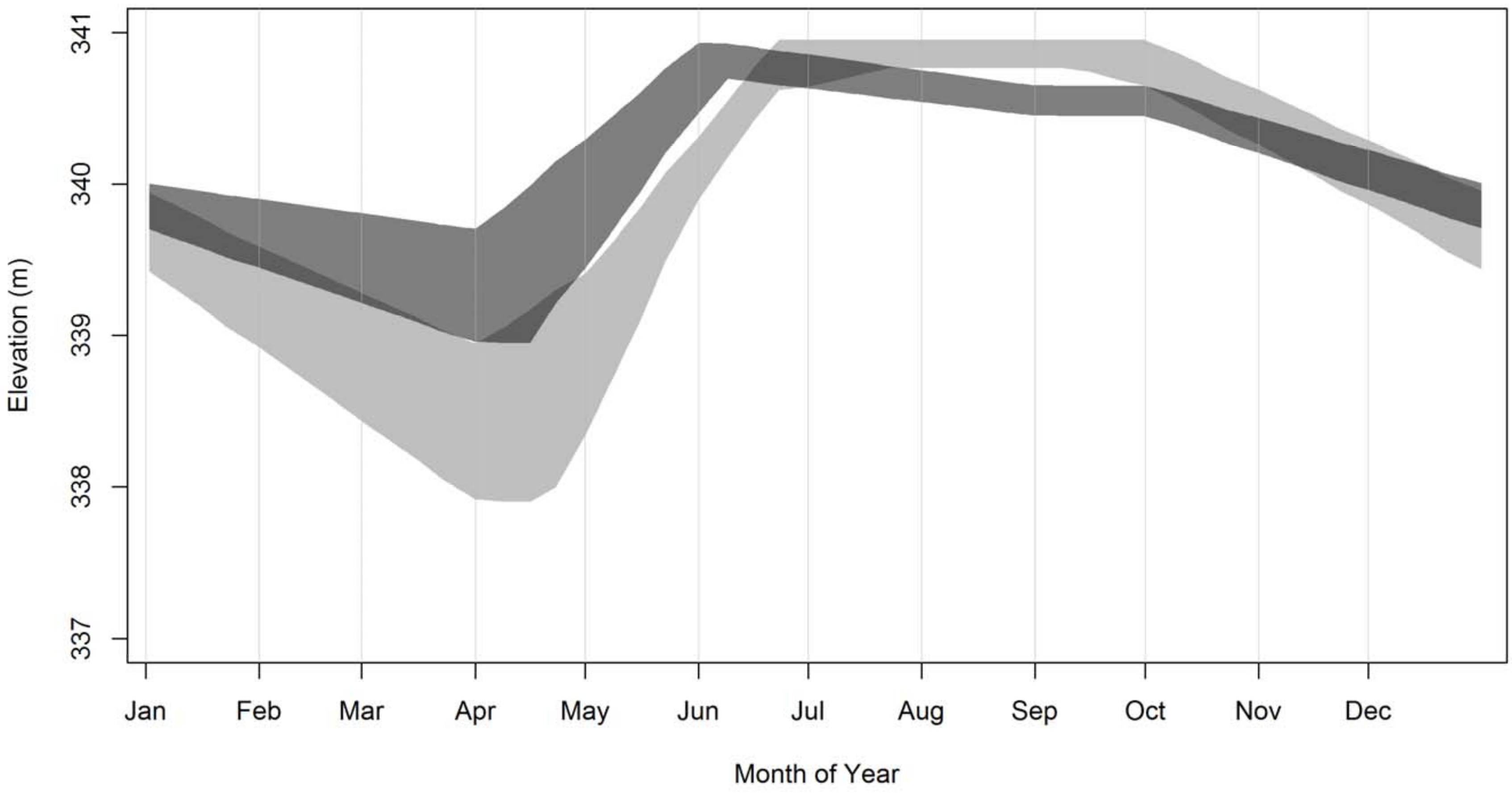

Figure 1.2. Hydrographs for the 1970 rule curve (in effect from 1970-1999; light gray) and 2000 rule curve (in effect from 2000-present; dark gray) on the Namakan Reservoir. Dam operators control outflows by targeting elevations at the middle of the shaded areas. Vertical elevations are relative to the USC&GS 1912 datum.

Chapter 2

The effects of water level policies in the Namakan Reservoir on the physical forces that maintain walleye spawning habitat[1]

Summary

Water level management on reservoirs affects the timing and depth of wave and ice forces that help to maintain walleye spawning habitats. We studied how two water level management policies ('1970 rule curve' and '2000 rule curve') have affected those forces in the Namakan Reservoir, an international waterway on the border of Ontario, Canada and Minnesota, USA. We surveyed substrate at 44 spawning locations and spatially modeled wave energy and ice scour over preferred walleye spawning substrates to compare the effects of the rule curves. Wave energy over spawning substrates increased significantly (18% using observed water levels and 6% using modeled water levels, $P < 0.01$) during the 2000 rule curve and did not vary by lake. The improvement resulted from a small increase (0.1 m) in mean water levels during open water seasons. The interaction of ice with preferred substrates on Lake Kabetogama decreased 11% ($P < 0.01$) during the 2000 rule curve, resulting from a decrease in the mean range (0.7 m) of water level elevations during winter. However, ice scour was still affecting those substrates used most frequently by walleye during typical spawning seasons. These findings suggest that the 2000 rule curve has improved the maintenance of spawning habitat by forces that remove fine sediments, and is likely to improve the reproductive success of walleye in the Namakan Reservoir.

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[1] This chapter has been prepared as a manuscript for publication. Co-authors include Paul A. Venturelli and Tim Cross. I will use the plural pronouns "we" or "our" instead of the singular "I" or "my" in reference to co-authorship in this chapter.

Introduction

Dam construction for the purpose of storing water is one of the oldest examples of humans engineering their environment (Baxter 1977). However, the quantity and size of global reservoirs has increased dramatically since the 1700s. A recent estimate of the total number of reservoirs exceeds 500,000 and covers 260,000 km^2 (Downing et al. 2006), an area roughly equivalent to New Zealand. Total reservoir area is likely to increase due to the growing demand for electricity, as well as the need for reliable sources of irrigation and drinking water. Even proposals to mitigate climate change have included the use of reservoirs due to their high carbon storage potential (Dean and Gorham 1998).

The intense and varied demands placed on reservoirs by humans (e.g., irrigation, navigation, energy, and flood control) dictate fluctuations in water levels and alter limnological characteristics (Thornton et al. 1990). Flooding of reservoirs stimulates microbial production of greenhouse gasses like methane and carbon dioxide, and increases methylation of inorganic mercury (Kelly et al. 1997). Reservoirs also have larger watershed to waterbody ratios than natural lakes, confounding the management of water quality characteristics (e.g., sedimentation) (Straskraba et al. 1993, Pegg et al. 2015). These limnological changes often lead to changes to fish populations. For example, several studies have shown that water level fluctuations in North American reservoirs are correlated with mercury levels in percids (Therriault and Schneider 1998, Sorensen et al. 2005). Water levels also affect the movement and distribution of fishes in reservoirs by altering the availability of certain habitat types (Hubert and Lackey 1980).

Walleye (*Sander vitreus*) are prevalent in North American boreal reservoirs and exhibit reproductive characteristics that make them particularly susceptible to water level fluctuations. Walleye spawn near shorelines at depths of 0.1 to 1.0 m, and prefer homogenous, clean, wind-swept gravel, cobble, and rubble (16 to 256 mm diameter) (Niemuth et al. 1959, Priegel 1970, Raabe and Bozek 2012). A benefit of coarse, homogenous substrates is the provision of interstitial spaces that allow eggs to develop in an oxygen-rich environment while being protected from siltation, transport, abrasion, and predation (Bozek et al. 2011b). The removal of particulates (both organic and inorganic) by repetitive cleaning of these substrates is therefore necessary to maintain these interstitial regimes, and is an important factor in the survival of walleye eggs (Johnson 1961).

Both wind and ice are known to impart physical forces that remove littoral debris from shorelines (Bailey and Hamilton 1997, Scrosati and Heaven 2006). Water levels in reservoirs determine the vertical distribution of wind-generated wave energy, and are strong determinants of the distribution of sediments and the depths of mud boundaries (Cooley and Franzin 2008). The rise and fall of lake levels also determines the range in elevation of the ice-substrate interface (i.e., ice foot) in littoral zones and affects the spatial distribution of forces imparted on substrates (i.e., ice scour) along the interface (Rearic et al. 1990, Woodworth-Lynas et al. 1991). Thus, policies that dictate water level management in reservoirs (henceforth ‘rule curves’) can be crucial in determining the timing, location, and magnitude of cleaning of walleye spawning substrates.

The Namakan Reservoir (Figure 2.1) is an international waterway that falls under the jurisdiction of the International Joint Commission (IJC). Walleye are prevalent in this boreal reservoir and have major ecological, cultural, and economic significance (Kallemeyn et al. 2003). Since 1970, water levels in the reservoir have been successively managed under two separate rule curves (Figure 2.2) (Kimmett et al. 1999). The 1970 rule curve was in place from 1970 to 1999. The 2000 rule curve was established in 2000 with the intent of improving habitat conditions for walleye and other species. The 2000 rule curve differs from the 1970 rule curve in three important ways: (1) a narrower range of water levels during the ice season (~November through April), (2) higher water levels during the springtime (~April through June), and (3) reduced water levels throughout summer (~June through November). Due to the unique combination of walleye prevalence and rule curve changes, the Namakan Reservoir is an ideal system in which to examine the effects of water level management on those forces that maintain walleye spawning substrates.

In this study, we compared the effects of the two rule curves on factors that maintain walleye spawning habitat (i.e., wind-generated waves and ice scour) during the study period 1970-2014. Our goal was to determine if one rule curve was more effective at exposing preferred spawning substrates to forces that assist in the suspension and/or removal of fine particulates. Our hypothesis is that water levels are important, not only in determining the depth of littoral habitats, but also in determining the magnitude and location of physical forces that maintain spawning habitat suitability. Our results can also inform future water level management policies with respect to fine particulates and fish habitat, both within and outside of the Namakan Reservoir.

Methods

Site selection

In the spring of 2012, we conducted spawning surveys at 109 locations throughout the three large lakes within the Namakan Reservoir: Lake Kabetogama (10425 ha), Namakan Lake (10170 ha), and Sand Point Lake (3580 ha). We chose these locations based on the likely presence of spawning as determined by agency reports (Osborn et al. 1978, Osborn and Ernst 1979), current local knowledge, and location/appearance. We focused on lacustrine (as opposed to riverine) shoreline locations because lake habitats were of greater interest to a larger, IJC funded study. We used scap nets at each site to determine the presence/absence of walleye eggs at depths ranging from 10 to 150 cm. We re-surveyed for eggs at these same locations during the 2013 and 2014 spawning seasons, and based our final site selection on the consistency of spawning as demonstrated by three consecutive years of egg detection, and a minimum shoreline length of 20m. To the extent possible, we also selected sites across all three lakes and between both countries in a way that maximized morphological diversity (e.g., shoreline lengths, slope, and aspect).

Substrate surveys and habitat modeling

From May 2013 to August 2013, we used snorkel gear to survey substrate at each study site by establishing transects perpendicular to the shoreline at 5 m-intervals and sampling substrate at 2 m-intervals along each transect (Figure 2.3a). We collected five substrate class measurements for each sample within a 60 cm quadrat: one at each corner and one in the center. Each substrate measurement was classified according to the Wentworth scale modified for boreal lacustrine shoreline habitat (Table 2.1) (Jones 2011, Raabe 2006).

We created substrate class and substrate variability rasters at each site by computing the class mean and standard deviation for each survey quadrat and spatially interpolating among quadrats using inverse distance weighting (cell size = 1 m, power = 3, variable radius, points = 8, distance = 20 m) (Figure 2.3b-c). Walleye prefer to spawn on gravel, cobble and rubble (Eschmeyer 1950, Johnson 1961, Priegel 1970); therefore, we reclassified substrate class rasters into two subgroups with classes in the range 2-4 (gravel, cobble, and rubble) reclassified as suitable (assigned pixel value 1) and all others reclassified as unsuitable (assigned pixel value 0) (Figure 2.3d). We also reclassified rasters into two groups based on standard deviation, with standard deviations <2 reclassified as suitable (assigned pixel value 1) and >2 reclassified as unsuitable (assigned pixel value 0) (Figure 2.3e). Finally, we multiplied these two raster datasets to create a final spawning substrate raster in which pixel values of 1 and 0 identified suitable and unsuitable spawning substrate, respectively (Figure 2.3f).

During the study period, the reservoir underwent episodes of both flooding and drought in which water levels were at elevations that were above and below those that were accessible during the 2013 snorkel survey. We used Gaussian functions to predict suitable substrates beyond surveyable elevations (100 m upslope and downslope of measured substrate at all sites). Gaussian functions are commonly used to describe the distribution of habitat along physical gradients (e.g., elevation) (Gauch and Chase 1974, Gauch et al. 1974). We generated lake-specific and reservoir-wide Gaussian functions by fitting non-linear least squares to observed substrate data and a digital elevation model (DEM) resampled to 1 m^2 using bilinear interpolation (Morin et al. 2014) (Figure 2.4). The observed substrate suitability raster was then overlaid onto the predicted substrate suitability raster to create a hybrid raster (i.e., based on both observed and predicted substrates) that could be used to model the effects of wind and ice on habitat over a wider range of elevation (Figure 2.5a-c).

Wave modeling

To model wave energy (and therefore sediment suspension) at each study site, we first had to determine the timing and duration of open water seasons. For all study years, we used archival ice-out dates that were based on both ground and areal observations of various lakes within the reservoir. These dates represent best estimates that are likely to be accurate to within one week of actual ice-out. We predicted freeze-up dates from average daily air temperatures taken from the International Falls International Airport weather station (NOAA 2015) using a linear regression model (Shuter et al. 2013). We calibrated the model using freeze-up dates established from public satellite imagery of the Namakan Reservoir from 2007 to 2014 (SSEC 2014).

Because the re-suspension of fine sediments relies on factors other than water levels (e.g., wind speeds/directions), we compared the 1970 and 2000 rules curves in two ways: using observed water levels (serial comparison) and using a hydrologic model (Thompson 2013) (parallel comparison). The hydrologic model allowed us to assume parallel time-scales (one in which the 1970 rule curve was in place from 1970-2014 and another in which the 2000 rule curve was in place from 1970-2014) and therefore control for climatic variability. So that both comparisons were computationally feasible, we aggregated daily wind speed, wind direction, and water levels (both observed and modeled) into 7-day (hence-forth ‘weekly’) means during the study period. We obtained daily wind speeds and directions from the International Falls International Airport weather station (NOAA 2015), and water levels from the Lake of the Woods Control Board (LWCB 2014).We used the cosine method to calculate mean weekly wind direction (ranging from 0 to 359°).

Two important components of wave energy are bathymetry and wind fetch. We created bathymetric rasters of our study sites (5 m resolution) during each aggregate week of the study period (1,376 weeks) by subtracting the water elevation (assumed to be planar throughout the reservoir) from our DEM (resampled using bilinear interpolation). To minimize the number of model iterations necessary, we rounded water elevations to the nearest 10 cm for all analyses. We then created fetch rasters for each wind direction (in 30° increments) at both observed and modeled water elevations during each week using the fetch model in Rohweder et al. (2012). We used the model's single direction method to quantify wind fetch distances. This method ignores near-shore processes such as wave shoaling, breaking, reflection, refraction, and diffraction (Rohweder et al. 2012).

