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Lake Characteristics Influencing Spawning Success of Muskellunge in Northern Wisconsin Lakes

ASHLEY J. RUST*[1] AND JAMES S. DIANA

University of Michigan, School of Natural Resources and Environment,
Ann Arbor, Michigan 48109-1115, USA

TERRY L. MARGENAU

Wisconsin Department of Natural Resources, 810 West Maple,
Spooner, Wisconsin 54801, USA

CLAYTON J. EDWARDS

U.S. Forest Service, North Central Research Station,
5985 County Highway K, Rhinelander, Wisconsin 54501, USA

Abstract.—We determined the physical, chemical, biological, and land use characteristics that distinguish northern Wisconsin lakes with self-sustaining populations of muskellunge *Esox masquinongy* from lakes where stocking is required to maintain populations. Lakes that supported self-sustaining muskellunge populations were characterized by fewer shoreline alterations and by spawning habitats with softer, organic-nitrogen-rich sediments. Lakes that required stocking had extensively developed shorelines. The direction of water level change during the spawning period, percentage of spawning area sediment covered by woody debris, number of deadfall trees per kilometer of shoreline, and percentage of shoreline that was totally developed were the most important variables for classifying the level of muskellunge reproduction a lake could support. A linear discriminant function correctly classified 83% of the lakes with self-sustaining muskellunge populations and 89% of the lakes requiring stocking to sustain or enhance muskellunge populations. Lake managers wishing to use muskellunge stocking programs to reestablish self-sustaining populations should critically review each candidate lake by considering our model and that of Dombeck et al. (1986).

The spawning of muskellunge *Esox masquinongy* occurs in shallow water (less than 1 m deep) over organic sediment, woody debris, and submersed vegetation (Scott and Crossman 1973; Dombeck 1979; Dombeck et al. 1984; Zorn et al. 1998). Spawning muskellunge pair off and release sperm and eggs simultaneously. The eggs are nonadhesive and sink into the substrate (Scott and Crossman 1973). Previous studies indicate that low dissolved oxygen concentrations in spawning habitats (Dombeck et al. 1986; Zorn et al. 1998), competition with congeneric northern pike *Esox lucius* (Inskip and Magnuson 1983), and human development of shoreline habitat (Trautman 1981; Dombeck 1986; Jennings et al. 1999) may contribute to reduced natural reproduction of muskellunge.

Muskellunge reproductive success is often insufficient to sustain populations in their historically native lakes in Wisconsin (Dombeck et al. 1986; Hanson et al. 1986). Many of these waters are either stocked with hatchery-reared muskellunge to supplement natural recruitment or as the sole means of sustaining the population. Dombeck et al. (1986) categorized a large set of Wisconsin, Michigan, and Minnesota lakes according to the level of muskellunge reproduction that each lake supported. The authors related four levels of muskellunge reproduction to ecological variables such as rising spring water level, alkalinity, drainage or seepage status, northern pike abundance, and shoreline development factor. The Dombeck et al. (1986) classification provided a basis for our classification of muskellunge lakes.

Our objective was to identify the physical, chemical, and biological characteristics that are correlated with the reproductive success of muskellunge in northern Wisconsin lakes. We identified the effects of human alterations of the landscape on muskellunge reproduction by quantifying development along the shoreline and within the watershed of each study lake. Our ultimate goal was to develop a lake classification model suitable

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* Corresponding author: ashleyrust@hotmail.com

[1] Present address: 1425 South Elizabeth Street, Denver, Colorado 80210, USA.

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for predicting good and poor natural reproduction of muskellunge and to compare it to the one developed by Dombeck et al. (1986).

Methods

Muskellunge spawning activity, spawning site characteristics, shoreline development, and watershed development were surveyed on 23 study lakes in northern Wisconsin during 1998 and 1999. Muskellunge spawning was observed for approximately 2 weeks in mid-April of each year. Each lake was visited at least once, and a subset of lakes was visited in both years. Data from field measurements taken in 1998 and 1999 were combined for analysis. Biologists in Wisconsin had previously classified lakes into three categories based on their knowledge of muskellunge reproduction (WDNR 1996). We separated lakes into two groups: those with self-sustaining muskellunge populations (category 1 in WDNR 1996) and those requiring stocking of hatchery-reared fish to supplement or maintain a muskellunge population (categories 2 and 3). Thirteen lakes were classified as being in reproductive category 1, and 10 lakes were classified as being in reproductive categories 2 or 3. Each lake historically had a naturally reproducing population of muskellunge. The lakes did not differ significantly in size: category 1 lakes averaged 150 ha (SD = 143; range = 52–582 ha) in surface area, while category 2 and 3 lakes averaged 849 ha (SD = 1,644; range = 50–5,418) in surface area ($t = -1.7$, df = 21, $P = 0.11$). Two large category 2 and 3 lakes skewed the average; all other lakes in the study were approximately 150 ha. All selected lakes were classified by the WDNR (1996) as prime (class A) muskellunge fishing waters. Additionally, to simplify logistics of the study, the lakes that we selected were in relatively close proximity to each other.

