



A comparison of the effects of water-level policies on the availability of walleye spawning habitat in a boreal reservoir

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ABSTRACT

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Water levels in reservoirs can affect the quantity and quality of the habitat that is available for spawning fish and their eggs. We studied how a change in the water-level management policy (“rule curve”) in 2000 affected the availability of walleye (*Sander vitreus*) spawning habitat in 3 lakes (Kabetogama, Namakan, and Sand Point) that make up a large, boreal reservoir between Canada and the United States. According to observed water-level data, available spawning habitat on known Lake Kabetogama spawning sites increased 95% ($P < 0.01$) with the 2000 rule curve, but did not change on Namakan or Sand Point lake spawning sites. However, when using modeled water-level data to control for confounding weather events, habitat availability at known spawning sites increased significantly ($P < 0.01$) on all 3 lakes (179%, 92%, and 93%, respectively). Habitat availability improved because the 2000 rule curve increased mean spring water levels by 0.5 m, and water levels rose more slowly (2.2 vs. 3.0 cm/d) during egg incubation. Our findings suggest that, although water-level management on large reservoirs can be a challenge, carefully designed policies can improve walleye spawning habitat conditions and help to achieve fisheries management goals.

KEYWORDS

Adaptive management; Namakan Reservoir; rule curve; *Sander vitreus*; spawning habitat; walleye

The walleye (*Sander vitreus*) is a well-studied and ecologically, culturally, and economically important game fish in north-central North America (Scott and Crossman 1973, Colby et al. 1979, Barton 2011). A great deal of walleye 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). This research suggests that seasonal water-level fluctuations in most natural lakes are relatively small and therefore unimportant for walleye reproduction (Raabe and Bozek 2014). However, water-level fluctuations in reservoirs can be substantial and have more pronounced effects on spawning habitat. For example, Papenfuss et al. (2017) found that water-level fluctuations in a North American boreal reservoir affected wind and ice forces that assist in the maintenance of habitat through wave energy and ice scour. Water levels may also limit the availability of habitat during spawning if suitable substrates are too deep or shallow (Colby

et al. 1979). Although the artificial manipulation of water levels is one of the most widespread problems facing walleye populations (Kerr et al. 1997), relatively few studies have examined the effects of water-level management on walleye (e.g., Chevalier 1977, Kallemeyn 1987, Cohen and Radomski 1993, Larson et al. 2016), or their spawning habitat.

Fluctuating water levels are especially important during the spawning season because they determine the depth and configuration of the littoral substrates that are available for lacustrine-spawning walleye (Osborn et al. 1978, Osborn and Ernst 1979). Suitable substrates tend to be sediment-free and of specific grain size (6–300 mm diameter; Eschmeyer 1950, Priegel 1970, Bozek et al. 2011b, Raabe and Bozek 2012) and spawning over these substrates increased the survival rate of walleye eggs in a boreal lake (Johnson 1961). Typical 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

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contact with relatively warm, oxygen-rich, surface water, but not so shallow that they are subject to wave-induced resuspension or desiccation (Raabe and Bozek 2014). Dissolved oxygen (DO) is critical to the survival and development of walleye eggs and varies with depth (i.e., water levels; Daykin 1965). Dissolved oxygen concentrations $>5\text{--}6$ mg/L are optimal for walleye egg incubation (Oseid and Smith 1971), while concentrations <3 mg/L result in high egg mortality (Auer and Auer 1990). Therefore, rising water levels during the spawning season can influence egg survival by slowing development rates and starving eggs of DO, while receding water levels can expose eggs to abrasion, transport, or desiccation.

In this study, we compared the effects of 2 water-level management policies (“rule curves”) on the availability of walleye spawning habitat during spawning seasons. Our goal was to determine if the 2000 rule curve was more effective at providing walleye with access to substrates at depths and temperatures known to be optimal for walleye spawning and egg incubation in boreal lakes. This study is an important step in understanding how the timing and duration of water-level fluctuations influence the quality and quantity of spawning habitat available to walleye in reservoirs in which human demands on water are varied and intense (e.g., hydroelectricity, irrigation, flood control, navigation; see Taylor et al. 2016). Improving this understanding can help to balance these competing demands in reservoirs across North America.

Study site

The Namakan Reservoir (Fig. 1) is an international waterbody that lies on the border between Minnesota, USA, and Ontario, Canada. The total area of the reservoir is 22,916 ha and comprises 3 lake basins: Lake Kabetogama (area = 9726 ha, mean/max depth = 9.1/24.3 m), Namakan Lake (9739 ha, 13.6/45.7 m), and Sand Point Lake (3450 ha, 12.0/56.1 m). Two dams were built in the early 20th century to manage water levels for industrial use downstream on the Rainy Reservoir. The reservoir lies largely within the boundaries of Voyageurs National Park (est. 1975) and is managed primarily to maintain the region's ecological integrity. Currently, there is very little residential shoreline development and no industrial water use or effluent discharge on the Namakan Reservoir.

Since 1970, water levels in the reservoir have been successively managed under 2 rule curves (Fig. 2; Kimmett et al. 1999). The 1970 rule curve was in place from 1970 to 1999. The 2000 rule curve was established in 2000 to improve habitat conditions for walleye and other species. The 2000 rule curve differs from the 1970 rule curve in 3 important ways: (1) a narrower target range of water levels during the ice-cover season (\sim Nov through Apr), (2) higher water levels during the walleye spawn (\sim Apr through Jun), and (3) reduced water levels throughout summer (\sim Jun through Nov). The unique combination of abundant walleye, rule curve changes, and lengthy time series of water-level data in the reservoir make it an ideal system in which to examine the effects of water-level management on the availability of spawning habitat.