Finally, we used the bathymetry rasters, fetch rasters, weekly wind speed, and weekly wind direction as inputs to the wave model to create weekly estimates of sediment suspension probability (estimated as 1 or 0). The wave model first quantifies the height, period, length, and maximum orbital velocity of waves for a given period. Given a threshold velocity of 0.1 m/s (the velocity required to suspend fine particulates typical of the Namakan Reservoir) (Hakanson and Jansson 2002), the model then uses these predicted wave characteristics as inputs to create weekly sediment suspension rasters.

Wave summary and analyses

To estimate the total number of days of sediment suspension at each site, we summed weekly sediment suspension rasters over open water seasons and multiplied the sum by 7. To provide weighted estimates of the number of days that preferred substrates were exposed to wave velocities sufficient to suspend fine particulates (0.1 m/s), we spatially multiplied seasonal suspension rasters (resampled to 1 m using the nearest neighbor method) by our habitat suitability rasters and summed the products over sites. We accounted for variation in site size by dividing each weighted sum by the total area of the site. Because the response demonstrated non-normality, we normalized via a $\log_{10}(Y+C)$ transformation, where C is the minimum non-zero response (Zuur et al. 2009, Warton and Hui 2011).

Because we were primarily interested in the effect of the rule curves on the cleaning of spawning habitat, we employed mixed ANOVA to model the log-transformed interaction of wave energy and substrate suitability. First, we used observed water level data to predict wave induced substrate cleaning as a function of rule curve (fixed effect) and study site (random effect). Second, we used modeled water level data to predict wave-induced substrate cleaning as a function of water level models (fixed effect) and study site (random effect). We also included a lake interaction term in each model to determine if the effect of rule curve/model varied by lake. We defined study sites as mixed effects to control for temporal pseudo-replication, and because the study locations were a subset of all available spawning sites in the reservoir.

Ice scour measurement

To measure and subsequently model the magnitude of ice scour over study years and sites, we deployed measuring devices following Scrosati and Heaven (2006). This involved using marine epoxy (A-788 Splash Zone Compound: Z-Spar) to affix ~1 cm^3 wire cages (constructed from 23 gauge galvanized hardware cloth with ¼ inch openings; Figure 2.6a) to existing substrate at 30 cm depth intervals along transects. We deployed five transects at each site, and sampled 13 sites in total (325 total cages, all on Lake Kabetogama). We deployed cages in late summer (August – September) and collected them in late spring (May – June). To quantify the intensity of ice scour at each depth interval, we measured the maximum angle of defection from vertical (0 to 90°) of the four sides and the location of each cage (Figure 2.6b). Cages at a single site (site 78) were deployed during the winter of 2012-2013 as a pilot study. Cages at the 12 remaining sites were deployed during the winter of 2013-2014.

To predict ice scour as a function of ice elevation, we plotted cage deflection against cage elevation (Figure 2.7a-b). Because this deflection-elevation relationship was highly variable (see results), we modeled the presence/absence of scour (S) using a step function that was based on our observed data:

$$S_i(elev) = \begin{cases} 1\ if\ elev\ \in A \\ 0\ if\ elev\ \notin A \end{cases} \tag{2.1}$$

$$where\ A\ \rightarrow (MIN\ ICE_i + 0.089m) \leq elev \leq (MAX\ ICE_i + 0.288m),$$

$elev$ is the elevation of the cage during measurement (i.e., after ice out), $MIN\ ICE$ is the minimum elevation of the ice during winter, and $MAX\ ICE$ is the maximum elevation of the ice during winter, and i is the study year. Finally, we used this step function and the DEM to reclassify elevation into yearly rasters (1970 – 2013) that indicated the presence (reclassified as 1) or absence (reclassified as 0) of ice scour.

Ice scour summary and analyses

To estimate the cleaning effect of ice on suitable substrate over all study years, we spatially multiplied yearly ice scour rasters by our habitat suitability rasters. We then summed cells over sites to give estimates of the area of suitable spawning substrate affected by ice scour during each season. We accounted for variation in site size by dividing the total area affected by scour at each site by the total area of each site. Because the response demonstrated non-normality, we applied a $\log_{10}$ transformation to normalize the distribution. Similar to the wave analysis, we employed mixed ANOVA to model ice-induced substrate cleaning as a function of the two rule curve (fixed effect) and study site (random effect).

All statistical analyses were performed in R, version 2.15.1 (package lme4) (Bates et al. 2012, R Core Team 2012), and all spatial analyses were performed in ArcGIS, version 10.0. We geo-referenced substrate measurements and ice scour measurements with a Trimble® GeoXT capable of sub-meter resolution and employed a combination of real-time and post-processed differential correction methods.

Results

Of the 109 locations surveyed in 2012, we selected 44 study sites (Table 2.2, Figure 2.1): 17 in Lake Kabetogama, 19 in Namakan Lake, and 8 on Sand Point Lake. The majority of these sites (32) were in U.S. territory. A summary of the site characteristics is as follows: total surveyed area 36,501 m^2 with a site mean of 830 ± 311m^2 SD (range 441 to 1512 m^2), mean shoreline length 54 ± 19 m SD (range 25 to 100 m), mean slope 2.5 ± 1.0° SD (range 0.6 to 4.8°), and mean elevation 339.8 ± 0.3 m SD (USGSC 1912 datum; range 338.9 to 340.4 m). Incidentally, all of the sites previously surveyed by agency staff (i.e., Osborn et al. 1978, Osborn and Ernst 1979) that were also surveyed as part of this study demonstrated evidence of spawning. This result indicates that walleye frequently spawned at our sites prior to our surveys in 2012 – 2014.

In total, we collected 21,940 individual substrate measurements. The mean substrate class across all sites was 3.7 ± 1.5 SD (i.e., rubble/cobble). After substrate measurements were interpolated, reclassified, and then combined for each site, the resulting total area of suitable substrate was 10,431 m^2 (28.6% of total sampled area). The Gaussian functions used to estimate habitat suitability predicted maximum habitat suitability for Kabetogama, Namakan, and Sand Point at elevations of 340.8 m (pseudo-r^2 = .82), 341.2 m (pseudo-r^2 = .92), and 341.6 m (pseudo-r^2 = .93) respectively (Figure 2.4a-c). The reservoir-wide maximum suitability occurred at an elevation of 341.1 m (pseudo-r^2 = .93) (Figure 2.4d).

We found a significant, linear relationship between air temperature and freeze-up ($r^2 = 0.58$, $F_{1,6} = 8.36$, $P = 0.028$) that is given by

$$F = 93.8 + 0.72(YDAY), \qquad (2.2)$$

where F is the day of the year of first ice formation (1 – 365) and $YDAY$ is the day of the year that the 30-day moving average of daily air temperature falls below 0 °C. Figure 2.8 summarizes the open water periods for each year of the study period. The mean observed date of ice-out was April 28 ± 9.8 days SD, and the mean predicted date of freeze-up was November 21± 5.8 days SD. According to a Welch two-sample t-test, the length of the open water seasons did not vary between rule curves ($CI = [-13.6, 4.3]$, $P = 0.3$).

Wind speed during open water seasons was significantly higher during the 2000 rule curve (1970 rule curve: 6.85 ± 2.05 $m \cdot s^{-1}$ SD, $n = 6196$; 2000 rule curve: 7.75 ± 2.38 $m \cdot s^{-1}$ SD, $n = 2976$; $t = -17.7$, df = 5169, $P = 2.2e-16$). However, wind bearing did not appear to vary significantly and was predominantly west-northwest during both rule curves (Figure 2.9a-b).

Our analysis of observed water levels suggested that, on average, the cleaning of walleye spawning substrates by wave energy increased during the 2000 rule curve by a factor of 1.18 ± 0.013 SD ($n = 1980$, $t = -14.7$, df = 1933, $P = 2e-16$). However, the modeled water level analysis suggested that substrate cleaning only increased by a factor of 1.06 ± 0.009 SD ($n = 3872$, $t = 7.26$, df = 3827, $P = 4.6e-13$). The effect of the 2000 rule curve on cleaning did not vary by lake in either case. Random site effects indicated that the interaction between wave energy and suitable spawning substrates was site-specific and was greatest, on average, at site 34 (Namakan Lake) and lowest at site 40 (Namakan Lake) for both observed and modeled water level data (Figure 2.10a-b).

Validation of our wave cleaning model demonstrated normality of the response and homogeneity of the residuals (for both observed and modeled water levels).

The ice scour model suggested that, on average, the level of interaction between lake ice and suitable spawning habitat decreased during the 2000 rule curve by a factor of 0.89 ± .02 SD ($n = 572$, $t = 5.89$, df = 558, $P = 2e\text{-}16$). Random site effects for ice scour over suitable substrates were less variable than for waves, and were greatest, on average, at site 24 and lowest at site 23 (both Lake Kabetogama sites) (Figure 2.10c). Model validation demonstrated normality of the response and homogeneity of the residuals.

Discussion

Gravel, cobble, and rubble substrates that are cleaned by various physical forces during open water seasons are important to walleye spawning success (Johnson 1961, Colby et al. 1979). Our study provides insight into the ways in which water level management policies can affect the location and timing of those forces. For example, a policy change to the 2000 rule curve resulted in an 18% increase in wave-induced cleaning of suitable spawning substrates when using modeled water level data. However, this result was confounded by a significant increase in wind speed observed during the period that the 2000 rule curve was in place. When controlling for wind speed using modeled water level data, there was a smaller (6%) increase in wave-induced cleaning.

The small but significant increase in wave-induced cleaning that resulted from the 2000 rule curve is counter-intuitive. Previous research, which examined the relationship between water levels and year-class strength of walleye in the Namakan Reservoir, suggested that a summer drawdown of 0.6 m would provide spawning habitat at lower elevations by allowing suitable substrate types to be cleaned by wave action at lower lake levels (Kallemeyn 1987). That recommendation, which led to the current policy, did not consider the relationship between elevation and the occurrence of suitable walleye spawning substrates, or that wave-induced cleaning occurs over the entire open water season (as opposed to only summer and fall). Surprisingly, in spite of the 0.6 m summer drawdown that occurs under the 2000 rule curve, the mean elevation of water levels during open water seasons is still higher (1970 rule curve: 340.4 m, 2000 rule curve:

340.5 m; $n = 9172$, $t = -7.34$, df = 13449, $P = 2.3\text{e-}13$). This increase in mean elevation is the result of an earlier rise in the reservoir in the spring than what was typical during the 1970 rule curve. Consequently, it appears that the cleaning of fewer substrates during the summer and fall seasons is offset by an earlier rise in water levels in spring, which provides more cumulative wave energy over suitable substrates.

While the mechanism by which wind-induced waves suspend and distribute fine particles is fairly well studied (e.g., Osborne and Greenwood 1993, Bailey and Hamilton 1997, Rohweder et al. 2012), the mechanism(s) by which ice can influence substrates is less understood. Many researchers have studied the ecological disturbances caused by moving ice, particularly in marine intertidal zones (Barnes 1999, Brown et al. 2004, Scrosati and Eckersley 2007); however, those studies have tended to focus on the responses of benthos to ice scour. Fewer studies have examined the effects of ice movement on sediment re-suspension in marine habitats (e.g., Rearic et al. 1990, Woodworth-Lynas et al. 1991). To our knowledge, however, there are no published studies that examine the effects of ice movement on lacustrine freshwater habitats. Using a very basic form of measurement, we showed that forces imparted by ice scour on freshwater littoral substrates are quite significant (Figure 2.6b). These results, combined with the dearth of related research, suggest that ice scour is an overlooked mechanism of habitat disturbance that is important to the maintenance of habitat in larger freshwater systems.

Our model suggests that the interaction of suitable substrates and ice scour forces decreased 11% in the Namakan Reservoir, and that the decrease was due to the raising of minimum water level elevations during ice cover dictated by the 2000 rule curve. Given that the maximum water elevations during ice cover remained similar for both rule curves, it is likely that suitable substrates at higher elevations were still receiving some degree of ice scour. The intensity of forces imparted on those substrates from ice scour may be sufficient to ensure that fine sediments that can impair spawning habitat are re-suspended each winter. To optimize substrate cleaning during winter, future research should examine more closely (1) the mechanisms by which lake ice imparts forces on substrate, (2) the scale of those forces, and (3) the degree to which those forces act to remove fine sediments.

Although waves and ice help to maintain walleye spawning habitats and are important factors in successful reproduction, water level fluctuations in reservoirs also affect the depth at which spawning and incubation occur. Depth mediates the concentrations of dissolved gasses, water temperature, and wave energy at the substrate interface, all of which are important to egg survival (Niemuth et al. 1959, Daykin 1965, Raabe and Bozek 2014). Therefore, understanding how water level policies affect depth during spawning is equally important to reservoir management. In Chapter 3, I quantify and compare the availability of spawning habitat (by depth) during spawning seasons over the 1970 and 2000 rule curves. An examination of habitat conditions during spawning seasons, in addition to the factors that maintain it (i.e., waves, ice), will inform a more comprehensive approach to reservoir management.

Management Recommendations

Our analysis suggests that hydrologic rule curves in the Namakan Reservoir affect more than just lake levels; they also affect the physical forces that maintain spawning habitat for walleye. The information gathered about the elevations at which preferred substrates are likely to occur is crucial to understanding how these forces might interact with, and maintain, those substrates. Interestingly, the occurrence of suitable spawning substrates in the Namakan Reservoir is highest at elevations that are not attained by either the previous or current rule curves. Therefore, maintaining ice-free lake levels at or near those elevations with the highest occurrence of suitable substrates for as long as possible will provide the greatest cumulative cleaning by wind induced wave energy. Similarly, having a wide range of water levels that include those at relatively high elevations during the ice covered months will ensure that the greatest amount of substrates are subject to ice scour, helping to dislodge and redistribute fine sediments.

Table 2.1. The classification scale used in surveying boreal lacustrine shoreline habitat in the Namakan Reservoir. Substrate classes were modified from the typical Wentworth scale (Raabe 2006). Sample codes were used to geo-reference sample locations and for quantifying substrate means and variance.

inorganic substrate type (class)	size (mm)	sample code
Silt	< 0.2	0
Sand	0.2 – 6.4	1
gravel	6.4 – 76.0	2
cobble	76.0 – 150.0	3
rubble	150.0 – 304.0	4
small boulder	304.0 – 610.0	5
large boulder	> 610.0	6
bedrock	consolidated	7

Table 2.2. Summary of Namakan Reservoir study site characteristics. Study sites each demonstrated three consecutive years (2012-2014) of walleye spawning as determined by the presence of walleye eggs. Sites were located on the three large lake bodies of the Namakan Reservoir: Lake Kabetogama (KAB), Namakan Lake (NAM), and Sand Point Lake (SP). Thirty sites were located in U.S. (US) territory and 14 were located in Canadian (CAN) territory. Morphological site characteristics were estimated using the DEM, rather than actual on site measurement. Site coordinates are in UTM Zone 15N projection.

site ID	lake name	country	area of surveyed substrate (m^2)	shoreline length (m)	mean slope (°)	mean elevation (m)	mean aspect (°)	northing (m)	easting (m)
0	KAB	US	658	35	1.9	339.7	241	5368411	501939
4	KAB	US	1213	60	1.7	339.8	228	5368102	499808
5	KAB	US	731	65	2.5	339.9	178	5368079	500438
7	KAB	US	1190	75	3.1	339.8	218	5370393	500452
9	KAB	US	1140	80	2.6	340.0	207	5371492	499377
10	KAB	US	870	55	2.6	339.8	103	5372838	495454
12	KAB	US	1176	60	1.9	339.8	230	5372657	494864
14	KAB	US	1050	40	1.7	339.7	219	5371408	495985
16	KAB	US	810	60	2.4	340.0	237	5372398	496535
17	KAB	US	1512	75	1.4	339.9	314	5371634	496689
18	KAB	US	563	40	2.5	340.0	57	5365029	504991
21	KAB	US	1338	70	1.1	340.2	51	5365252	503839
23	KAB	US	632	60	3.7	340.1	176	5367255	504848
24	KAB	US	1503	100	1.7	340.1	199	5367529	505205
25	KAB	US	932	90	2.9	340.3	260	5365436	508242
26	KAB	US	1037	100	3.4	340.4	254	5365531	508579
78	KAB	US	530	40	2.5	340.1	204	5372733	494030
27	NAM	US	469	40	3.6	339.8	157	5366112	515268

Table 2.2 Cont.