Spawning habitat and lake characteristics.—Muskellunge spawning sites were located by means of the night visual observation method of Zorn et al. (1998). A spawning area was defined as a location where two or more muskellunge were observed near each other. To verify that spawning occurred within the areas defined as spawning habitat, we searched for muskellunge eggs in daylight, following Zorn et al. (1998).

Spawning habitat characteristics were measured from a boat anchored in two to four random locations within each spawning area, with the number of locations dependent upon the size of the area. At each site, a 75-cm-diameter weighted hoop was submerged on each of the four sides of the boat. Woody debris, dissolved oxygen, substrate composition, and substrate softness were then measured within the hoop.

The percentage of spawning area covered by woody debris was quantified by recording an image of the substrate within each hoop with a submersible video camera. The video image was then transferred onto the Fusion Recorder 1.0.2 program for Macintosh (VideoFusion, Inc.). Images were isolated, saved, and transferred into Adobe Photoshop, version 5.0.2 (Adobe Systems, Inc. 1998). The ruler tool in Adobe Photoshop was used to measure the percentage of the substrate area within the hoop occupied by woody debris.

Dissolved oxygen (DO) at both the substrate–water interface and 5 cm above the substrate was measured at the center of each hoop. Dissolved oxygen was measured between 0800 and 1200 hours. The probe of a Yellow Springs Instruments model 54A oxygen meter was attached to an adjustable tripod set on the lake bottom and was agitated during measurements. Dissolved oxygen was also measured on a subset of six spawning sites at dawn and in the late afternoon, to quantify daily DO fluctuations.

Substrate samples were collected by hand within each hoop, dried, ground to a fine powder, weighed, and then analyzed with an elemental analyzer to determine the percentage of nitrogen content by weight.

The softness of the sediment in the spawning habitat (henceforth termed penetrability) was measured with a length of polyvinyl chloride pipe equipped with a flat metal base. The pipe was held at the sediment–water interface within each hoop and then allowed to penetrate the sediment by gravity. The depth penetrated was measured, and penetrability values were averaged for each lake.

Water level fluctuation was monitored during the spawning and hatching period at one location in each study lake. A stake was driven into the lake sediment in 1 m of water and marked at the water level. The stakes were removed 30 d after spawning was observed, and the change in water level was measured. The stake at Upper Clam Lake (Ashland County) was missing when we attempted to retrieve it, so no data on water level change were available for this lake.

Lake managers were surveyed to determine ranked abundance of muskellunge, northern pike, walleyes *Stizostedion vitreum*, largemouth bass *Micropterus salmoides*, panfishes (Centrarchidae), bullheads (Ictaluridae), and yellow perch *Perca flavescens* in each study lake. The managers were

TABLE 1.—Mean values (SD) of characteristics related to muskellunge spawning habitat quality and results of two-sample *t*-tests comparing 13 category 1 lakes (which have self-sustaining populations) with 10 category 2 or 3 lakes (which require stocking to sustain populations), including degrees of freedom, *t*-statistics and *P*-values. Data were from 23 northern Wisconsin lakes (except where missing data is noted) in 1998 and 1999.