Materials and methods

Site selection

In spring 2012, we conducted spawning surveys at 109 shoreline locations in Kabetogama, Namakan, and Sand Point lakes. 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 lake (as opposed to riverine) habitats because they are directly impacted by water-level management and were therefore of greater interest to the larger, international effort to evaluate the 2000 rule curve (Kallemeyn et al. 2009). We used scap nets (flat, square, open-faced nets for disturbing the substrate) at all 109 sites to determine the presence/absence of walleye eggs at depths ranging from 10 to 150 cm. White sucker (*Catostomus commersoni*) are present in the reservoir (Kallemeyn et al. 2003) and have similar spawning temperatures and habitats (Corbett and Powles 1986), so we used egg size (1.63–1.73 mm diameter for walleye vs. 2.0–3.0 mm for white sucker; Becker 1983, Raabe 2006) to distinguish between the eggs of these species. All netted eggs were assumed to be from walleye due to their size and the observed presence of walleye at several survey sites. During the 2013 and 2014 spawning seasons, we resurveyed sites at which we detected walleye eggs in 2012. We based our final site selection on the consistency of spawning as demonstrated by egg detection over all 3 yr and a minimum

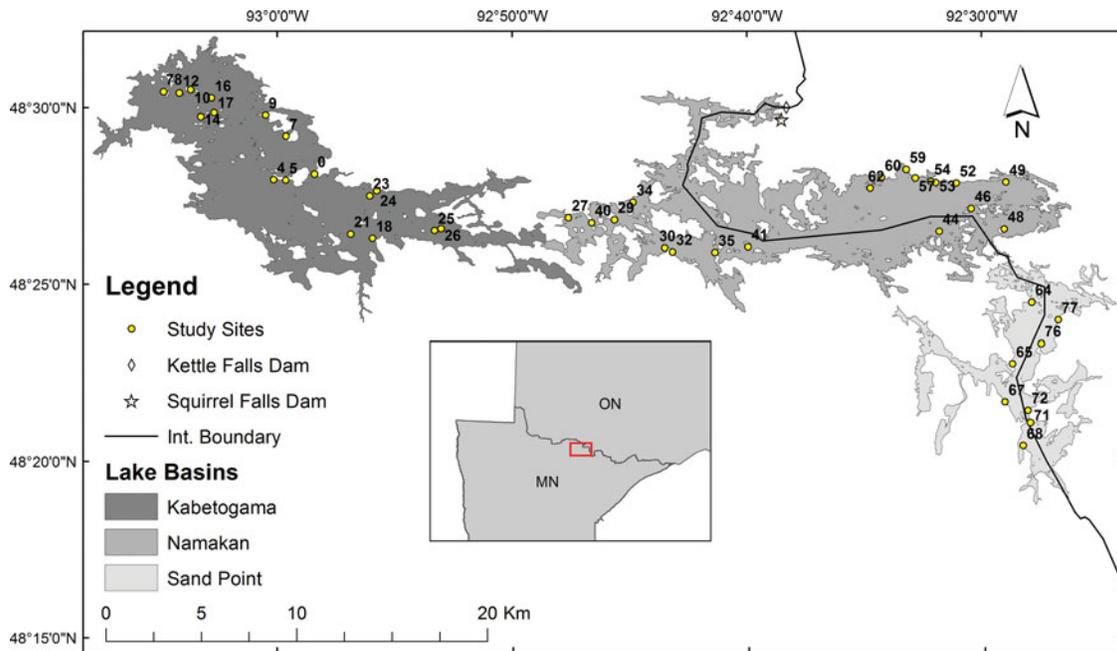


Figure 1. Map of the large lakes of the Namakan Reservoir: Lake Kabetogama, Namakan Lake, and Sand Point Lake. The 44 study sites are labeled with the site ID number and the inset shows the location of the reservoir relative to Lake Superior, Minnesota, and Ontario.

shoreline length of 20 m. To the extent possible, we also selected sites from all 3 lakes and both countries to maximize morphological (e.g., shoreline lengths, slope, and aspect) and political diversity.

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 then sampling substrate at 2 m intervals along each transect (Fig. 3a). The minimum and maximum transect lengths were 10 and 20 m, respectively, and each transect extended to an approximate lake depth of 3 m (the maximum depth at which samples could be taken with snorkel gear). At each location along a transect, we classified substrates at 5 locations within a 60 cm quadrat: 1 at each corner and 1 in the center. We classified substrate according to the Wentworth scale modified for boreal

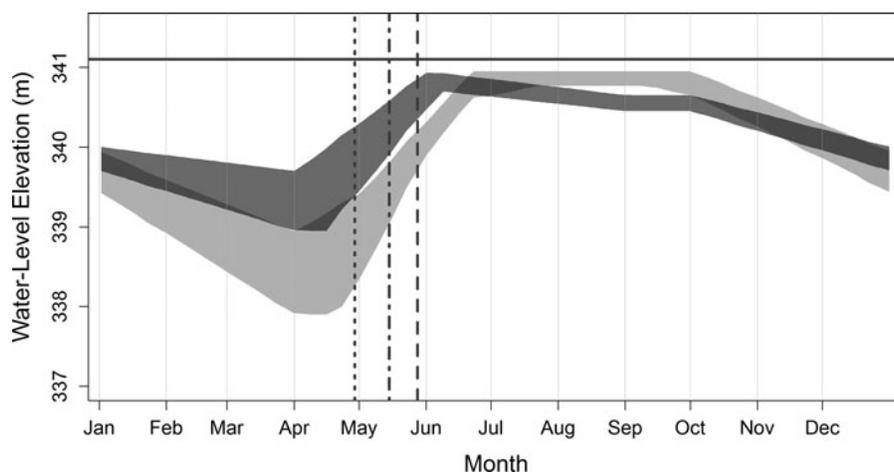


Figure 2. Hydrographs for the 1970 rule curve (in effect from 1970 to 1999; light gray) and 2000 rule curve (in effect from 2000 to present; dark gray) on the Namakan Reservoir. Dam operators control outflows by targeting elevations at the middle of the shaded areas. The solid horizontal line indicates the elevation of 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 (28 Apr \pm 10d SD), peak walleye spawn (14 May \pm 6d SD), and peak walleye hatch (27 May \pm 5d SD), respectively. Vertical elevations are relative to the USC&GS 1912 datum.