29	NAM	US	631	70	3.2	340.1	147	5365981	517651
30	NAM	US	511	40	4.5	340.0	234	5364528	520317
32	NAM	US	730	45	3.5	339.7	110	5364315	520724
34	NAM	US	441	40	2.2	338.9	215	5366929	518647
35	NAM	US	1166	60	2.4	339.7	254	5364283	522951
40	NAM	US	1002	70	3.1	339.8	164	5365846	516475
41	NAM	US	815	60	4.8	339.7	171	5364589	524682
44	NAM	US	474	40	1.1	339.1	111	5365404	534707
46	NAM	CAN	560	40	0.8	339.6	183	5366601	536383
48	NAM	CAN	1013	60	2.6	339.9	52	5365527	538121
49	NAM	CAN	503	45	0.6	339.4	169	5367984	538200
52	NAM	CAN	1402	60	2.1	340.1	153	5367930	535604
53	NAM	CAN	553	30	1.7	340.0	134	5367964	534518
54	NAM	CAN	578	30	1.6	340.2	233	5368020	534263
57	NAM	CAN	950	50	2.0	340.1	194	5368204	533444
59	NAM	CAN	649	30	1.1	339.5	220	5368645	532971
60	NAM	CAN	715	50	2.7	339.9	220	5368227	531672
62	NAM	CAN	445	25	1.6	340.1	189	5367656	531087
64	SP	US	1183	75	2.8	339.9	181	5361690	539559
65	SP	US	537	40	2.9	339.7	93	5358474	538548
67	SP	US	667	55	3.2	339.4	59	5356481	538165
68	SP	US	726	25	1.3	339.4	160	5354191	539112
71	SP	CAN	460	35	3.6	340.4	242	5355394	539482
72	SP	CAN	551	40	4.1	340.1	258	5356037	539369
76	SP	CAN	761	60	3.3	339.5	106	5359532	540062
77	SP	CAN	1124	60	2.8	339.5	233	5360759	540953

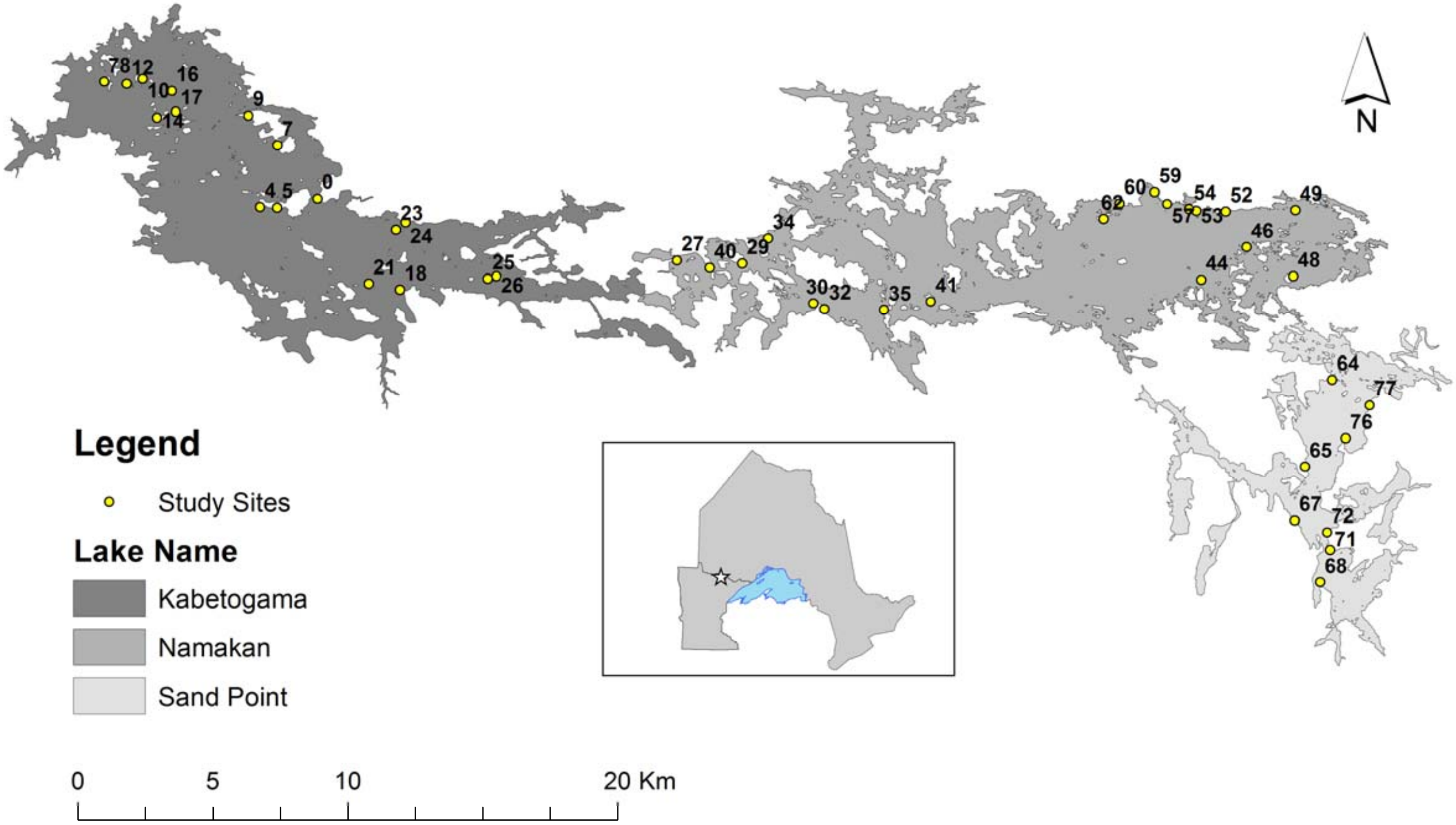

Figure 2.1. Map of the large lakes of the Namakan Reservoir: Lake Kabetogama, Namakan Lake, and Sand Point Lake. The 44 study sites are labeled with the site ID number and the inset shows the location of the reservoir relative to Lake Superior, Minnesota, and Ontario.

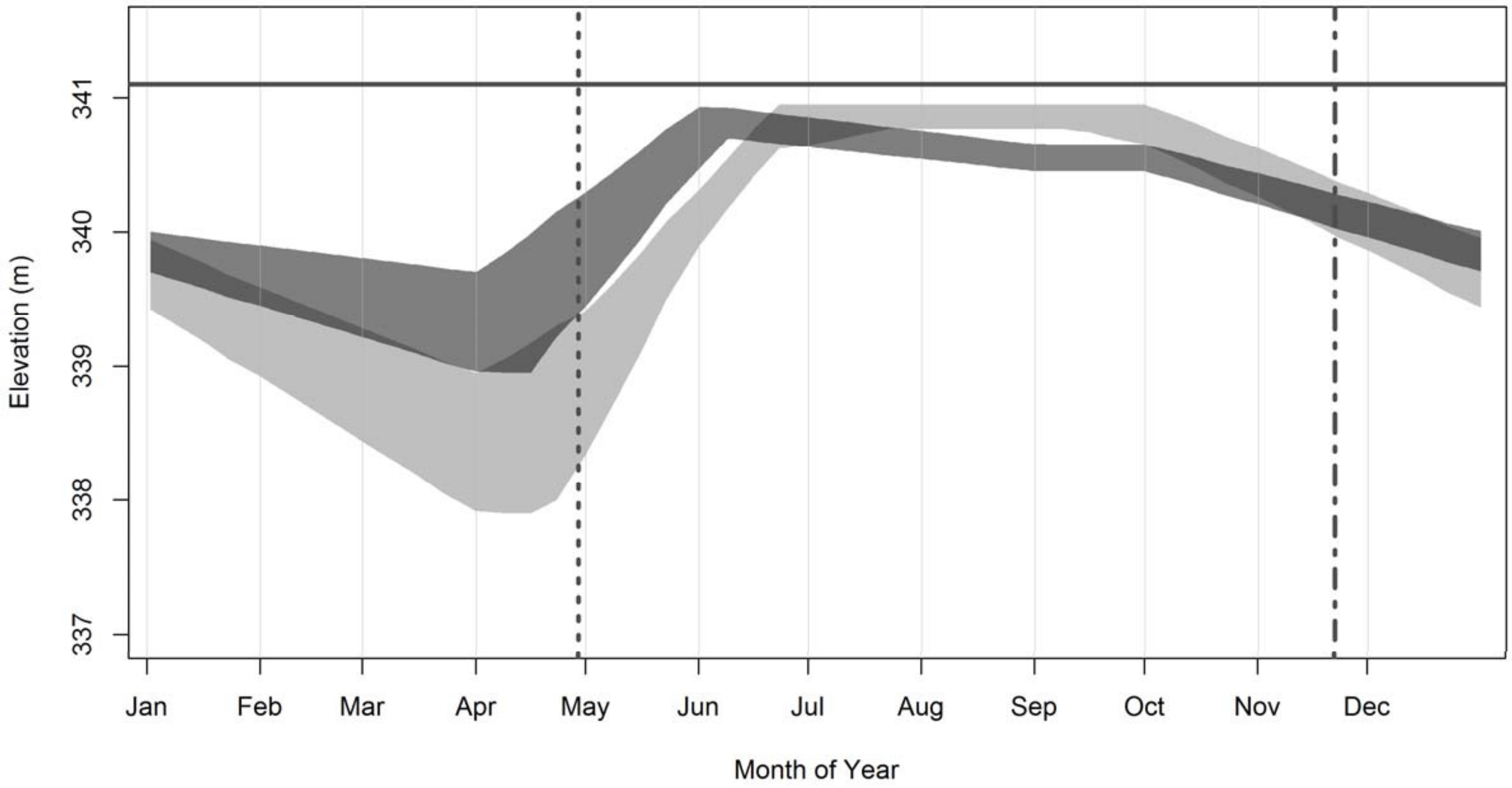

Figure 2.2. Hydrographs for the 1970 rule curve (in effect from 1970-1999, light gray) and 2000 rule curve (in effect from 2000-present, dark gray) on the Namakan Reservoir. Dam operators control outflows by targeting elevations at the middle of the shaded areas. The solid horizontal line indicates the elevation with the highest estimated proportion (reservoir-wide) of suitable spawning substrate (341.1 m, 51%). The dotted, and dot-dashed vertical lines indicate the mean observed date of ice-out (SD = 9.8 days), and mean predicted date of freeze-up (SD = 5.8 days) (i.e., open water seasons), respectively. Vertical elevations are relative to the USC&GS 1912 datum.

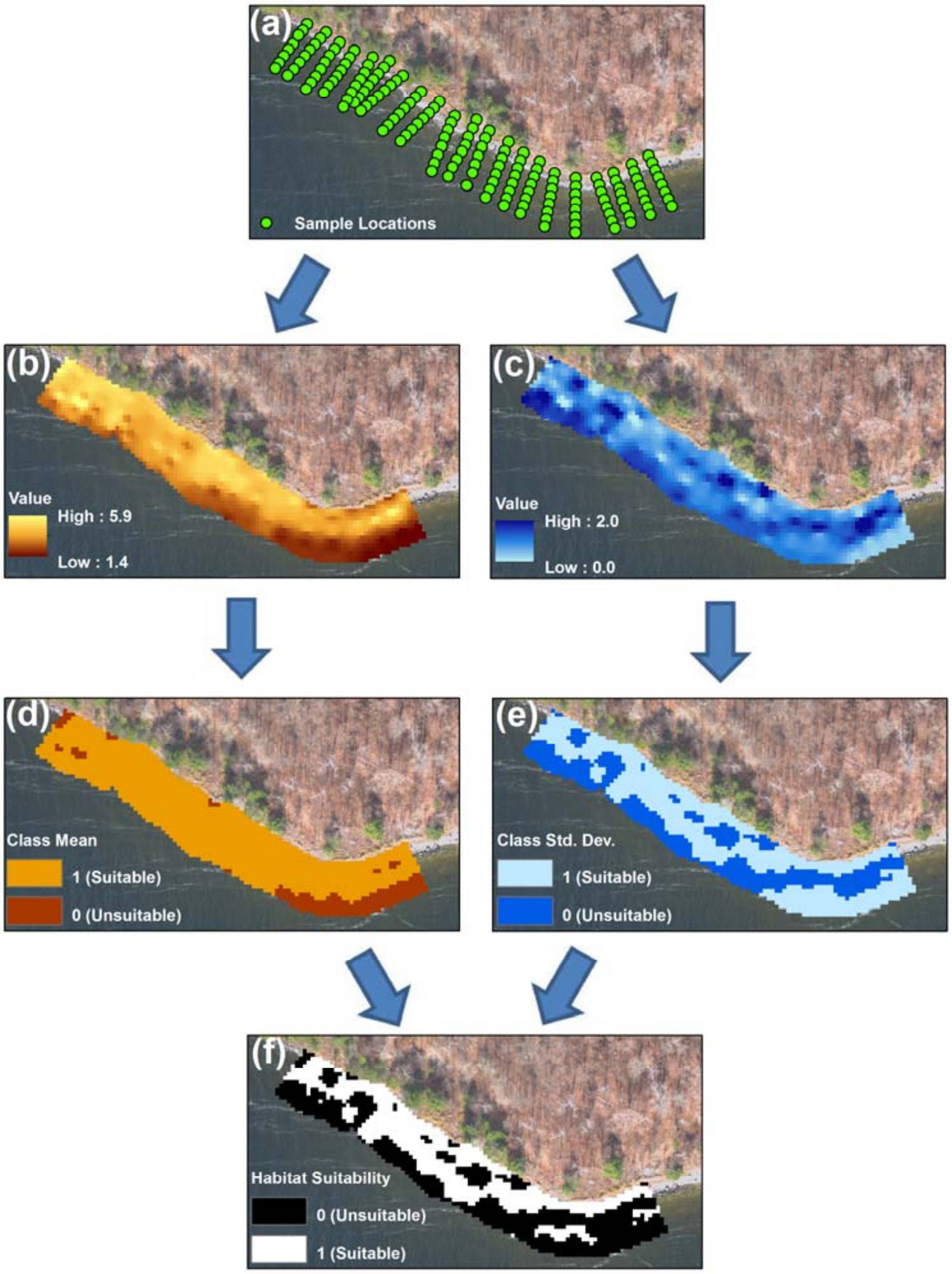

Figure 2.3. A flow diagram for creating observed substrate suitability rasters at site 24. Map (a) depicts the locations of substrate samples collected at the site. Maps (b) and (c) are interpolations of the sample means and sample standard deviations, respectively. Sample means and sample standard deviations were then reclassified. Means greater than 2 and less than 4 were reclassified as suitable (d), and standard deviations less than 1 were reclassified as suitable (e). Finally, (d) and (e) were spatially multiplied to produce the substrate suitability raster (f). All maps are drawn to the same scale (1:1000) and oriented so that north is up.