	Mean value (SD)		*t*-test		
Characteristic	Category 1 lakes	Category 2/3 lakes	*P*-value	df	*t*-statistic
Lake size (ha)	150 (143)	849 (1,644)	0.11	21	−1.7
Woody debris in spawning habitat (%)	4 (3.4)	1.8 (3.4)	0.14	21	1.5
Dissolved oxygen at substrate–water interface (mg/L)	6.3 (2.6)	6.7 (3.4)	0.76	21	−0.31
Organic nitrogen in sediment (%)	1.2 (0.75)	0.6 (0.53)	0.04	21	2.17
Spawning sediment penetrability (cm)	15 (6.4)	4 (2.3)	0.04	21	2.2
Water level change (cm)[a]	2.5 (5.91)	20.3 (7.75)	0.04	20	−1.8
Deadfall trees per kilometer	8.6 (6.7)	4.9 (6.1)	0.2	20	1.32
Emersed vegetation (%)[b]	8.4 (7)	15.4 (17)	0.19	20	1.35
Undeveloped shoreline (%)[b]	80 (17.8)	59 (24.3)	0.03	20	2.3
Developed shoreline (%)[b]	20 (17.8)	41 (24.3)	0.03	20	−2.3
Partially developed shoreline (%)[b]	13 (9.9)	14 (10.9)	0.065	20	−0.46
Totally developed shoreline (%)[b]	7 (9.3)	26 (17.5)	0.0	20	−3.2
Forest in watershed (%)	94.4 (6.2)	91.3 (13.8)	0.48	21	0.71
Urban land use in watershed (%)	0.01 (0.007)	0.03 (0.04)	0.11	21	−1.7
Ranked abundance of muskellunge	7 (2.5)	5 (2.7)	0.02	21	2.5
Ranked abundance of northern pike	1 (1.6)	4 (2.4)	0.0	21	−3.9

[a] Data for Upper Clam Lake are not included.

[b] No data were recorded on the Turtle–Flambeau flowage because the shoreline was too long.

asked to rank abundance of each taxonomic group on a scale from 0 (not present) to 10 (abundant) based on their previous surveys of the lakes.

Shoreline and watershed characteristics.—Aerial surveys were used on each study lake to determine the amount of physical structure available as nursery habitat for young muskellunge. An airplane was flown around the perimeter of each study lake to videotape the shoreline. The videotape was then used to determine the number of deadfall trees per kilometer of shoreline and the percentage of shoreline with one type of emersed vegetation (bulrushes *Scirpus* spp.). The shoreline of the Turtle–Flambeau flowage (Iron County) was too long (250 km) to videotape, and was not characterized.

We visually quantified the percentages of undeveloped (marsh or forest), partially developed, and totally developed shoreline and determined the percentage of altered shoreline. Shoreline was defined as totally developed if the entire shore area had been changed; in most cases, a mowed lawn lined the shore instead of a forested or wetland area. Partially developed shoreline was land with a structure on it but which was not otherwise dramatically changed. Altered shoreline was the amount of actual shoreline covered in riprap, railroad ties, or additional sand. Developed shoreline was the sum of partially and totally developed shoreline. We measured shoreline attributes from a boat travelling at slow speed and maintaining a constant distance from shore. We used a fish finder to record the length of the shoreline in order to note points where the shoreline landscape changed on a paper chart. Later, the paper chart from the fish finder was correlated with the lake map and the percentage of shoreline in each landscape category was calculated from the chart. Shoreline data were not recorded for the Turtle–Flambeau flowage due to the length of the shoreline.

Watershed development was quantified with the aid of a Geographic Information Systems software program. Land use coverages and watershed boundaries were found on GEODISC 3.0, which was produced by the Wisconsin Department of Natural Resources (WDNR) in 1998. We adopted the land use categories defined in GEODISC 3.0. The urban and agricultural areas in each watershed were summed separately and used to calculate the percentages of each type of development within the watershed of each lake.

Statistical analysis.—Statistical analysis for all measurements was performed with SYSTAT 7.0 (SPSS 1997). We began by evaluating summary statistics of each variable for the two classes of lakes. All percentage data were arcsine transformed to obtain normality. As all variables used in the analysis were normally distributed, parametric statistics were used. A *P*-value of 0.05 or less was considered statistically significant in all analyses. Physical, chemical, and biological characteristics used as dependent variables are listed in Table 1; *t*-tests were performed on each dependent variable to determine whether values differed between lake types.

Discriminant analysis was used to create a linear combination of the original variables into a new variable that would best separate the lakes into two classes. The *F*-to-remove values determined the relative importance of variables included in the model. The *F*-value for a variable measures the extent to which it uniquely contributes to prediction of group membership. Individual lake data were reanalyzed in the model to test how well the lakes were classified according to the selected variables. The equations were then used to calculate scores for each lake. In the classification matrix, each lake was grouped into the class where it scored the highest. Upper Clam Lake and the Turtle–Flambeau flowage were omitted from the model because of missing data.