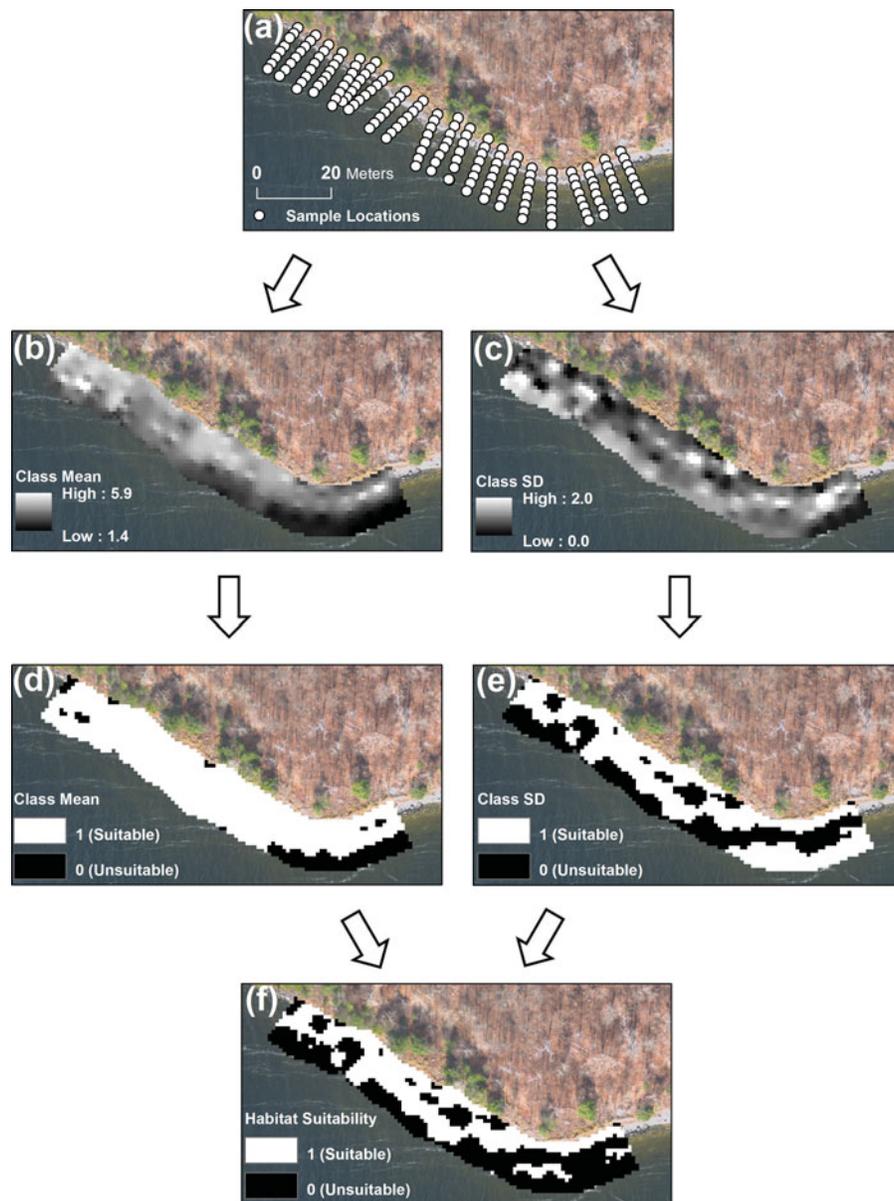


Figure 3. A flow diagram for creating observed substrate suitability maps at site 24 (Lake Kabetogama). Map (a) depicts locations of substrate samples. Maps (b) and (c) are interpolations of the sample means and sample standard deviations, respectively. Sample means and sample standard deviations were 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 map (f). All maps are drawn with the same extents, to the same scale (1:1000), and oriented so that north is up.

lacustrine shoreline habitat (Table S1; Raabe 2006, Jones 2011).

We created 5 distinct substrate class and substrate variability maps at each site by computing the class mean (average of the 5 substrate measurements for each sample) 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; Fig. 3b–c). Because walleye prefer to spawn on gravel, cobble, and rubble (Eschmeyer 1950, Johnson

1961, Priegel 1970), we reclassified those substrates as suitable (assigned pixel value 1) and all other substrate classes as unsuitable (assigned pixel value 0; Fig. 3d). We then reclassified substrate samples with standard deviations < 2 as suitable (assigned pixel value 1) and all other standard deviations as unsuitable (assigned pixel value 0; Fig. 3e). Finally, we spatially multiplied these 2 maps to create a spawning substrate map in which pixel values of 1 and 0 identified suitable and unsuitable spawning substrate, respectively (Fig. 3f).

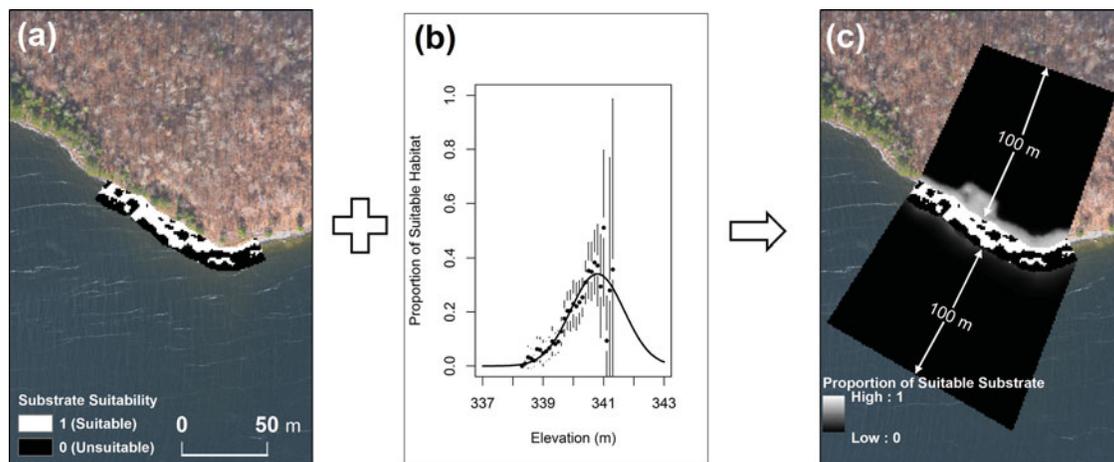


Figure 4. A flow diagram for creating substrate suitability maps at site 24 (Lake Kabetogama) at increased range of elevations. Map (a) depicts the observed substrate suitability (see Fig. 3). Plot (b) is the Gaussian model used to predict substrate 100 m upslope and downslope from the observed data. Map (c) is the observed suitability overlaid onto the predicted suitability. Both maps are drawn to the same scale and oriented so that north is up.