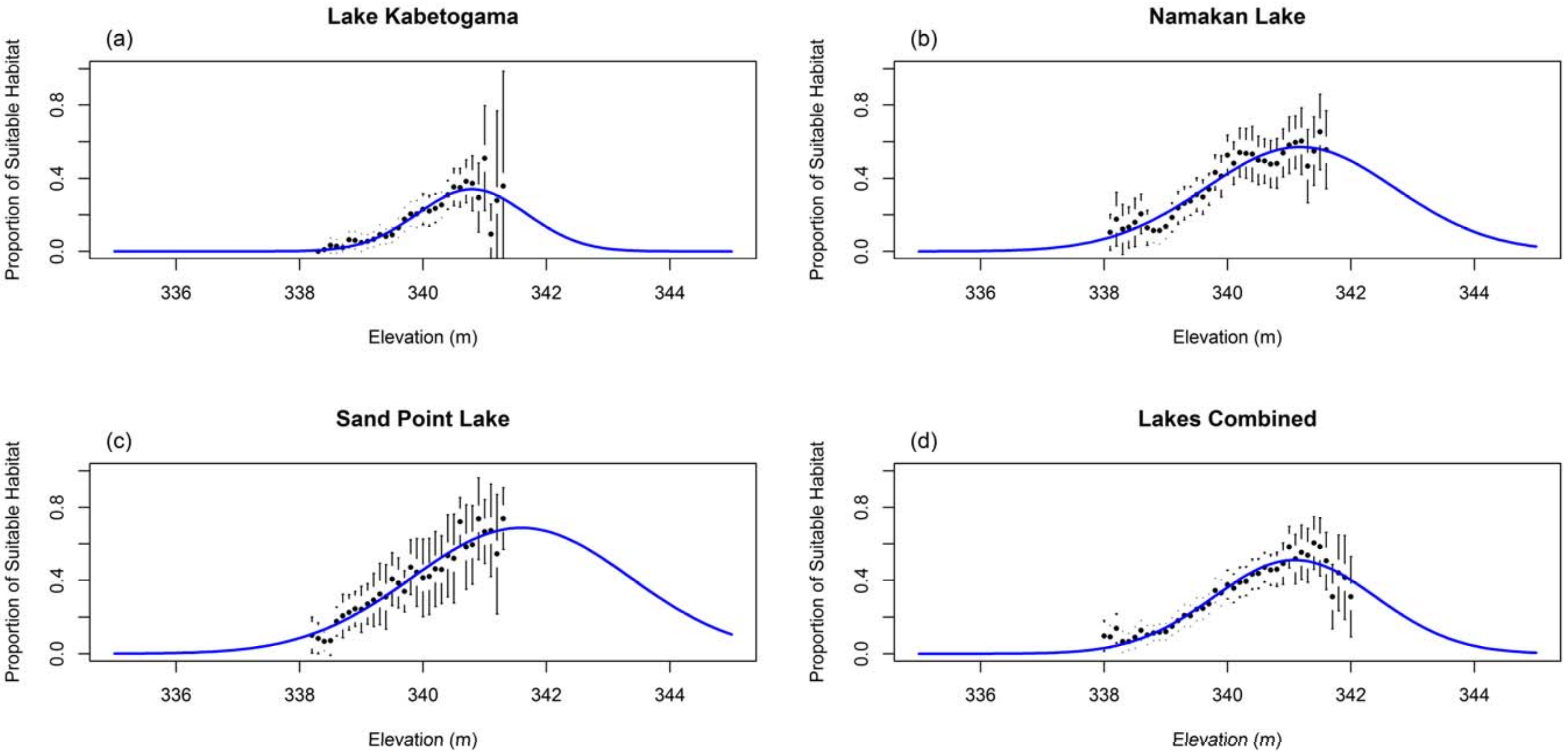

Figure 2.4. We fit Gaussian functions to observed substrate suitability data using nonlinear least squares fitting. The fit was performed for each large lake in the reservoir (a-c). A Gaussian function was also fit to the aggregate (reservoir-wide) suitability data (d).

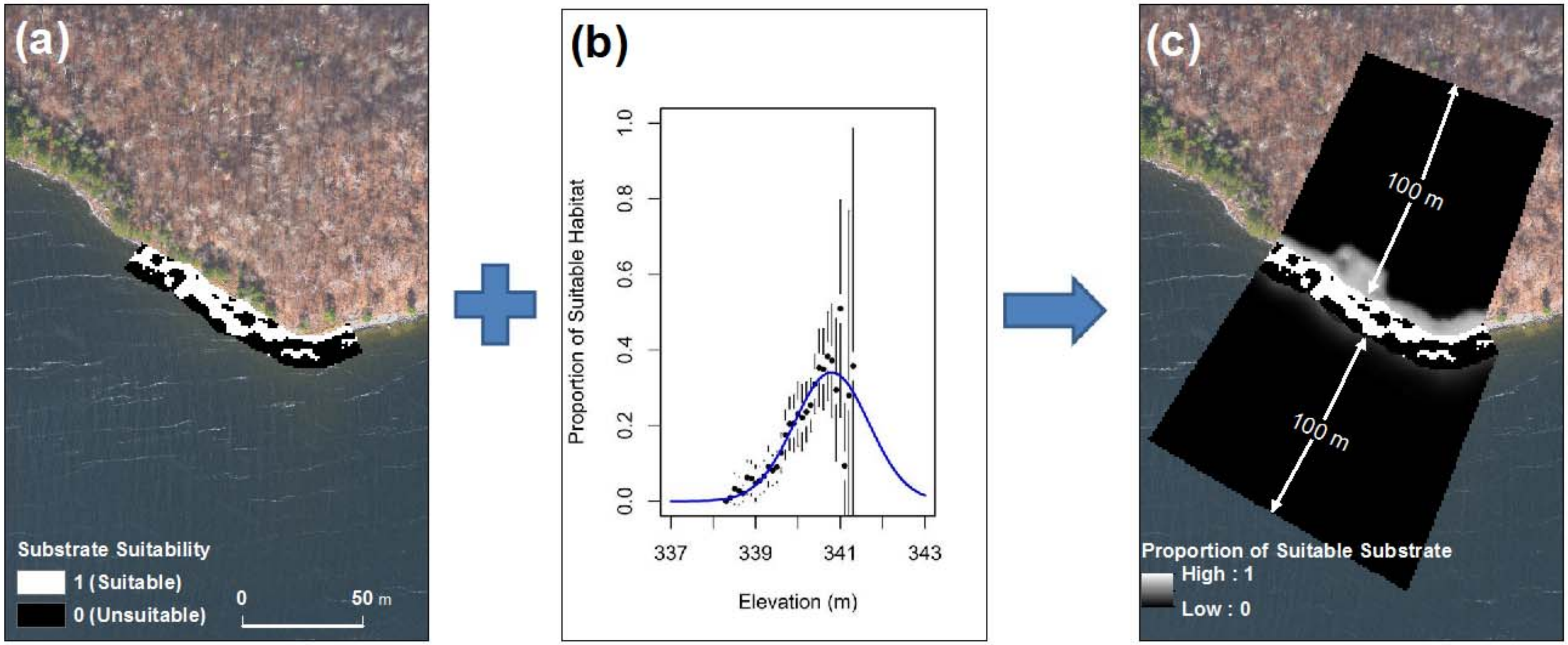

Figure 2.5. A flow diagram for creating substrate suitability rasters at site 24 at increased range of elevations. Map (a) depicts the observed substrate suitability (see Figure 2.3). Plot (b) is the Gaussian model used to predict substrate 100 m upslope and downslope from the observed data. Map (c) is the observed suitability overlaid onto the predicted suitability. Both maps are drawn to the same scale (1:1000) and oriented so that north is up.

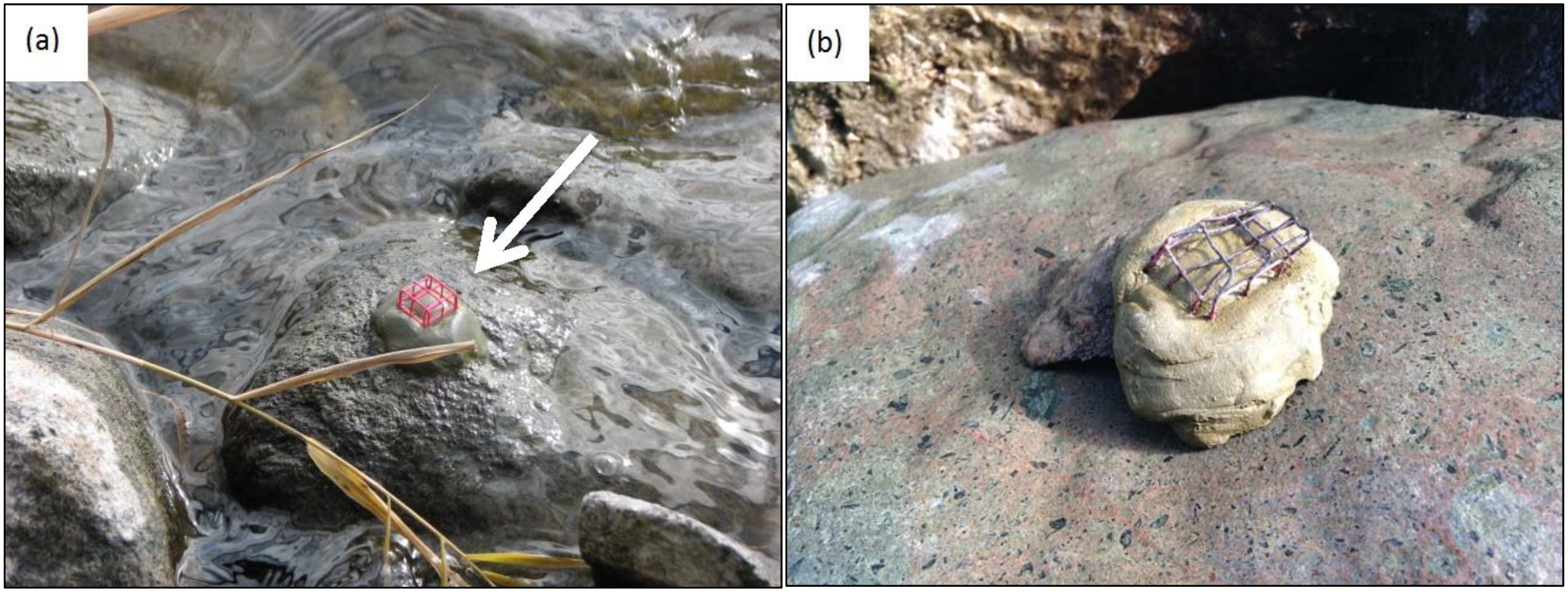

Figure 2.6. Photograph (a) shows an ice scour cage affixed to typical spawning substrate prior to 2012-2013 winter season on Lake Kabetogama. The epoxy resin used to hold the cage to the substrate can be seen underneath the cage. Photograph (b) shows the cage after ice scour with an 80° defection. All cages and resin compound were removed from the reservoir in the spring following deflection measurement.

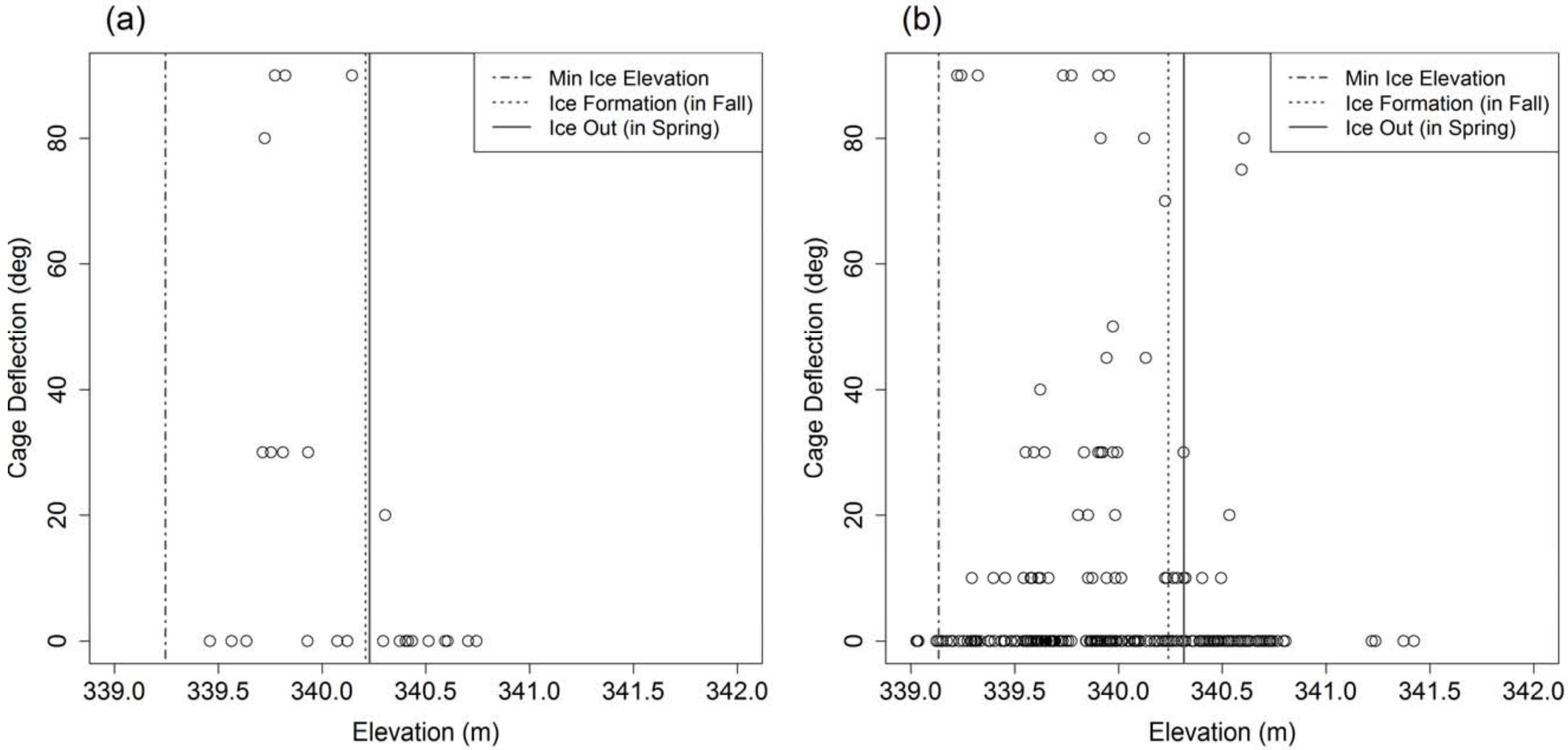

Figure 2.7. Summary of raw ice scour data for a pilot site (a) and the remaining 12 sites (b) on Lake Kabetogama. Cages were deployed at the pilot site (site 78) during the 2012-2013 winter season. Cages at the remaining sites were deployed during the 2013-2014 winter season.