Dombeck et al. (1986) also used discriminant analysis to create a model for predicting the probability of each level of muskellunge reproduction a lake could support, though theirs was based on a different set of lakes and different lake characteristics. We used that model (programmed into a Microsoft Excel spreadsheet by J. Breck, Michigan Department of Natural Resources) to predict the level of muskellunge reproduction our study lakes could support, based on rising spring water level, alkalinity, drainage or seepage status, northern pike abundance, and shoreline development factor. Shoreline development factor relates the length of the shoreline to the surface area of a lake to quantify whether the shoreline is convoluted or smooth. The Dombeck et al. (1986) model classified lakes into four reproductive levels: poor, low, moderate, and high. We combined the poor and low reproductive levels into one category (poor reproduction) and the moderate and high reproductive levels into a second category (good reproduction) for purposes of our data analysis. We then compared results from our discriminant analysis classification to the results from the Dombeck et al. (1986) model.

Results

Spawning Habitat and Lake Characteristics

From one to three spawning sites were identified along the shores of each study lake, and muskellunge eggs were found in 61% of the spawning sites. No eggs were found during searches conducted later than 18 d after spawning, probably due to hatch, decomposition, or predation.

The average percentage of spawning habitat area covered by woody debris was 1–4%, and it did not differ significantly between lake category 1 and categories 2 and 3. Dissolved oxygen at the substrate–water interface did not differ significantly among lake categories. Dissolved oxygen levels also did not vary at the substrate–water interface between dawn and afternoon (t = 0.3, df = 3, P = 0.81). The percentage of organic nitrogen (N) in spawning sediments was significantly higher in category 1 lakes than in category 2 and 3 lakes. Category 1 lakes had significantly higher sediment penetrability than category 2 and 3 lakes. Water levels dropped after the spawning period in 6 of 12 category 1 lakes, whereas water levels rose after the spawning period in 9 of 10 category 2 and 3 lakes. Shoreline nursery habitat was similar for both lake types. Deadfall trees per kilometer and emersed vegetation did not differ significantly between lake types.

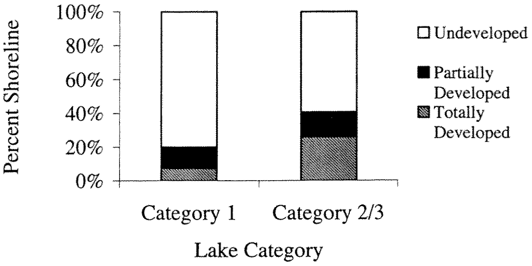

FIGURE 1.—Average percent of shoreline that was undeveloped, partially developed, and totally developed in 23 northern Wisconsin lakes with category 1 and category 2 or 3 muskellunge reproduction in 1998 and 1999.

Shoreline and Watershed Characteristics

The percentage of undeveloped shoreline was significantly higher for category 1 lakes (80%) than for category 2 and 3 lakes (59%; Figure 1). Both lake types had similar percentages of partially developed shoreline, but category 2 and 3 lakes had more totally developed shoreline than category 1 lakes (Figure 1). The percentage of altered shoreline was low on average in both lake types and was not significantly different between the two types. The number of docks per kilometer of shoreline was similar between the two types (t = −1.7, df = 20, P = 0.09). Few measures of human development in the watershed differed significantly among the two lake types. In fact, more than 90% of the land between 10 m of shore and the watershed boundary was forested in both lake types. Muskellunge were significantly more abundant in category 1 lakes (average ranking, 7) than

TABLE 2.—Eigenvalues of discriminant models used to classify lakes according to muskellunge reproductive potential and *F*-to-remove values showing the relative importance of each variable in the model. The model was derived from data on 21 northern Wisconsin lakes in 1998 and 1999.

Variable	Eigenvalues: Category 1 lakes	Eigenvalues: Category 2/3 lakes	*F*-to-remove value
Constant	−2.950000	−4.704000	
Totally developed shoreline (%)	0.105009	0.205756	3.29
Water level change (cm)	−0.043687	0.152294	1.70
Woody debris in spawning habitat (%)	0.259902	0.218924	0.97
Deadfall trees per kilometer	0.310228	0.221395	0.45

in category 2 and 3 lakes (average ranking, 5), where they were common but not abundant. Furthermore, northern pike were considered to be more abundant in category 2 and 3 lakes than in category 1 lakes.