During the study period from 1970 to 2014, water levels in the reservoir infrequently rose above or fell below those accessible during the 2013 snorkel survey. For example, water levels reached a study period maximum of 341.6 m in June 2014 (an elevation that flooded shoreline areas), and a study period minimum of 338.1 m in April 1972 (an elevation too deep for the 2013 snorkel survey). In all, exceptionally low open-water (after ice-out) elevations occurred in 1972 and 1978, and exceptionally high open-water elevations occurred in 2001, 2008, and 2014. To account for these 5 instances, we used Gaussian functions to predict suitable substrates beyond surveyable elevations (100 m linear distance 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 nonlinear least squares to observed substrate data and a digital elevation model (DEM) resampled to 1 m² using bilinear interpolation (Morin et al. 2014). The observed substrate suitability map was then combined with the predicted substrate suitability map to create a single map for modeling the effects of water levels over a wider range of elevation (Fig. 4a–c). Because we were also interested in the effects of site characteristics (as covariates) on habitat availability, we used a DEM to estimate the length, area, mean slope, and mean elevation of each site (Morin et al. 2014).

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 suitable depth range of spawning walleye in the Namakan Reservoir, we randomly selected 10 study sites and measured the occurrence of eggs by depth over suitable substrates (gravel, cobble, and rubble). We performed these measurements during the May 2014 spawning period. We established 5 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 suspended by the boot motion. If a net appeared to contain <50 walleye eggs, we counted all eggs in the sample. If a net appeared to contain >50 walleye eggs, we randomly sampled 20% of the net area and extrapolated.

Seasonal spawning 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 3 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 that is 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 daily average air temperatures taken from a local weather station (NOAA 2015) as inputs, and calibrated the model using 28 yr of biweekly water temperature measurements taken at a depth of 1 m from a monitoring site on Lake Kabetogama.

Walleye can begin to spawn at temperatures as low as 2.0 C (Hokanson 1977); therefore, we used ice-out dates supplied by local agency observers to indicate the start of the spawning season in each year. Because ice-out dates were based on both ground and aerial observations of lakes in the reservoir, they represent best estimates that are accurate to within 1 week of actual ice-out. Peak spawning activity for walleye typically occurs within 5.6–10.0 C (Niemuth et al. 1959, Becker 1983). We selected 10 C as the peak spawning temperature in the Namakan Reservoir 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 on a given day as:

$$DD = T_w - T_o \quad (1)$$

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 d (Venturelli PA, University of Minnesota, Jan 2014, unpubl. data). We assumed that the date on which this threshold was reached was the date of peak hatch. Because newly hatched larvae are capable of vertical movement after ~ 1 d (Scott and Crossman 1973, Li and Mathias 1982), we added a single day after peak hatch to account for swim-up (i.e., larvae disassociating from the substrate). Accordingly, the total estimated spawning and incubation period for each year of the study period spanned all days from ice-out to the 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 by combining the DEM (Morin et al. 2014) with our estimated spawning periods and water levels that we assumed were planar throughout the reservoir (LWCB 2015). We used bilinear interpolation to resample the DEM to 1 m so that it was at the same resolution as our suitable substrate maps (Fig. 4c). We created suitable spawning depth maps (1 m resolution) by reclassifying the DEM into suitable depths (assigned pixel value 1) at both the peak spawn and swim-up dates. Suitable depths were defined by our spawning depth validation (see section above). Overlapping these 2 maps identified the total area of habitat that was at a suitable depth for the entire period between peak spawn to swim-up. Finally, we spatially multiplied these depth suitability maps by the suitable substrate maps referenced above. Each 1 m cell of the output raster indicated the area within that cell that was at a suitable depth and over suitable substrate during the spawning season (Fig. 5a–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). Therefore, in addition to comparing the rule curves for observed water levels, we also used a hydrologic model (Thompson 2015) to compare the rule curves with modeled water-level inputs. 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 potentially confounding factors. The hydrologic model uses a conservation of mass approach (i.e., storage estimates, measured inflows, and measured outflows) to predict a time series of water levels (from 1950 to 2014) using either the 1970 or 2000 rule curve. The model also uses a quarter-monthly time step; therefore, 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 each site and accounted for variation

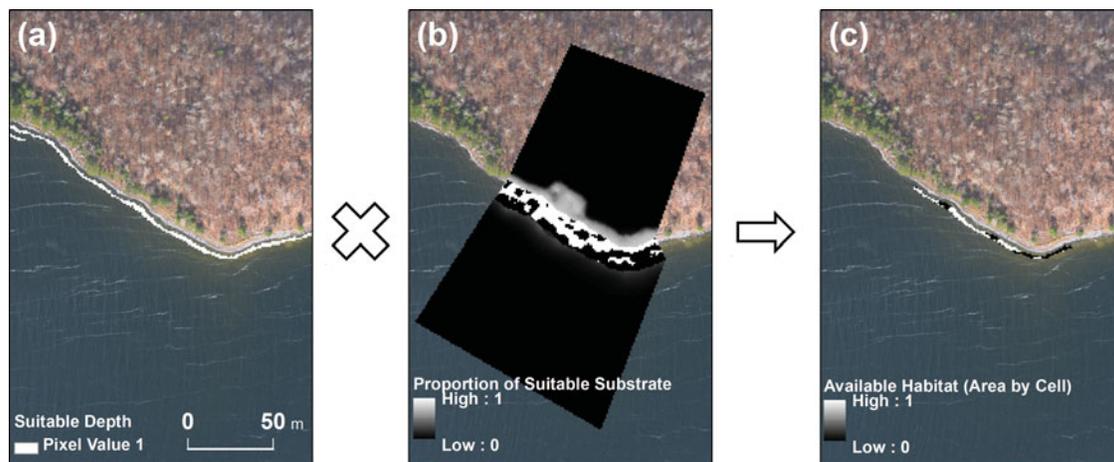


Figure 5. A flow diagram for creating an available habitat raster at site 24 (Lake Kabetogama, Namakan Reservoir) using observed water levels during the 1970 spawning season. Maps depict habitat suitability based on (a) water depth (0.1–1.0 m), (b) substrate, and (c) both criteria. All maps are drawn to the same scale (1:1000) and are oriented so that north is up.