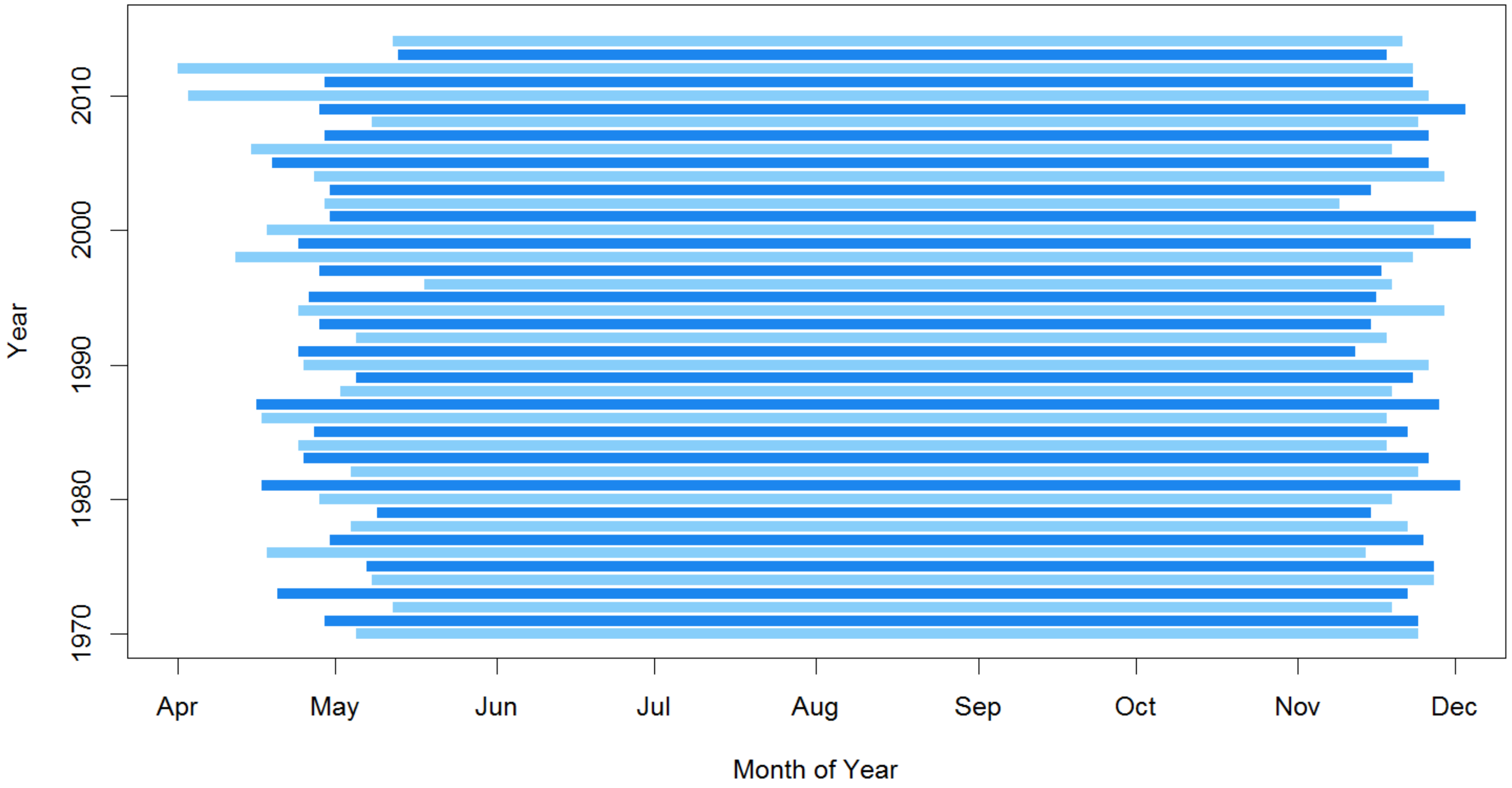

Figure 2.8. Summary of ice-free durations on the Namakan Reservoir during each year of the study period (1970-2014). Freeze-up dates were predicted using a linear regression model (Shuter et al. 2013) that was calibrated to the Namakan Reservoir using publicly available satellite imagery to ascertain actual freeze-up dates. Ice-out dates are from historical observations of Lake Kabetogama ice-out.

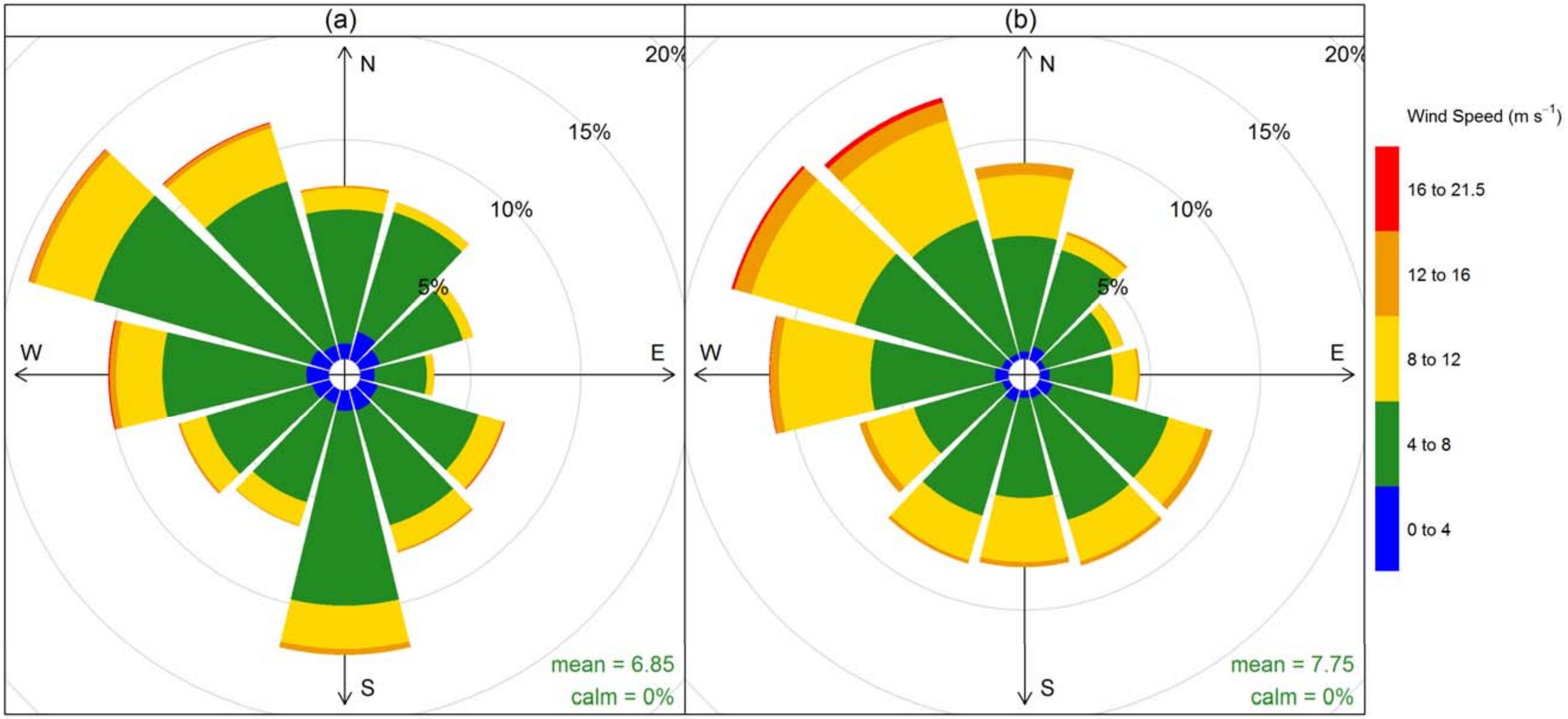

Figure 2.9. Windrose diagrams for the 1970 rule curve (a, 1970-1999) and 2000 rule curve (b, 2000-2014). The diagrams plot the frequency of mean daily wind by both speed and direction. The predominant wind direction for both periods is from the west-northwest. Data are from the International Falls International Airport weather station. The station is approximately 20 km to the nearest point of the Namakan Reservoir.

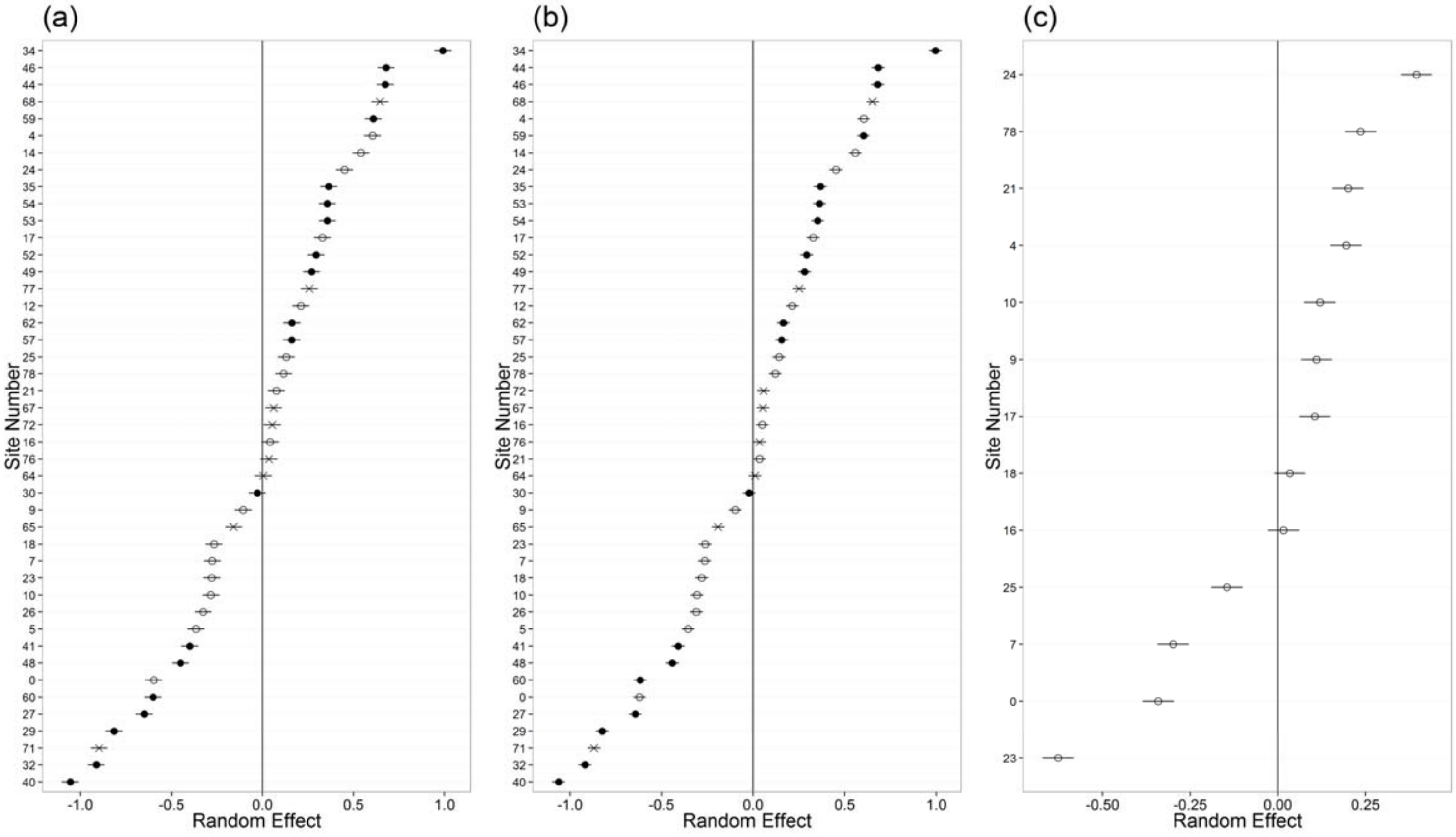

Figure 2.10. Estimates of the random site effects generated by mixed ANOVA for the 44 Namakan Reservoir study sites. Estimates are of the random effects of wave induced cleaning over suitable spawning substrates for both observed (a) and modeled (b) water levels, and (c) ice scour forces over suitable spawning substrates. Results are shown by lake: Lake Kabetogama (○), Namakan Lake (●), and Sand Point Lake (×). Predictions intervals are shown as black bars.

Chapter 3

The effects of water level policies in the Namakan Reservoir on the availability of walleye spawning habitat during spawning seasons[2]

Summary

Water level policies in reservoirs significantly affect the quantity of habitat available for spawning walleye (*Sander vitreus*) and moderate the depth at which eggs incubate. We studied how two water level management policies (‘1970 rule curve’ and ‘2000 rule curve’) have affected the availability of spawning habitat on three large lakes in the Namakan Reservoir, an international waterway on the border of Ontario, Canada and Minnesota, USA. We modeled habitat availability at 44 spawning locations throughout the reservoir during estimated spawning seasons, and compared the effects of rule curves via both observed and modeled water level data. Observed water level data suggested that available spawning habitat on Lake Kabetogama increased 95% ($P < 0.01$) because of the 2000 rule curve, but availability on Namakan Lake and Sand Point Lake was unaffected. However, when using modeled water level data to control for confounding weather events, spawning habitat availability increased significantly ($P < 0.01$) on all three lakes (Kabetogama = 179%, Namakan = 72%, Sand Point = 93%). Habitat availability improved because the 2000 rule curve increased mean springtime water levels by 0.5 m, and water levels rose more slowly (2.2 vs. 3.0 cm/day) while eggs were incubating. The former created more overlap between proper spawning depth regimes and preferred spawning substrates, while the latter probably reduced the stranding of eggs in water that is too deep and/or cold. Our findings suggest that controlling reservoir water levels can be challenging, but carefully planned water level management can lead to improved spawning conditions and reproductive success of walleye.

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[2] This chapter has been prepared as a manuscript for publication. Co-authors include Paul A. Venturelli and Tim Cross. I will use the plural pronouns “we” or “our” instead of the singular “I” or “my” in reference to co-authorship in this chapter.

Introduction

The walleye (*Sander vitreus*) is an ecologically, culturally, and economically important fish species in north central North America; therefore, its biology, habitat, and life history characteristics are well studied (Colby et al. 1979, Scott and Crossman 1973, Barton 2011). Much of this research has focused on the relationships between abiotic factors (e.g., water temperatures, storm events, wind energy) and walleye reproduction (often year-class strength) in natural lakes (Busch et al. 1975, Madenjian et al. 1996, Raabe and Bozek 2014). Seasonal water level fluctuations in natural lakes are relatively small and therefore unimportant for walleye reproduction (Raabe and Bozek 2014). However, water level fluctuations in managed reservoirs can vary considerably. These fluctuations tend to maintain the abundance and quality of suitable habitat through wind energy and ice scour (ref. Chapter 2), but may also limit the extent of preferred habitat during spawning if suitable substrates are unevenly distributed across elevation (Colby et al. 1979). The artificial manipulation of water levels is one of the most widespread problems facing walleye populations (Kerr et al. 1997). However, in spite of the ubiquity of reservoirs across North America (Downing et al. 2006) where walleye are prevalent, few studies have focused on the relationships between water level management and walleye (e.g., Chevalier 1977, Kallemeyn 1987, Cohen and Radomski 1993).

Fluctuating water levels are especially important during the spawning season because they dictate the depth and spatial arrangement of the littoral substrates that are available for spawning walleye (Osborn et al. 1978, Osborn and Ernst 1979). Preferred substrates consist of clean, wind-swept gravel, cobble, and rubble (16 to 256 mm diameter) (Eschmeyer 1950, Priegel 1970, Bozek et al. 2011a, Raabe and Bozek 2012). Spawning over these substrates increased the survival rate of walleye eggs in a boreal lake (Johnson 1961). Preferred spawning depths range from approximately 30 to 75 cm (Eschmeyer 1950, Johnson 1961, Priegel 1970, Raabe and Bozek 2012), and reflect the advantage of depositing eggs shallow enough that they are in contact with relatively warm, oxygen-rich, surface water, but not so shallow that they are subject to wave-related processes or desiccation (Raabe and Bozek 2014). Dissolved oxygen is critical to the survival and development of walleye eggs, and varies with depth (i.e., water levels)

(Daykin 1965). Concentrations >5-6 mg/L are optimal for walleye egg incubation (Oseid and Smith 1976), while concentrations <3 mg/L result in high egg mortality (Auer and Auer 1990). Therefore, increasing water levels during the spawning season can influence egg survival by starving eggs of dissolved oxygen, while decreasing water levels can expose eggs to abrasion, transport, desiccation, etc.