The direction of the water level change, number of deadfall trees per kilometer of shoreline, percentage of sediment area covered by woody debris, and percentage of totally developed shoreline were the most important variables in differentiating between the two lake types. The percentage of totally developed shoreline was the most important variable in determining whether a lake had good reproduction or not ($F = 3.29$, df = 16, $P = 0.02$; Table 2). Ten of the 12 category 1 lakes included in the model were classified correctly as category 1 lakes according to the discriminant analysis model (Table 3). Grand Portage Lake and Pine Lake (Iron County) were incorrectly classified as category 2 and 3 lakes by the model. Eight of the nine category 2 and 3 lakes included in the model were classified correctly as category 2 and 3 lakes (Table 3), with Moose Lake (Iron County) as the exception. According to the classification method based on the four variables, 86% of all lakes were assigned to the correct category (Table 3).

The Dombeck et al. (1986) model predicted that 77% of our category 1 study lakes would support moderate or high muskellunge reproduction and 23% would support poor or low reproduction (Table 4). The model assigned 50% of our category 2 and 3 lakes to a poor or low muskellunge reproduction classification and 50% to moderate or high reproduction (Table 4). Overall, 65% of the study lakes were placed in the correct category by the Dombeck et al. (1986) model.

TABLE 3.—Results of a discriminant analysis model classifying study lakes according to muskellunge reproductive potential and agreement of the model with the Wisconsin Department of Natural Resources' (WDNR 1996) classification. Data for the model were collected from 21 northern Wisconsin lakes in 1998 and 1999.

WDNR classification	Model class: 1	Model class: 2/3	% correct
Category 1	10	2	83
Category 2/3	1	8	89
Total	11	10	86

Discussion

We found that lakes with self-sustaining muskellunge populations were mostly surrounded by forest, whereas lakes that required stocking had less shoreline in a natural state and more with human development. Previous studies have also indicated that human development affects muskellunge reproductive success and overall numbers (Trautman 1981; Dombeck et al. 1984). Development along the shoreline had the greatest negative correlation with spawning habitat suitability in this study, while development within the watershed was not correlated with spawning habitat suitability. However, all our lakes were located in areas where watersheds were mostly forested (>90%). Expansion of this data set with data from

TABLE 4.—The number of study lakes classified as having poor, low, moderate, and high reproductive potential by the Dombeck et al. (1986) model and the percent of classifications that were correct. Data used in this comparison were collected from 23 northern Wisconsin lakes in 1998 and 1999.

Dombeck prediction class and % correct	Observed class: 1	Observed class: 2/3
Poor (1)		
Low (2)	1	5
	2	0
Moderate (3)	3	3
High (4)	7	2
Total	13	10
% Correct[a]	77	50

[a] Computed as (3 + 7)/13 for observed class 1, 5/10 for observed class 2/3.

more developed regions may show greater correlation between land use in the watershed and muskellunge reproductive success.

The number of deadfall trees per kilometer of shoreline was positively related to suitability of the spawning habitat and reproductive success of muskellunge in the 23 study lakes. MacGregor et al. (1960) also found that muskellunge elected to spawn over areas where deadfalls, stumps, and driftwood were available. Deadfall trees also provide age-0 muskellunge with shelter from predators and a source of prey (Hanson and Margenau 1992).

We found that the percentage of spawning habitat area covered by woody debris was also correlated with muskellunge reproductive success. Both Zorn et al. (1998) and Dombeck et al. (1984) found higher muskellunge egg survival on sediments with woody debris than on bare sediments. The sediments in self-sustaining muskellunge lakes were also softer and had more organic nitrogen than did sediments in lakes requiring stocking. The soft organic sediments may protect muskellunge eggs from predation by camouflaging the eggs as they sink into the sediment. Soft sediments may also allow low flows of water to circulate, providing dissolved oxygen to eggs. Our results suggest that more deadfall trees, woody debris, and rich organic sediments occurred in lakes less affected by human development.

The direction of water level change during the spawning period was related to suitability of spawning habitat and muskellunge spawning success. The damming of rivers and creation of reservoirs apparently cause a deviation from natural water level fluctuations. In self-sustaining lakes, spring flooding enhanced muskellunge access to organically rich vegetative areas during the spawning period. Access to aerated sediments and vegetative areas has been identified as a critical factor for muskellunge spawning success (Scott and Crossman 1973; Dombeck 1986). Water levels continued to rise after spawning in category 2 and 3 lakes, resulting in the submergence of sediment in these lakes throughout the spring. Sediments not exposed to air during spring fail to become properly aerated between spawning events. Dombeck (1986) suggested that aeration of sediments in spawning habitat is necessary to reduce biochemical oxygen demand of the sediments.