in site size by dividing each sum by the total site area. The responses in both scenarios demonstrated non-normality; therefore, we applied a $\log_{10}(Y+C)$ transformation, where C was the minimum nonzero response (Zuur et al. 2009, Warton and Hui 2011). We then used 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 random 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 Development Core Team 2012) using the lme4 package (Bates et al. 2012). A predictive methodology (as opposed to other methods such as pairwise comparisons), and the factors chosen for study, were contractually mandated by our funding agencies who intend to use the predictive models to estimate habitat availability under alternative rule curve scenarios. All spatial analyses were performed in ArcGIS, version 10.0. We georeferenced egg validation measurements with a Trimble GeoXT capable of submeter resolution

and used a combination of real-time and postprocessed differential correction methods to improve positional accuracy.

Results

Of the 109 locations surveyed in 2012, we selected 44 study sites (Table S2): 17 in Lake Kabetogama, 19 in Namakan Lake, and 8 on Sand Point Lake (Fig. 1). Thirty-two of the 44 sites were located in the United States. A summary of the site characteristics is as follows: total surveyed area 36,501 m² with a site mean of 830 ± 311 m² SD (range 441–1512 m²), mean shoreline length 54 ± 19 m SD (range 25–100 m), mean slope $2.5 \pm 1.0^\circ$ SD (range 0.6–4.8°), and mean elevation 339.8 ± 0.3 m SD (USC&GS 1912 datum; range 338.9–340.4 m). Incidentally, the 6 sites that were surveyed by agency staff in the 1970s (i.e., Osborn et al. 1978, Osborn and Ernst 1979) that were also surveyed as part of this study showed evidence of spawning by walleye. This finding suggests that walleye consistently spawned at study sites before our surveys in 2012–2014. Additionally, each site contained substrate typical of walleye spawning as determined by previous studies of walleye reproduction (Eschmeyer 1950, Johnson 1961, Priegel 1970).

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 m² (28.6% of total sampled area). The Gaussian functions that we used to estimate

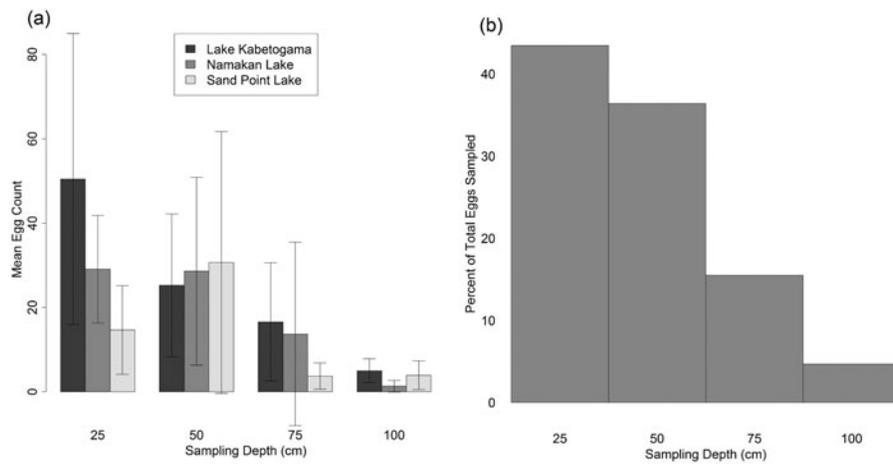


Figure 6. Summary of egg depth surveys conducted at 10 sites in the Namakan Reservoir (4 on Lake Kabetogama, 3 on Namakan Lake, and 3 on Sand Point Lake) during the 2014 spawning season. Panel (a) shows mean egg counts per sample by lake with confidence intervals (black bars). Panel (b) shows a histogram of eggs sampled (aggregated over all sites and lakes) by depth as a percentage of the total number of eggs sampled.

habitat suitability predicted maximum habitat suitability for Kabetogama, Namakan, and Sand Point at elevations of 340.8 m (pseudo- $r^2 = 0.82$), 341.2 m (pseudo- $r^2 = 0.92$), and 341.6 m (pseudo- $r^2 = 0.93$), respectively (Fig. S1). The reservoir-wide maximum suitability occurred at an elevation of 341.1 m (pseudo- $r^2 = 0.93$).

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 at site 25 (Lake Kabetogama). Egg counts on both Kabetogama and Namakan lakes peaked at 25 cm and decreased with both decreasing and increasing depth; however, egg counts on Sand Point Lake peaked at 50 cm (Fig. 6a). Over 90% of the eggs that we sampled were collected at depths of 25–75 cm (Fig. 6b), which corroborates published estimates of a suitable depth range of 30–75 cm (Eschmeyer 1950, Johnson 1961). We created our suitable spawning depth maps assuming a suitable depth range of 10–100 cm. This expanded depth range accounted for variation in water levels within and between lakes in the reservoir during times of rapid water level changes that were common in spring.