The Namakan Reservoir, located on the border between Minnesota, USA, and Ontario, Canada, is a boreal reservoir that has undergone changes in water level management policies ('rule curves'). Water levels have been managed under two separate rule curves (Kimmett et al. 1999) (Figure 3.1): the 1970 rule curve, which was in effect from 1970 to 1999; and the 2000 rule curve, which has been in effect from 2000 to present. The 2000 rule curve was implemented, in part, to optimize walleye productivity. It differed from the 1970 rule curve in three important ways: (1) a narrower range of water levels during the ice season (~November through April), (2) higher water levels in spring (~April through June), and (3) reduced water levels in summer (~June through November). The increase in springtime water levels was intended to improve spawning conditions for walleye by flooding preferred habitat, which was presumed to occur at higher elevations, earlier in the spring. Although surveys in the Ontario waters of Namakan Lake in 2004 and 2005 suggested that walleye abundance improved after 2000 (McLeod and Trembath 2007), later surveys in all lakes suggested that spawning success has remained low, and may be declining in Lake Kabetogama (MNDNR unpublished data, Jackson 2015). Unclear is the extent to which the 2000 IJC rule curve and attendant changes in the availability of spawning habitat are responsible for these disparate responses.

In this study, we compared the effects of the two rule curves on the availability of habitat during spawning seasons. Our goal was to determine if one rule curve was more effective at providing walleye with access to preferred substrates at depths shallow enough to provide an oxygen-rich environment, but deep enough to provide protection from wave energy and desiccation. The timing and duration of water level fluctuations are important determinants of the quality and quantity of spawning habitat available to walleye in reservoirs, where human demands are also varied and intense (e.g., hydroelectricity, irrigation, flood control, navigation). Improving our understanding of how water levels affect habitat can help to balance these competing demands.

Methods

Spawning habitat: Sites, surveys, and modeling

To compare the effects of rule curves on the availability of walleye spawning habitat, we first had to estimate the spatial distribution of preferred substrates at spawning sites throughout the reservoir. Chapter 2 describes our procedure for selecting study sites, describing the substrate at those sites, and predicting spawning substrate suitability at elevations not surveyable with snorkel gear. In brief, we (1) selected study sites from a larger set of known spawning locations based on site length and morphological diversity (Table 2.2, Figure 2.1), (2) conducted substrate surveys at those sites during the 2013 open-water season, and (3) used lake-specific functions describing the elevational distribution of suitable substrate to predict the probability of suitable substrate at inaccessible elevations. Because we were also interested in the effects of site characteristics (as covariates) on habitat availability, we used a digital elevation model (DEM) (Morin et al. 2014) to estimate the length, area, mean slope, and mean elevation of each site.

Egg depth validation

The depth range over which walleye spawn is relevant to water level management and an important factor in modeling the availability of habitat during spawning. To estimate the preferred depth range of spawning walleye in the Namakan Reservoir, we randomly selected 10 study sites and surveyed preferred substrates (gravel, cobble, and rubble) at each site for the occurrence of eggs by depth. We established transects perpendicular to the shoreline at 5 m intervals, and sampled points along those transects at depth intervals of 25, 50, 75, and 100 cm. Because eggs normally incubate in the interstitial spaces between substrates, we modified the protocol for sampling freshwater benthic invertebrates described in Barbour et al. (1999) to collect and count walleye eggs. Specifically, we used the heel of a boot to sample benthos by manually disturbing substrates such that eggs were suspended in the water column. We used a single jab with a scap net to sample any eggs that were suspended by the boot motion. If a net appeared to contain <50 eggs, we counted all eggs in the sample. If a net appeared to contain >50 eggs, we used a placard to divide the net into 25 equal area sections, counted the number of eggs in five randomly selected sections, and then multiplied that number by 5 to estimate the total number of eggs sampled.

Seasonal modeling

Water temperature in the littoral zones of boreal reservoirs is a major factor in the timing and duration of walleye spawning and incubation of walleye eggs (Eschmeyer 1950, Scott and Crossman 1973, Becker 1983). We estimated the timing and duration of walleye spawning seasons in the Namakan Reservoir in three stages: initiation of spawn, peak spawn, and peak hatch. We first estimated water temperatures in the Namakan Reservoir from 1970 to 2014 via a water temperature model described in Matuszek and Shuter (1996). This model uses 5- and 15-day moving averages of daily air temperatures and year-day to predict water temperature at 1-2 m depths. We used the daily average air temperatures taken from the International Falls International Airport Weather Station as inputs (NOAA 2015), and calibrated the model using 28 years of bi-weekly water temperature measurements taken at a depth of 1 m at the Grave Island monitoring site on Lake Kabetogama.

Walleye can begin spawning at temperatures as low as 2°C (Hokanson 1977); therefore, we used ice-out dates to indicate the start of the spawning season. Because ice-out dates were based on both ground and areal observations of lakes in the reservoir, they represent best estimates that are roughly accurate to within one week of actual ice-out. Peak spawning activity for walleye typically occurs within the range of 5.6 to 10°C (Niemuth et al. 1959, Becker 1983). We selected 10°C as the peak spawning temperature in the Namakan in order to capture the greatest variability in water levels during spawning seasons. Finally, we used cumulative degree-days (DD) to predict peak hatch. We calculated degree-days in a given day as

$$DD = T_w - T_o, \tag{3.1}$$

where T_w is the average daily water temperature and T_o is the base temperature below which egg development is assumed to be negligible. Starting at peak spawn date, we summed DD daily assuming a T_o of 2.13°C until the cumulative sum reached a threshold value of 138.3°C·days (Venturelli and Cabrini, in revision). We assumed that the date that this threshold was reached was the date of peak hatch. Because newly hatched larvae are capable of vertical movement after ~1 day (Scott and Crossman 1973, Mathias and Li 1982), we added a single day to peak hatch to account for swim-up (i.e., larvae disassociating from the substrate). Accordingly, the total estimated spawning period for each year of the study period spanned the duration from ice-out to swim-up of larvae.

Habitat modeling, summarization, and analysis

Walleye spawning and egg development occur over a narrow range of depths, and are highly dependent on water levels during a critical period that is defined by temperature (Niemuth et al. 1959, Johnson 1961, Priegel 1970). Therefore, we spatially modeled the availability of spawning habitat via a DEM (Morin et al. 2014), our estimated spawning periods, and water levels that were assumed planar throughout the reservoir (LWCB 2014). We used bilinear interpolation to resample the DEM to 1 m so that it was at the same resolution as suitable substrate rasters that were created in Chapter 2. We created suitable spawning depth rasters (1 m resolution) by reclassifying the DEM into suitable depths (assigned pixel value 1) at two time points: peak spawn and swim-up. Suitable depths were defined by our spawning depth validation. Overlapping these two rasters identified the total area of habitat that was a suitable depth from peak spawn to swim-up. Finally, we spatially multiplied these depth suitability rasters by the substrate suitability rasters from Chapter 2. Each 1 m cell of the output raster indicated the area within that cell that was at a suitable depth and over preferred substrate during the spawning season (Figure 3.2a-c).

Water level fluctuations dictate the availability of spawning habitat, but these fluctuations also depend on factors other than rule curves (e.g., rainfall, drought). If one or more of these factors vary with rule curve periods (e.g., more or less rainfall after 1999) then a rule curve comparison is confounded. To control for confounding factors, we used a hydrologic model (Thompson 2013) to compare the rule curves with modeled water level inputs as well as observed water level inputs (similar to the analysis in Chapter 2). Using observed water level inputs allowed us to compare the rule curves in series, while using the modeled water level inputs allowed us to compare the 1970 rule curve (modeled from 1970 to 2014) to the 2000 rule curve (modeled from 1970 to 2014) in parallel, and therefore independent of confounding factors. The hydrologic model uses a conservation of mass approach to predict a time series of water levels (from 1950 to 2014) using either the 1970 or 2000 rule curve. Because the model uses a quarter-monthly time step, we linearly interpolated between intervals to obtain daily time series for our analyses.

To predict the available habitat under both scenarios (observed and modeled water levels), we summed the area available at sites and accounted for variation in site size by dividing each sum by the total site area. Because the responses in both scenarios demonstrated non-normality, we applied a $\log_{10}(Y+C)$ transformation, where C was the minimum non-zero response (Zuur et al. 2009, Warton and Hui 2011). We then employed a mixed ANCOVA to model the log-transformed proportion of available habitat. In the first scenario, we used observed water level data to predict the proportion of available habitat as a function of rule curve (fixed effect), site area, site length, site slope, mean site elevation (all covariate fixed effects), and study site (random effect). Because we were interested in the lake-specific responses to the rule curves, we also included a lake-rule curve interaction term as a fixed effect. In the second scenario, we used modeled water level data to predict the proportion of available habitat as a function of water level model (fixed effect). We included a lake-model interaction term in this model as well, and left all other predictors the same. We defined study sites as a mixed effect to control for temporal pseudo-replication, and because the study locations represented a subset of all available spawning sites in the reservoir.

All statistical analyses were performed in R, version 2.15.1 (R Core Team 2012) using the lme4 package (Bates et al. 2012). All spatial analyses were performed in ArcGIS, version 10.0. We geo-referenced egg validation measurements with a Trimble®

GeoXT capable of sub-meter resolution and employed a combination of real-time and post-processed differential correction methods.

Results

Egg counts in our egg depth surveys ranged from 0 to 315 eggs per sample, with the maximum count observed at a depth of 25 cm on site 25 (Lake Kabetogama). Egg counts on both Kabetogama and Namakan lakes peaked at 25 cm and decreased with both increasing depth; however, egg counts on Sand Point peaked at 50 cm (Figure 3.4a). We suspect that eggs on Sand Point were spawned earlier in the season (Sand Point tends to ice-out the earliest) while water levels were rising. Over 90% of the eggs that we sampled were collected at depths between 25 and 75 cm (Figure 3.4b), which corroborates published estimates of a preferred depth range of 30 to 75 cm (Eschmeyer 1950, Johnson 1961). We created our suitable spawning depth rasters assuming a preferred depth range of 10-100 cm. This slightly expanded depth range was used to account for variation in water levels within and between lakes in the reservoir during times of rapid water level increases common in spring.

We found a significant ($r^2 = 0.89$, $F_{5,313} = 493$, $P < 2.2e\text{-}16$) linear relationship between air temperature and water temperature that was described by the equation:

$$T_1 = -21.2 + 0.348(ATEMP1) + 0.262(ATEMP2) + 0.313(YDAY) \\ -0.000732(YDAY)^2 - 342(INVAYD), \tag{3.2}$$

where *ATEMP1* is the 15-day mean air temperature, *ATEMP2* is the 5-day mean air temperature, *YDAY* is the day of the year, and *INVAYD* is the inverse of *YDAY* adjusted such that ice-out is standardized to *YDAY* 100.

We used equation (3.2) to estimate peak spawning dates in the reservoir. Peak spawning ranged from May 4 to May 27 (Figure 3.3), with a mean date of peak spawning over all 44 study years of May 14 ± 6 SD days. There was no significant difference in the mean dates of peak spawn across rule curves as determined by a Welch two-sample t-test (*CI* = [-5.0, 2.7], *P* = 0.54). We used equation (3.1) to estimate peak hatch dates that ranged from May 17 to June 7 (Figure 3.3), with a mean date of May 27 ± 5 days SD.

Similarly, the mean dates of peak hatch did not vary between rule curves ($CI = [-5.0, 2.2]$, $P = 0.42$).

Our analysis of habitat availability using observed water levels showed that the proportion of habitat available at Lake Kabetogama sites increased, on average, by a factor of 1.95 ± 0.15 SD ($n = 1980$, $t = -9.03$, df = 1933, $P = 2.0e-16$) as a result of the 2000 rule curve. However, the proportions of habitat available on Namakan Lake and Sand Point Lake were unaffected ($P > 0.01$). The same analysis with modeled water level data (which helped to control for confounding factors) showed that the proportion of habitat available increased, on average, by a factor of 2.79 ± 0.13 SD ($n = 3960$, $t = -22.1$, df = 3914, $P < 2e-16$) on Lake Kabetogama, 1.72 ± 0.11 SD ($n = 3960$, $t = -8.842$, df = 3914, $P = 2.0e-16$) on Namakan Lake, and 1.93 ± 0.11 SD ($n = 3960$, $t = -7.98$, df = 3914, $P = 2.0e-15$) on Sand Point Lake. The covariates site area, length, mean slope, and mean elevation did not contribute significantly ($P > 0.01$) in either analysis. Random site effects for both the observed and modeled water level analyses suggested that the proportion of preferred habitat was site-specific, and greatest at site 34 and lowest at site 60 (both sites on Namakan Lake) (Figure 3.5). Model validation (for both observed and modeled cases) demonstrated normality of the response and homogeneity of the residuals.

Discussion

Our results suggest that the 2000 rule curve increased the proportion of available spawning habitat at sites across all lakes by 28% using observed water level conditions, and by 96% under modeled water level conditions. While these improvements are likely to have a positive effect on spawning success, the effects vary significantly by lake. A post-hoc comparison of least-squares means (irrespective of rule curve) suggests that yearly spawning habitat availability on both Namakan Lake and Sand Point Lake is greater than Lake Kabetogama by a factor of approximately 3 ($P < 0.01$). However, the difference in habitat availability between Namakan Lake and Sand Point Lake is not significant ($P > 0.01$). These results are consistent with our observations of the distribution of preferred spawning substrates in the reservoir (Chapter 2, Figure 2.4). The narrower distribution (by elevation) of preferred substrates in Lake Kabetogama is consistent with a greater sensitivity to water level fluctuations. Thus, maintaining water levels within rule curve limits as much as possible is important, particularly on Lake Kabetogama because minor deviations from the rule curve alter habitat availability considerably.

Several studies have examined the dependence of walleye spawning success on spring water levels and found it to be an important factor in determining the abundance of subsequent year-classes. For example, Chevalier (1977) used commercial harvest records from the Rainy Reservoir for the period 1924 to 1975 to demonstrate a significant relationship between springtime water levels and walleye abundance 5 years later. Similarly, Kallemeyn (1987) found a significant relationship between age-0 walleye abundance and springtime water levels in Lake Kabetogama and Sand Point Lake from 1981 to 1985. However, Osborn et al. (1981) found no relationship between springtime water levels and year-class strength after 5 years on either the Rainy or Namakan Reservoirs. A comparable study found that walleye abundance was unrelated to water levels on Lake Erie from 1960 to 1970 (Busch et al. 1975). These contradictory results have been attributed to various factors. For example, it is unlikely that spawning habitat limits reproduction in Lake Erie, and Osborn et al. (1981) used data from a small area of their study lakes, thereby excluding a large segment of the lake-wide walleye population. Our study not only supports the link between springtime water levels and walleye abundance, but also provides crucial insight into how rule curves can improve habitat availability when it is a limiting factor in reproduction.

Two features of the 2000 rule curve likely led to improvements in the availability of walleye spawning habitat in the Namakan Reservoir. First, water levels are higher earlier in the spring under the 2000 rule curve, which raises the elevation at which walleye spawn. Over our study period (1970-2014), the actual observed water levels in the reservoir during the spawning seasons associated with the 1970 and 2000 rule curves were 340.0 and 340.5 m, respectively. Therefore, the 2000 rule curve places water level elevations closer to 341.1 m, the elevation at which substrate suitability is maximized (Chapter 2). Second, the 2000 rule curve prescribes a slower increase in water levels in spring. The mean observed rates of water level increase for the 1970 and 2000 rule curves between ice-out and peak hatch were 3.0 ± 1.0 and 2.2 ± 0.8 cm/day SD respectively. A relatively slower increase in water levels during spawning and development is less likely to strand eggs at sub-optimal depths (and therefore sub-optimal temperatures and oxygen concentrations). For example, during our 2014 spawning survey, abundant precipitation caused water levels to increase at a mean rate of 3.1 cm/day between ice-out and peak hatch (41% faster than the 2000 rule curve average). During this survey year, we observed more dead eggs, and eggs at depths deeper (particularly in Sand Point Lake) than in previous survey years.