The Dombeck et al. (1986) model correctly classified 77% of the self-sustaining muskellunge lakes in our study as supporting moderate or high levels of muskellunge reproduction. The model's results are similar to those from our discriminant analysis model, which correctly classified 83% of the self-sustaining lakes. Since the Dombeck et al. (1986) model was created with data from lakes different from those used here, we would not expect it to be as accurate as a model based on one data set. The Dombeck et al. (1986) model correctly classified only 50% of the study lakes requiring stocking, probably because it did not consider human development of the shoreline.

Our model incorrectly classified Moose Lake (Iron County), one of the nine lakes requiring stocking. Moose Lake has no human development and a high number of deadfalls per kilometer, characteristics of a self-sustaining muskellunge lake. However, the Dombeck et al. (1986) model did classify Moose Lake correctly, likely because northern pike are common there. The Turtle–Flambeau flowage was classified by the WDNR as requiring stocking, but the Dombeck et al. (1986) model predicted the lake would support good reproduction. The Turtle–Flambeau flowage has characteristics of a self-sustaining lake and could possibly support a muskellunge population through natural reproduction; yet the lake continues to receive stockings, possibly for social or political reasons, as Dombeck et al. (1986) speculated for Lake Chippewa (Sawyer County). Many of the muskellunge waters requiring supplemental stocking are large lakes that are intensively managed and more likely to be stocked (WDNR 1996). Some of these lakes, though stocked, could possibly support populations by natural reproduction. Unnecessary or excessive stockings are a concern that management agencies will need to address to maximize the contributions of cultured muskellunge (Margenau 1999).

Two of the 12 self-sustaining muskellunge lakes were not classified correctly by our model. Though the lakes were previously described as self-sustaining (WDNR 1996), their ability to support muskellunge reproduction should be reevaluated due to ongoing shoreline development and habitat alterations. Ideally, the WDNR lake classifications and muskellunge stocking program should be periodically updated to reflect changing conditions. Both our model and that of Dombeck et al. (1986) were based on subjective categorizations of muskellunge reproductive success by lake biologists, so each lake's reproductive status results from professional judgment and social or political factors as well as from the data itself. Zorn et al. (1998) based their study on the same WDNR (1996) classification system, and they compared spawning habitat characteristic of four lakes, three of which were included in this study. Zorn et al. (1998) performed electrofishing surveys of the four lakes in the fall to determine whether observed natural recruitment agreed with the classification system, and found a higher catch per effort of age-0 muskellunge in the two self-sustaining lakes than in the two lakes requiring stocking.

Our results did not suggest that northern pike interact negatively with muskellunge, as others have found. Numerous studies have suggested that northern pike prey upon age-0 muskellunge and compete for food resources and spawning sites (Caplin 1982; Inskip and Magnuson 1983, 1986; Inskip 1986). We included ranked abundance estimates for northern pike in our data analyses, but northern pike were not common in almost all study lakes and therefore did not appear to influence muskellunge reproductive success. Nevertheless, the relative abundances of northern pike in the two lake categories were statistically different, but not important in discriminating between self-sustaining lakes and those requiring stocking.

Management Recommendations

Muskellunge spawning habitats should be identified and protected from future perturbation. The physical properties of spawning areas in category 1 lakes, such as rich organic sediments, woody debris, and deadfall trees, should be maintained, as should normal seasonal fluctuations in the water levels, including spring flooding of nearshore areas. Minimal disruption of critical and delicate features of spawning habitat would allow self-sustaining muskellunge populations to continue.

The type of development taking place along the shorelines of muskellunge lakes was correlated with spawning success. The trends of completely altering the shoreline and clearing the landscape of vegetation appear detrimental to spawning habitats. Limiting such drastic development should be considered seriously as suitable muskellunge spawning habitat becomes scarcer.

Biologists intending to use muskellunge stocking to reestablish self-sustaining populations should critically review each candidate lake. The review should consider both the Dombeck et al. (1986) model, which takes into account northern pike abundance and the seepage or drainage status of each lake, and our model, which considers the habitat features and level of development. Lakes that support abundant northern pike populations and that have widespread shoreline development are unlikely to regain self-sustaining populations of muskellunge.

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