We found a significant ($r^2 = 0.89$, $F_{5,313} = 493$, $P < 2.2 \times 10^{-16}$) linear relationship between air temperature and water temperature that was described by:

$$T_i = -21.2 + 0.348 (ATEMP1) + 0.262 (ATEMP2) + 0.313 (YDAY) - 0.000732(YDAY)^2 - 342 (INVAYD) \quad (2)$$

where $ATEMP1$ is the 15d mean air temperature, $ATEMP2$ is the 5d 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 2 to predict a reservoir-wide peak spawning date in each year of the study assuming that peak spawning occurred at 10C in spring. Peak spawning dates ranged from 4 May to 27 May (Fig. S2) with a mean date of 14 May \pm 6d SD. A Welch 2-sample t -test found no significant difference in the mean peak spawning dates by rule curve ($CI = [-5.0, 2.7]$, $P = 0.54$). We used equation 1 to estimate peak hatch dates that ranged from 17 May to 7 June (Fig. S2), with a mean date of 27 May \pm 5d 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 known Lake Kabetogama spawning sites increased, on average, by a factor of 1.95 ± 0.15 SD ($t = -9.03$, $df = 1\,933$, $P = 2.0 \times 10^{-16}$) following the implementation of the 2000 rule curve. However, the proportions of habitat available on Namakan Lake and Sand Point Lake spawning sites were unaffected ($P > 0.01$; we used an alpha of 0.01 for this study to reduce the likelihood of Type I error). The same analysis with modeled water-level data showed that the proportion of habitat available at known spawning sites increased, on average, by a factor of 2.79 ± 0.13 SD ($t = -22.1$, $df = 3\,914$, $P < 2 \times 10^{-16}$) on Lake Kabetogama, 1.72 ± 0.11 SD ($t = -8.842$, $df = 3\,914$, $P = 2.0 \times 10^{-16}$) on Namakan Lake, and 1.93 ± 0.11 SD ($t = -7.98$, $df = 3\,914$, $P = 2.0 \times 10^{-15}$) 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 suitable habitat was site-specific, greatest at site 34, and lowest at site 60 (Fig. S3; both sites on Namakan Lake). 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 only on Lake Kabetogama when using observed water-level conditions, but on all 3 lakes under modeled (i.e., unconfounded) water-level conditions. 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 observations of the distribution of suitable spawning substrates in the reservoir (Fig. S1). The narrower distribution (by elevation) of suitable substrates in Lake Kabetogama is consistent with a greater sensitivity to water-level fluctuations. Thus, maintaining water levels within rule curve limits to the extent possible is particularly important on Lake Kabetogama, where 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 spring water levels and walleye abundance 5 yr later. Similarly, Kallemeyn (1987) found a significant relationship between age-0 walleye abundance and spring water levels in Lake Kabetogama and Sand Point Lake from 1981 to 1985. However, Osborn et al. (1981) found no relationship between spring water levels and year-class strength after 5 yr in 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. While our study does not support a direct causal link between water-level fluctuations and walleye abundance, it does provide insight into how rule curves can improve habitat availability in reservoirs in which 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 (Fig. S1). 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/d SD, respectively. A relatively slower increase in water levels during spawning and development is less likely to strand eggs at suboptimal depths (and therefore suboptimal temperatures and DO concentrations).

While our analysis demonstrated improvements in habitat availability resulting from the 2000 rule curve, we should avoid using water-level policies as a solution for enhancing habitat in reservoirs. Walleye use a diversity of habitat types that vary both annually and by life stage (Bozek et al. 2011a). Timing water-level 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 since recordkeeping began in 1932, 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 abundance and annual water-level elevation ranges (Cohen and

Radomski 1993) attributed to dynamic interactions at the community level. Above-average 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 (for the effects of water levels on abundance see Larson et al. 2016). We controlled for weather events and climate by modeling rule curves in parallel, but our study is still observational and subject to model error and potentially 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 significantly affected walleye populations over time and complicated 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*; Kerfoot et al. 2016) and rusty crayfish (*Orconectes rusticus*; Maki R, Voyageurs National Park, Apr 2015, pers. comm.) were discovered in the reservoir in 2006. 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, Miehl et al. 2009). For example, rusty crayfish can prey on incubating walleye eggs, and are able to significantly alter the composition of littoral habitats (Weisbord et al. 2012, Hansen et al. 2013). 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; however, these sites were only a small subset of the total number of potential spawning locations within the reservoir. The 3 large lakes in the reservoir comprise a large amount of littoral habitat. For example, Lake Kabetogama has an estimated 3100 ha of habitat that is <4.6 m deep (Kallemeyn et al. 2003) and our substrate surveys accounted for only 0.1% of that area. Additionally, sites may have undergone changes from wind, wave, and ice

forces acting to redistribute substrates (Papenfuss et al. 2017) over the study period. Therefore, future work should survey larger areas or model the total amount of suitable habitat on all 3 large lakes as a function of rule curves and regional morphometry and consider how sites may have changed over time. This work should also consider river spawning habitat if it is expected to contribute significantly to recruitment.

Further limitations included the extrapolation of substrate data necessitated by infrequent periods of flooding/drought and the nonrandom sampling of study sites. Although the extrapolated data were only required to model suitable habitat availability 5 out of 45 yr, they may have contributed to errors in our predictions. Similarly, our nonrandom sampling of study sites could have biased our study toward the impacts of rule curves on currently suitable and known spawning sites, while ignoring other potential spawning habitats.

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 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 noncompliance was the second-most important reason (after 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, there was less benefit to adopting the 2000 rule curve because prior water levels were often within the 2000 rule curve boundaries. Rule curves can also have competing effects; for example, lowering of water levels during summer may expose spawning habitat to forces that remove periphyton while simultaneously reducing nearshore habitat for juvenile walleye. We make these points not to suggest that management agencies should do a better job of directing water levels in the Namakan Reservoir, but to emphasize that water-level control in large reservoirs can be a challenge.

Despite the difficulty in adhering to the rule curves, our model predicted that the 2000 rule curve affected the quantity of spawning habitat available to walleye at our study locations. The quantification (by area) of the

change in habitat availability resulting from varied rule curves was a unique attribute of our study and similar approaches could be used to compare water-level policies in other reservoir systems. The ability to predict the effects of rule curves on walleye spawning habitat before they are implemented could be a useful tool in the management of water levels, both in the Namakan Reservoir and elsewhere.