While our analysis demonstrated improvements in habitat availability resulting from the 2000 rule curve, we should avoid making water levels policies a panacea for enhancing habitat in reservoirs. Walleye use a diversity of habitat types that vary both annually and by life stage (Bozek et al. 2011b). Timing water levels fluctuations to overlap with spawning and egg development requires that we know or can predict when these events occur. However, these events depend on climate and weather conditions that vary annually. For example, although the 2012 ice-out on the Namakan Reservoir was the earliest in recorded history, the 2013 and 2014 ice-outs were the second and third latest, respectively. Consistent, repetitive water level fluctuations may also be detrimental to habitat suitability over longer time-spans. A study on the Namakan and Rainy Reservoirs found significant, positive relationships between walleye populations and annual water level elevation ranges (Cohen and Radomski 1993) that were attributed to dynamic interactions at the community level. These greater-than-normal fluctuations were presumed to coincide with nutrient distribution, plant regeneration, and shoal cleaning; all of which may affect walleye reproduction in indirect ways.

Although it is tempting to conclude that increased spawning habitat availability following the establishment of the 2000 rule curve resulted in greater walleye abundance, this study does not establish a causal link. Even though we controlled for weather events and climate by modeling rule curves in parallel, our study is still observational in nature, and subject to model error and confounding factors such as harvest regulations. The Namakan Reservoir underwent changes in total catch quotas and angler slot regulations several times during the study period (McLeod and Trembath 2007). These changes could have a significant effect on walleye populations over time, and complicate the link between habitat and abundance. A second example is the introduction of several invasive species in the Reservoir since the 2000 rule curve. Spiny water flea (*Bythotrephes longimanus*) and rusty crayfish (*Orconectes rusticus*) were both discovered in the reservoir during the period 2004-2006 (R. Maki, Voyageurs National Park, personal communication). The introduction of non-native species affects changes in aquatic ecosystems (Crowl et al. 2008), and has been implicated in the decline and/or suppressed recovery of walleye in other large lakes (Schneider and Leach 1977, Miehls et al. 2009). These and other potentially confounding factors should be accounted for when assessing the relationship between walleye abundance and rule curves.

A second limitation of our study is the lack of knowledge of total available spawning habitat in the reservoir. We predicted habitat availability at sites where walleye were known to spawn consistently (Chapter 2). However, these sites were only a small subset of the total number of potential spawning locations within the reservoir. The three large lakes in the reservoir comprise a very large amount of littoral habitat. For example, Lake Kabetogama has an estimated 3100 ha of habitat that is <4.6 m deep (Kallemeyn 2003) and our substrate surveys accounted for only 0.1% of that area. If spawning habitat is not a limiting factor in walleye reproduction at typical water elevations in the Namakan Reservoir, then rule curves are unlikely to improve long-term walleye abundance. Therefore, future work should model the total amount of suitable habitat on all three large lakes as a function of rule curves and regional morphometry.

Finally, water level management can be simple in theory but difficult in practice. Weather events are unpredictable, and maintaining water levels within rule curve limits is a formidable challenge. For example, water levels in the Namakan reservoir were within the rule curve boundaries during walleye spawning seasons 75% of the time during the 2000 rule curve, and only 46% during the 1970 rule curve. Rule curve compliance was the primary reason (other than confounding environmental factors) that the observed water level analysis predicted habitat availability to be much less improved by the 2000 rule curve than the modeled water level analysis. Observed water levels during the spawning seasons of the 1970 rule curve were, in fact, within the 2000 rule curve limits

41% of the time. Thus, the benefit of switching to the 2000 rule curve was not fully realized, mainly because springtime water levels were already following the 2000 rule curve 41% of the time. We make this point not to suggest that management agencies should do a better job of directing water levels in the Namakan, but to emphasize that water level control in large reservoirs is extremely challenging. The ability to comply with a rule curve is partially inherent in the rule curve itself, and must be considered when planning for water level management.

Management Recommendations

Water level manipulation in the Namakan Reservoir has a direct effect on the quality and quantity of spawning habitat available to walleye, and this availability has improved because of the 2000 rule curve. The 2000 rule curve improvement resulted from an increase in water level elevations during spawning periods. However, the mean observed water level elevation during spawning (340.5 m) is still, on average, below the elevation with the highest probability of preferred substrates (341.1 m; Chapter 2). Therefore, raising the maximum springtime level by approximately 0.6 m would provide walleye with access to a greater amount of these preferred substrates.

Our study approach could also be used to forecast the availability of spawning habitat under alternative rule curves. The ability to quantify (by area) the change in habitat availability resulting from varied rule curves was a unique attribute of our study, and makes our approach ideal for comparing the effects of hypothetical rule curves. For example, under rule curves that dictate large and rapid increases in springtime water level elevations, this method could be used to predict the extent of egg stranding (i.e., eggs too deep) that occurs from rapidly increasing water levels, a factor that was considered important in this study. Our ability to predict the effects of rule curves before they are implemented could prove to be a useful tool in the management of water levels, both in the Namakan Reservoir, and throughout North America.

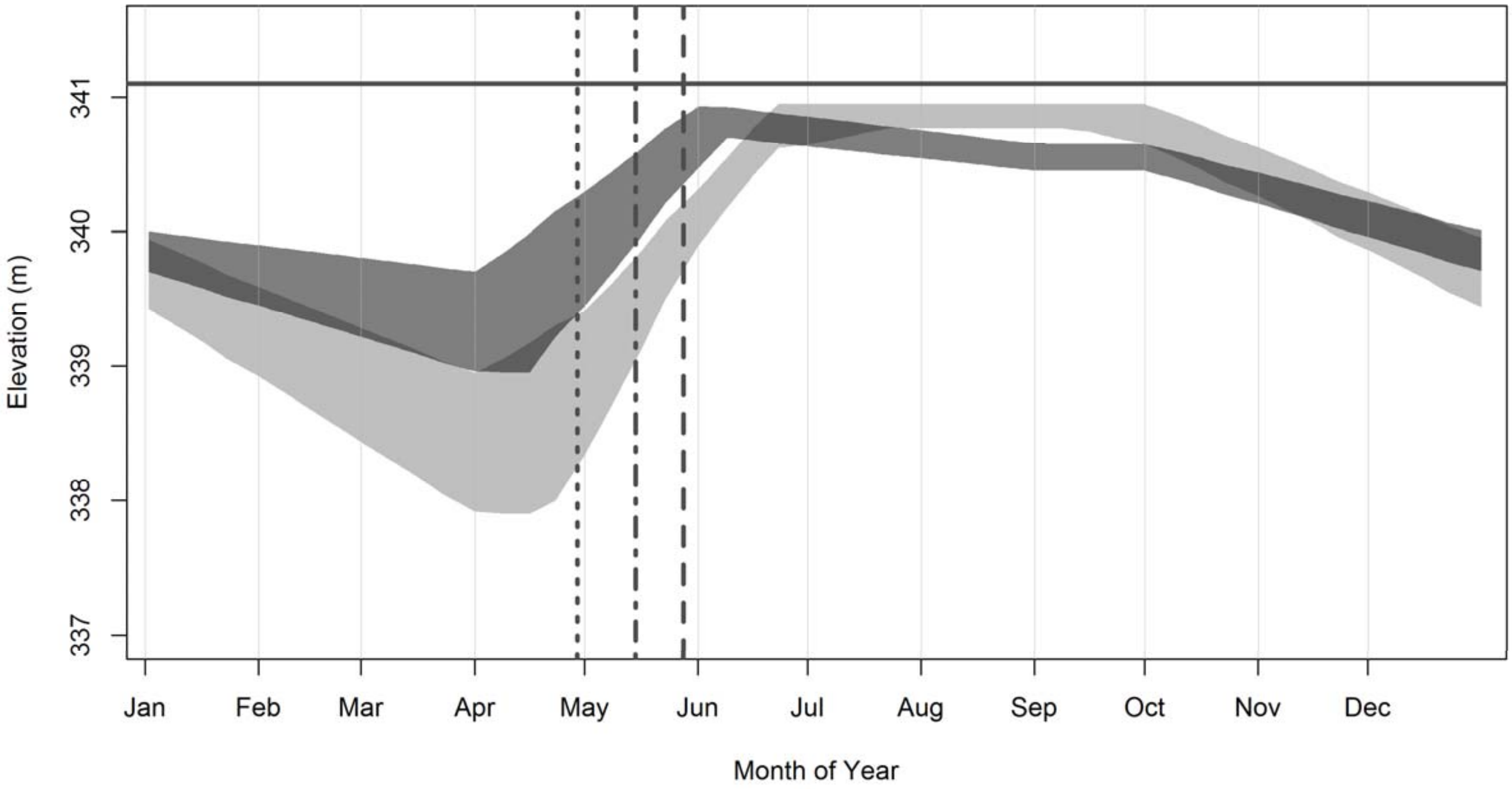

Figure 3.1. Hydrographs for the 1970 rule curve (in effect from 1970-1999; light gray) and 2000 rule curve (in effect from 2000-present; dark gray) on the Namakan Reservoir. Dam operators control outflows by targeting elevations at the middle of the shaded areas. The solid horizontal line indicates the elevation with the highest estimated, reservoir-wide proportion of suitable spawning substrate (341.1 m, 51%). The dotted, dot-dashed, and dashed vertical lines indicate the mean estimated dates of ice-out (April 28 ± 10 days SD), peak walleye spawn (May 14 ± 6 days SD), and peak walleye hatch (May 27 ± 5 days SD), respectively. The vertical elevations are relative to the USC&GS 1912 datum.

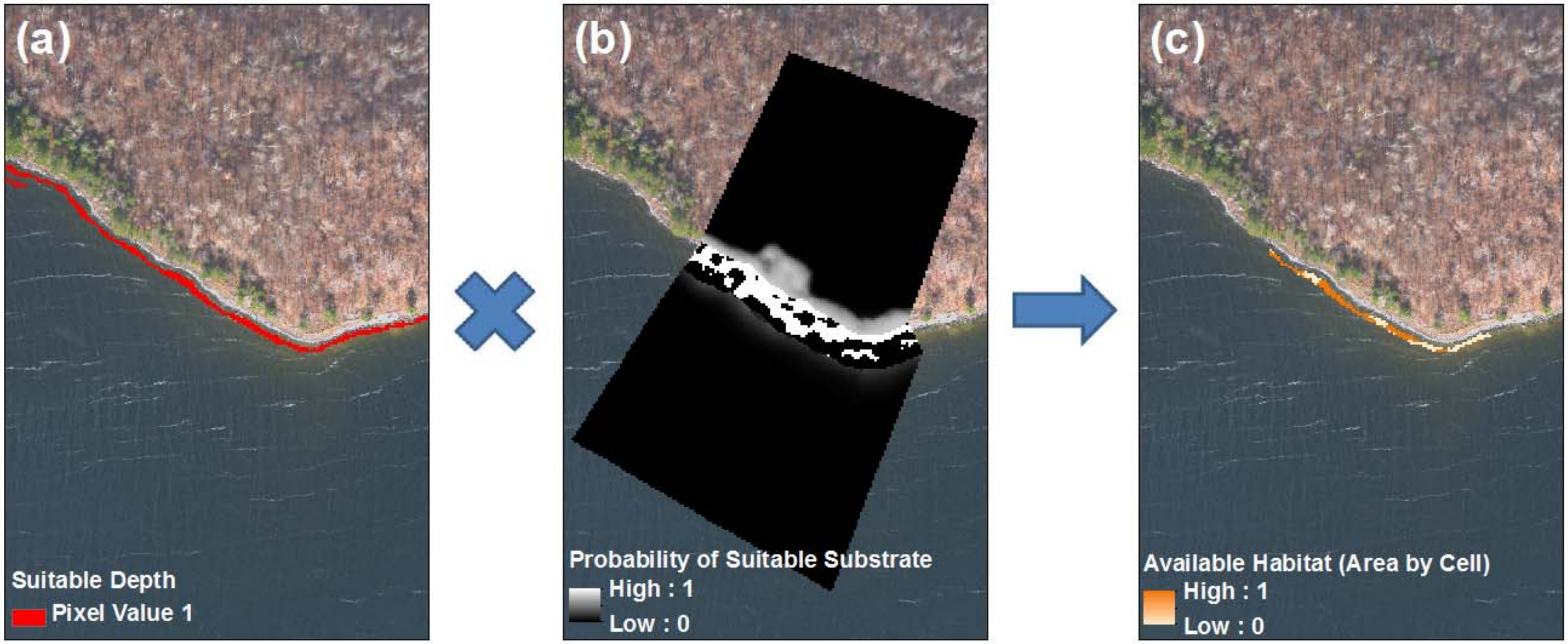

Figure 3.2. A flow diagram for creating an available habitat raster at site 24 (Lake Kabetogama, Namakan Reservoir) using observed water levels during the 1970 spawning season. Map (a) depicts the observed suitability by depth (0.1 to 1.0 m). Plot (b) is our habitat suitability rasters from Chapter 2. Map (c) is the observed available habitat during the 1970 spawning year. All maps are drawn to the same scale (1:1000) and are oriented so that north is up.

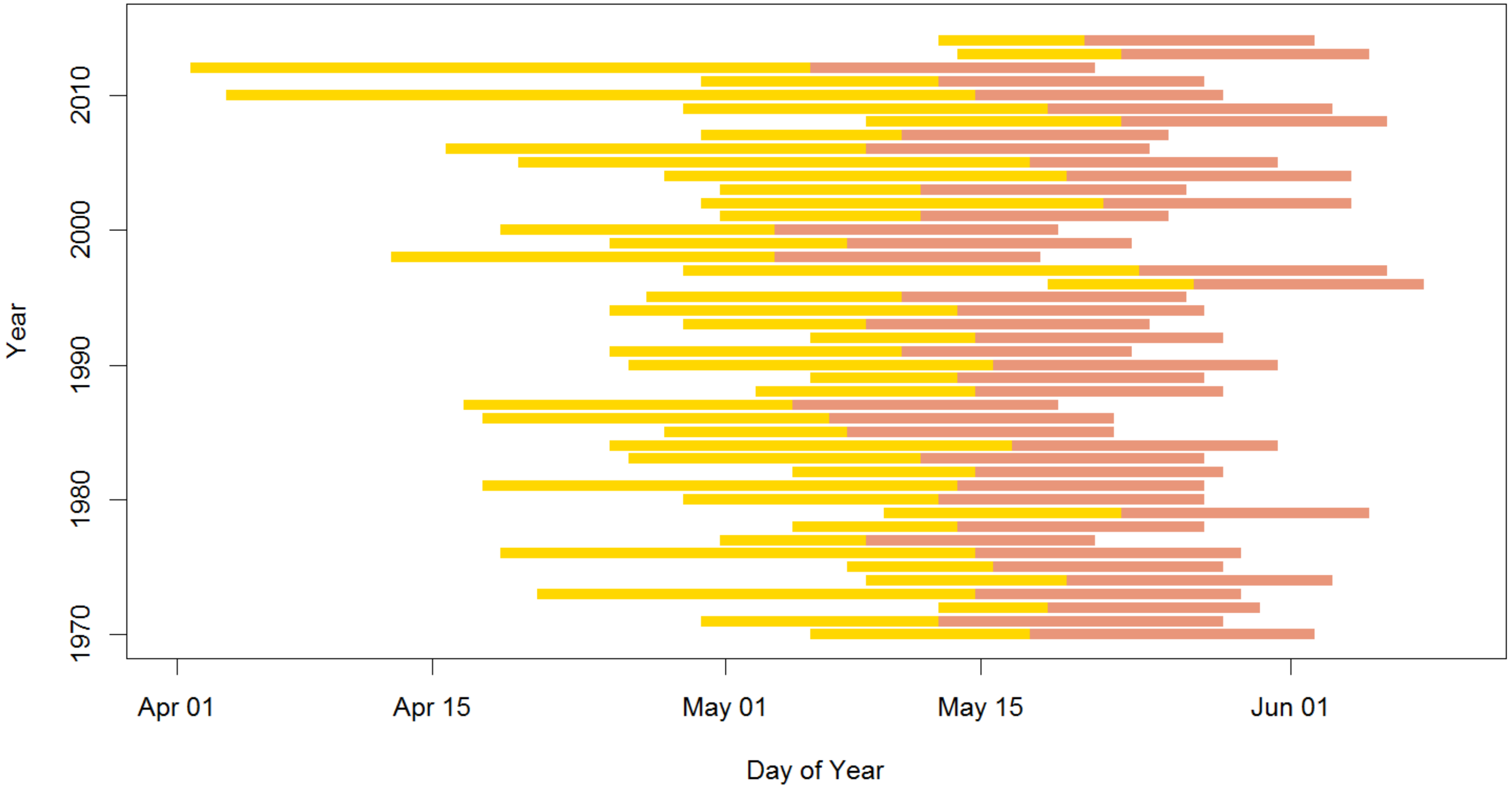

Figure 3.3. Estimated spawning seasons during each year of the study period (1970-2014). The yellow area indicates the period from ice-out to peak spawn, which occurs at a water temperature of 11 °C. The red area indicates the period from peak spawn to swim-up of newly hatched larvae, with peak hatch occurring 1 day before swim-up. Water temperatures were estimated using a linear model based on average air temperature (Matuszek and Shuter 1996), and egg development time was predicted via degree-days.

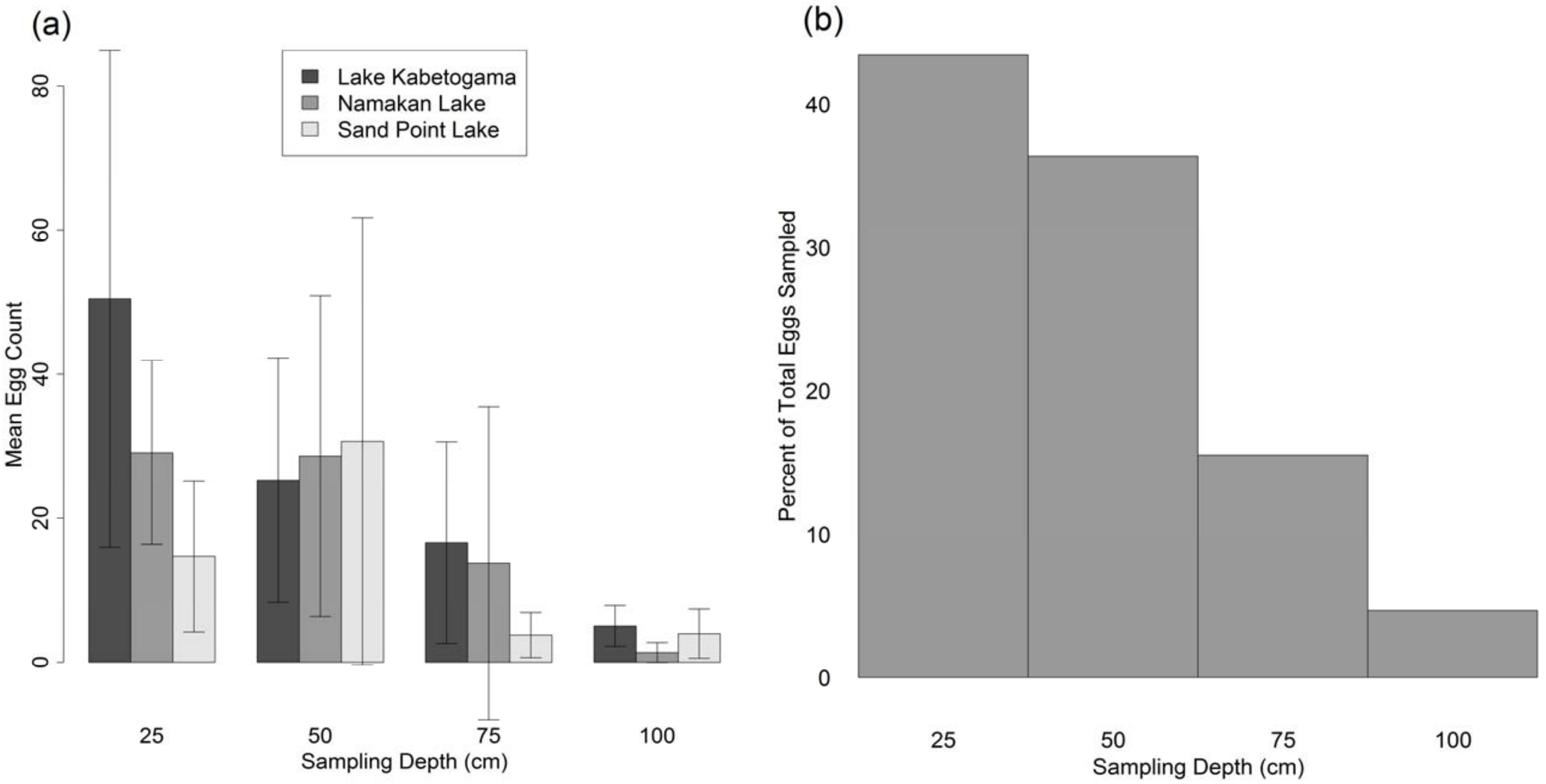

Figure 3.4. Summary of egg depth surveys conducted at 10 sites in the Namakan Reservoir (4 on Lake Kabetogama, 3 on Namakan Lake, and 3 on Sand Point Lake) during the 2014 spawning season. Panel (a) shows the mean egg counts per sample by lake with confidence intervals (black bars). Panel (b) shows a histogram of eggs sampled (aggregated over all sites and lakes) by depth as a percentage of the total number of eggs sampled.

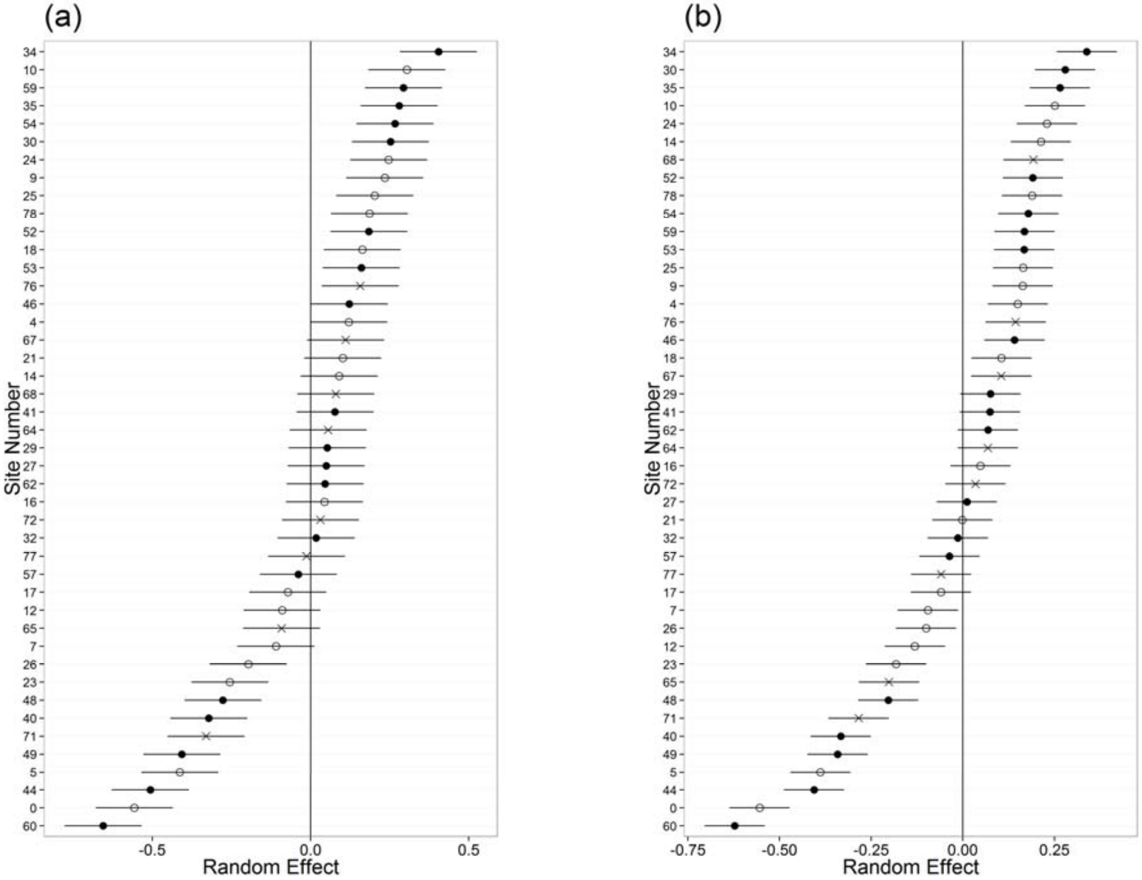

Figure 3.5. Estimates of the random site effects of the proportion of available preferred substrates during spawning seasons (1970-2014) on 44 sites in the Namakan Reservoir using observed (a) and modeled (b) water levels. Results are shown by lake: Lake Kabetogama (○), Namakan Lake (●), and Sand Point Lake (×). Error bars are predictions intervals.

Chapter 4

General discussion and conclusions

Globally, the number of reservoirs and the area that they occupy is growing (Downing et al. 2006). Reservoirs serve a variety of anthropocentric purposes including irrigation, hydroelectricity, flood control, and navigation (Thornton et al. 1990). Consequently, reservoirs are typically created and operated with little regard for Nature.

The effects of reservoir construction and operation on wildlife are well studied and diverse, and are often negative (Poff and Zimmerman 2010). Fish are particularly vulnerable in reservoirs, and a number of species are threatened or endangered because of reservoir impoundment and/or water flow manipulation. For example, the American eel (*Anguilla rostrate*) has declined substantially over its range in North America because spawning migrations are impeded by dams (Pratt and Threader 2011). The International Union for the Conservation of Nature (IUCN) has declared over 20 species of sturgeon as either endangered, or critically endangered (IUCN 2015), mostly due to the construction of dams. Impoundment and flow control has also been implicated in the functional extinction of baiji (*Lipotes vexillifer*), a river dolphin native to the Yangtze River in China (Wang et al. 2006).

The three large lakes of the Namakan Reservoir were impounded by two regulatory dams in 1914 in order to provide a buffer to water levels downstream in the Rainy Reservoir, where hydroelectricity is generated. Located on the border of Minnesota, U.S., and Ontario, Canada, the reservoir is unique in that the three large lakes are situated primarily within (~ 75%) the borders of Voyageurs National Park. Accordingly, the principal goal of managing the reservoir is to preserve the integrity of the Park’s natural resources, processes, systems, and values (Kallemeyn et al. 2003). Thus, the Namakan Reservoir is uniquely sheltered from the intense and varied demands placed on typical reservoir systems. Nevertheless, regulated lake levels and flow manipulation affect fish populations in the Namakan Reservoir, particularly those species that make extensive use of littoral habitats during their life cycle (e.g., walleye, perch, northern pike).

Walleye are prevalent in the large lakes of the Namakan Reservoir and are culturally, economically, and ecologically important. Walleye also use littoral habitats for spawning and egg development, and are sensitive to annual fluctuations in water levels (Chevalier 1977, Kallemeyn 1987, Cohen and Radomski 1993). Walleye populations in the Namakan have declined in recent decades, and regulation of water levels has been implicated as a possible cause (Kallemeyn 1987). While the 2000 rule curve was implemented, in part, to boost walleye reproductive success, post-2000 estimates of walleye abundance do not appear to be improving (MNDNR unpublished data, Jackson 2015). A major goal of this study was to elucidate the extent to which the 2000 rule curve has improved the maintenance and availability of habitat for walleye, and possibly shed light on the suppressed response of walleye abundance.

In Chapter 2, I modeled wave energy and ice scour over preferred walleye spawning substrates at 44 study sites to compare the effects of the 1970 and 2000 rule curves on the forces that maintain spawning habitat. Wave energy over spawning substrates increased significantly (18% for observed water levels and 6% for modeled water levels, $P < 0.01$) during the 2000 rule curve and did not vary by lake. The improvement resulted from a 0.1 m increase in mean water levels during open water seasons. The interaction of ice with preferred substrates at 13 spawning sites on Lake Kabetogama (other lakes were not sampled) decreased by 11% ($P < 0.01$) during the 2000 rule curve, resulting from a decrease in the mean range (0.7 m) of water level elevations during winter. However, ice scour still affects those substrates that are used most frequently by walleye during typical spawning seasons. These findings suggest that the 2000 rule curve improved the maintenance of spawning habitat by forces that remove fine sediments.

In Chapter 3, I modeled habitat availability during spawning at the same 44 study sites, and compared the effects of the 1970 and 2000 rule curves via both observed and modeled water levels. Observed water levels suggested that available spawning habitat on Lake Kabetogama increased 95% ($P < 0.01$) because of the 2000 rule curve, but availability on Namakan Lake and Sand Point Lake was unaffected. However, when using modeled water levels, which controlled for confounding weather events, habitat availability increased significantly ($P < 0.01$) on all three lakes (Kabetogama = 179%, Namakan = 72%, Sand Point = 93%). Habitat availability improved because the 2000 rule curve increased mean springtime water levels by 0.5 m, and water levels rose more slowly (2.2 vs. 3.0 cm/day) while eggs were incubating.

Despite of improvements to the maintenance and availability of walleye spawning habitat resulting from the 2000 rule curve, walleye abundance does not appear to be improving (MNDNR unpublished data, Jackson 2015). This contradiction highlights the difficulty in managing whole ecosystems and the challenge of establishing cause-and-effect relationships in ecosystem studies (Kallemeyn et al. 2009). Factors that may be confounding the relationship between habitat and walleye abundance include climate change and related weather patterns, angling regulations (McLeod and Trembath 2007), and harvest pressure (Kitchell and Koshinsky 1996); all which have changed in recent decades. Post-2000 non-native species introductions have also occurred in the reservoir (R. Maki, Voyageurs National Park, personal communication), further complicating management efforts. These factors underscore the need for ongoing monitoring and research into the complex relationships between climate and fish abundance. Additionally, research into the reservoir as a socio-ecological system is advised to elucidate the relationships between walleye abundance and angling/harvest pressures.

Despite the need for further research to optimize habitat in the Namakan and other reservoirs, this study clearly reveals the paradox of managing a reservoir for its natural integrity. Despite our intent to manage them as naturally as possible, reservoirs are indisputably altered ecosystems. This fact was highlighted in a Namakan Reservoir study (Cohen and Radomski 1993) in which the authors linked improved walleye abundance with periodic drought and flooding, both of which are more infrequent in managed reservoirs. Thus, even attempts to manage water levels in a way that optimizes habitat (i.e., rule curves) may be flawed in their consistency. This study also reveals that managing water levels in a large reservoir is challenging. Water levels during spawning seasons of the 1970 rule curve were within 2000 rule curve limits 41% of the time. This suggests that our ability to control water levels is limited, and depends on factors such as reservoir morphology, dam characteristics, and climate. Nevertheless, in the absence of dam removal (or creation) as a viable option to restoring natural integrity, managers should strive to mimic, as much as possible, fluctuations in water levels typical of pre-impoundment conditions.

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