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Table S1. 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 S2. Summary of Namakan Reservoir study site characteristics. Study sites each demonstrated 3 consecutive years (2012–2014) of walleye spawning as determined by the presence of walleye eggs. Sites were located on the 3 large lake bodies of the Namakan Reservoir: Lake Kabetogama (KAB), Namakan Lake (NAM), and Sand Point Lake (SP). Thirty sites were located in the U.S. (US) and 14 were located in Canada (CAN). 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 |

Table S2 Cont.

| | | | | | | | | | |
|----|-----|-----|------|----|-----|-------|-----|---------|--------|
| 78 | KAB | US | 530 | 40 | 2.5 | 340.1 | 204 | 5372733 | 494030 |
| 27 | NAM | US | 469 | 40 | 3.6 | 339.8 | 157 | 5366112 | 515268 |
| 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 |

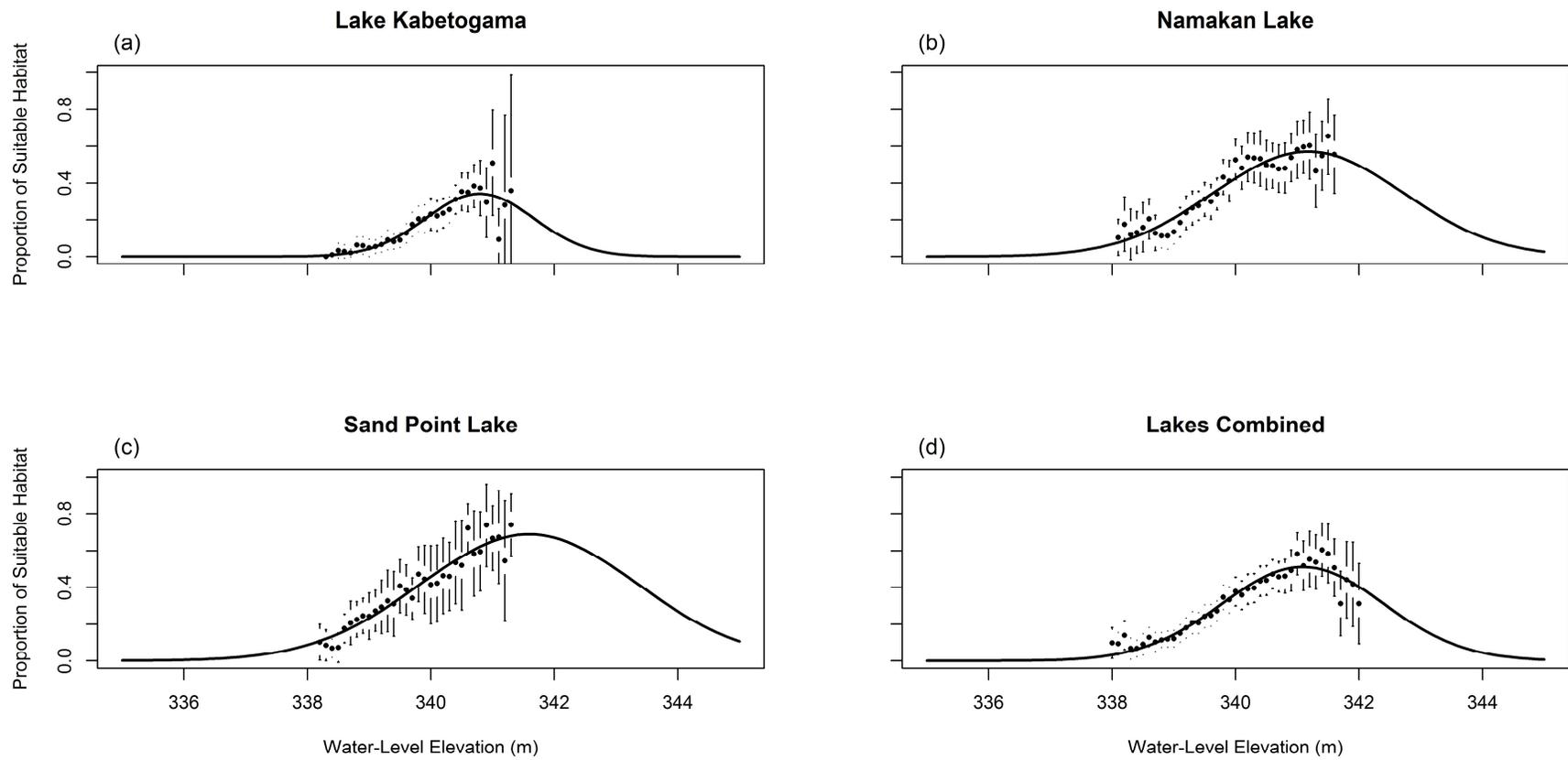


Figure S1. Gaussian functions (lines) fit to observed substrate suitability data (dots \pm CI) using nonlinear least squares for (a–c) each large lake in the reservoir, and (d) all data in aggregate.

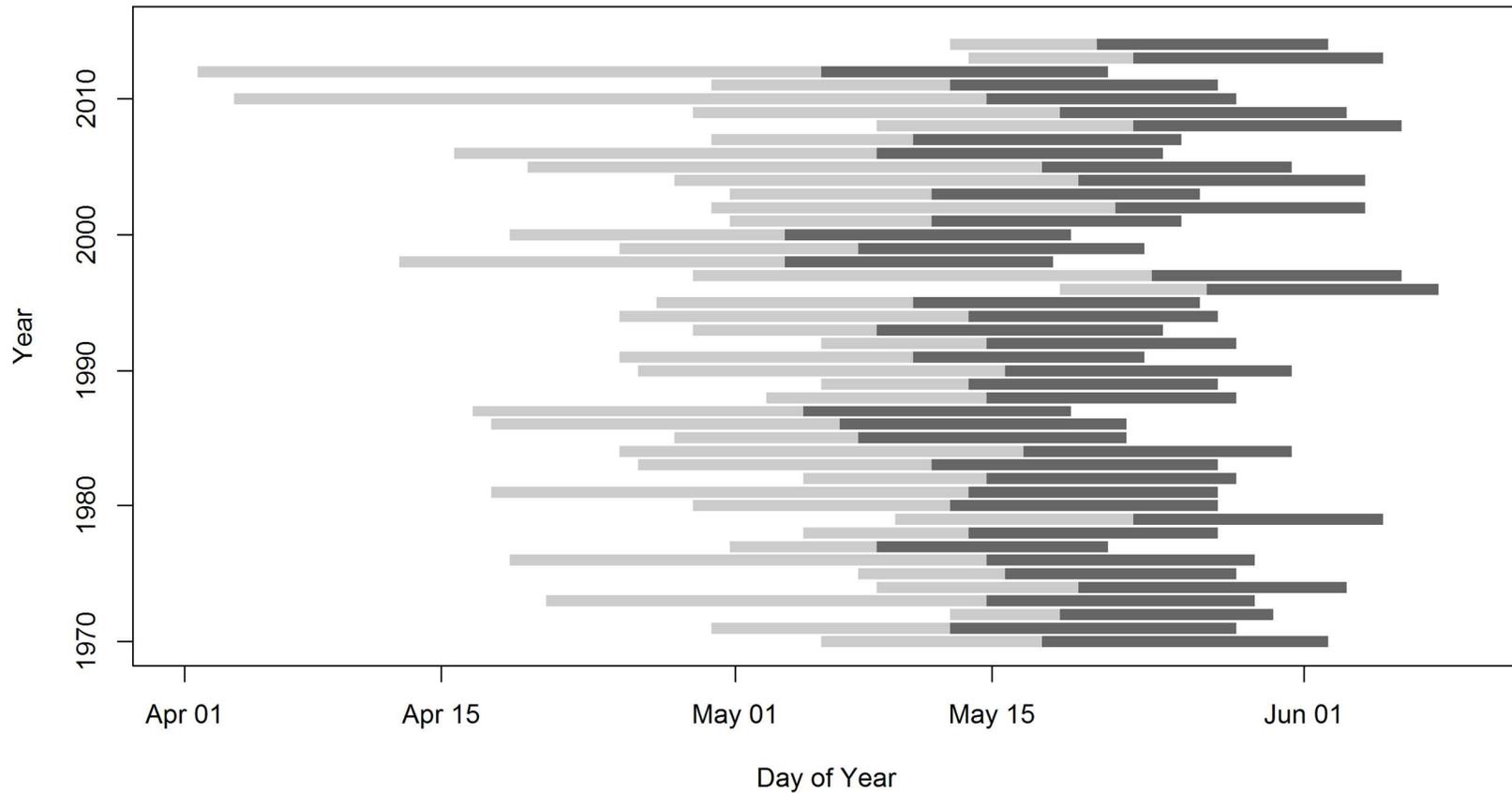


Figure S2. Estimated spawning seasons each year of the study period (1970-2014). Light gray bars are the period from ice-out to peak spawn and modeled at a water temperature of 10 C. Dark gray bars are the period from peak spawn to swim-up of newly hatched larvae, with peak hatch occurring 1 day before 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.

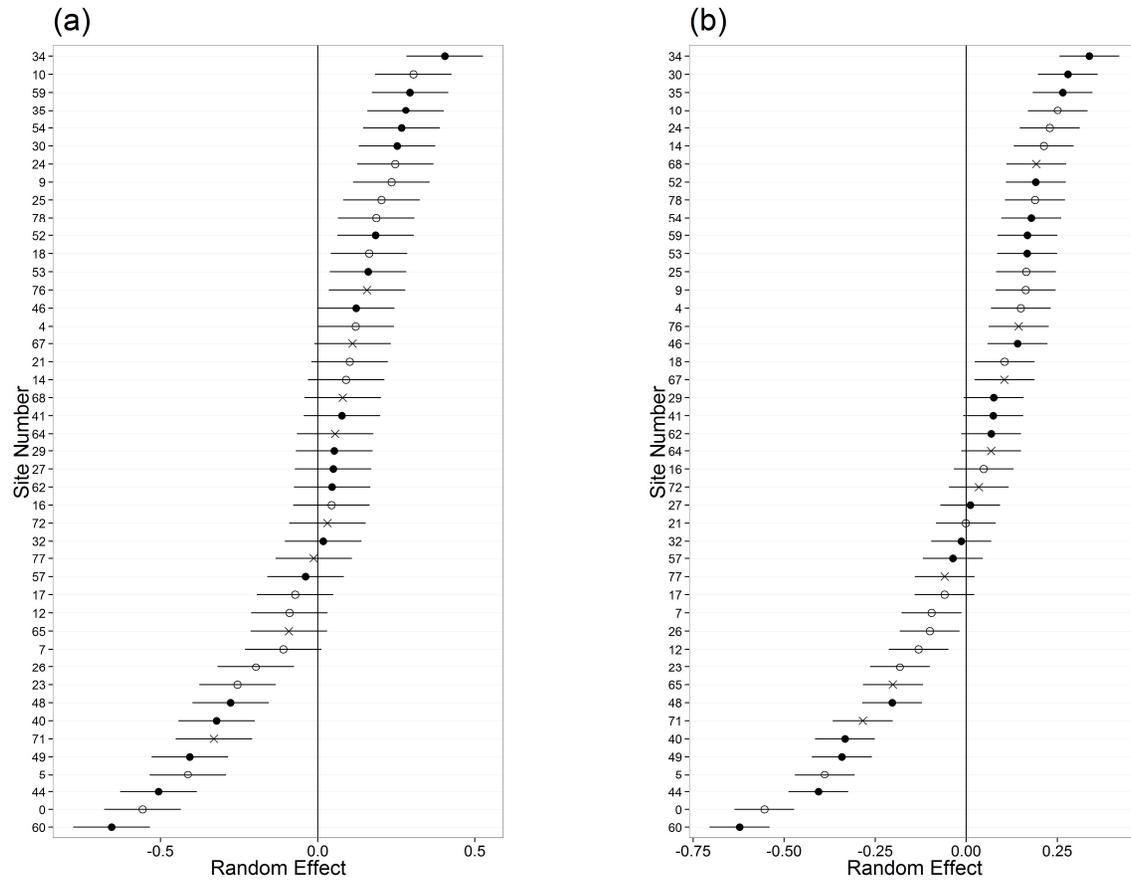


Figure S3. Estimates of the random site effects of the proportion of available preferred substrates during spawning seasons (1970-2014) on 44 sites in the Namakan Reservoir using observed (a) and modeled (b) water levels. Results are shown by lake: Lake Kabetogama (\circ), Namakan Lake (\bullet), and Sand Point Lake (\times). Error bars are predictions intervals.