

Predicting the Occurrence and Success of Walleye Populations from Physical and Biological Features of Northern Wisconsin Lakes

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Abstract.—We developed a linear discriminant function (LDF) using surface area, mean depth, fetch, and three substrate descriptors to discriminate the presence and absence of walleyes *Sander vitreus* (formerly *Stizostedion vitreum*) in 120 northern Wisconsin lakes. The resulting LDF correctly classified 90% of walleye lakes and 85% of nonwalleye lakes. For model validation, the model classified 90% of walleye lakes and 93% of nonwalleye lakes in an independent set of 100 randomly selected lakes. In contrast, within walleye lakes, an LDF using the same variables correctly classified only 60% of 30 self-sustaining walleye lakes and 50% of 30 stocked walleye lakes. For model validation, the model classified 30% of self-sustaining walleye lakes and 73% of stocked walleye lakes in an independent set of 40 randomly selected lakes. To further assess the differences between walleye lakes with self-sustaining and stocked populations, the angler catch rates for largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, northern pike *Esox lucius*, and muskellunge *E. masquinongy* obtained from creel surveys during 1990–2001 were analyzed by means of a principal components analysis. The first principal component explained 29% of the variation and represented a linear contrast between the relative abundance of walleyes and muskellunge and the relative abundance of largemouth bass and northern pike. High largemouth bass and northern pike densities characterized lakes with stocked walleye populations, whereas high walleye and muskellunge densities characterized lakes with self-sustaining walleye populations. We conclude that physical features may be used to discriminate lakes where walleyes presently occur from lakes where walleyes do not presently occur, and that fish community differences exist between stocked and self-sustaining walleye populations in northern Wisconsin.

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The presence and abundance of walleye *Sander vitreus* (formerly *Stizostedion vitreum*), a highly valued sport fish in much of North America, is often maintained or supplemented by stocking. In the last century, stocking has often been used to meet the increased demand for walleyes in North American waters, yet the survival of stocked fish is often unpredictable (Larman 1978). This unpredictable stocking success may be caused by interactions with naturally reproducing walleyes (Li et al. 1996), predation by other species on newly stocked walleyes (Santucci and Wahl 1993), and

variable environmental conditions at the time of stocking (Kampa and Jennings 1998), as well as the suitability of the lake habitat for walleyes. Variation in the natural recruitment of walleyes is common and often caused by a combination of environmental factors and interactions with other species (Madenjian et al. 1996; Hansen et al. 1998). Therefore, the management of self-sustaining and stocked walleye populations may be improved through a better understanding of the physical and biological features of lakes that support walleye populations.

Physical habitat characteristics may be useful for classifying lakes that are likely to support walleyes through annual stocking or through the establishment of self-sustaining populations. For example, lake area and depth were important for distinguishing lake types based on associations of walleye, northern pike *Esox lucius*, lake trout *Salvelinus namaycush*, and smallmouth bass *Micropterus dolomieu* for 2,496 Ontario lakes (Johnson et al. 1977). Kitchell et al. (1977) theorized that a percid habitat in lakes may be characterized by conditions analogous to those of temperate rivers where the species likely evolved, including sand or gravel substrate, low current velocity, reduced light penetration, temperatures optimal for growth (22–31°C), temperatures optimal for gonadal maturation (<12°C during winter), and well-oxygenated spawning substrate. Ryder and Kerr (1978) described the harmonic percid community in Canadian lakes as one that exists in moderately transparent mesotrophic lakes, with a Secchi depth visibility of 2–5 m and sufficient depth for temperature to stratify in spring and fall.

Species associations may also be useful for determining which lakes are likely to support self-sustaining walleye populations. Ryder and Kerr (1978) suggested that marginal abiotic conditions for percids would lead to increased competition and predation with other species that are more tolerant of prevalent abiotic conditions. For example, introduced northern pike reduced the abundance of the favored prey of walleyes, yellow perch *Perca flavescens*, and thereby may have caused the walleye population to decline in Horseshoe and Grace lakes, Minnesota (Colby et al. 1987). Also, predation by newly stocked smallmouth bass on juvenile walleyes may have been a factor in the decline of walleye populations in three of four northeastern Minnesota lakes (Johnson and Hale 1977). Lastly, predation by largemouth bass *M. salmoides* limited the survival of stocked walleyes



FIGURE 1.—Locations of 120 northern Wisconsin lakes used to determine walleye presence (dots) and absence (triangles) from physical lake characteristics.

in Ridge Lake, Illinois, a centrarchid-dominated impoundment (Santucci and Wahl 1993).

Our objectives were to (1) identify and quantify physical lake features associated with the presence of walleyes (stocked or natural) in lakes, (2) identify and quantify physical lake features associated with the presence of self-sustaining walleye populations, and (3) evaluate the differences in fish community patterns associated with the presence of self-sustaining and stocked walleyes in northern Wisconsin lakes. We expected that walleyes would be present in lakes with similar physical characteristics, and that self-sustaining walleye populations would likely be associated with different physical habitat or species than stocked walleye populations.

Methods

Study area.—The study area encompassed 22,400 square miles of northern Wisconsin (Figure 1; U.S. Department of the Interior 1991). Fisheries management in this part of the state relies on lake-specific tribal spearing quotas and angling bag limits, set annually on all lakes known to have walleye populations (Hansen 1989; Staggs et al. 1990). The presence or absence of walleyes and the source of walleye recruitment (i.e., stocked or natural) had been determined by state and tribal biologists from available fisheries survey data for all lakes (U.S. Department of the Interior 1991). For lakes known

TABLE 1.—Summary of limnological information used to discriminate walleye presence ($N = 60$) and absence ($N = 60$) in 120 northern Wisconsin lakes.

Variable	Walleye lakes			Non-walleye lakes		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Area (acres)	529.8	28.0	5,039.0	108.9	15.0	1,018.0
Fetch (mi)	1.6	0.3	8.1	0.7	0.2	3.5
Maximum depth (ft)	38.0	5.0	106.0	21.8	4.0	70.0
Bottom sand (%)	54.3	0.0	95.0	46.6	0.0	100.0
Bottom gravel (%)	14.2	0.0	58.0	9.3	0.0	50.0
Bottom muck (%)	22.6	0.0	90.0	40.4	0.0	100.0

to have walleye populations, classifications were used to describe the recruitment source and ranged from completely self-sustaining to completely dependent on stocking, with other categories for newly stocked or remnant populations (U.S. Department of the Interior 1991). For our first objective—predicting walleye presence versus absence—lakes were considered “walleye” lakes if their populations were either stocked or self-sustaining, whereas lakes were considered “non-walleye” lakes if they were newly stocked, contained remnant populations, or if they lacked walleyes. Previous research showed that the adult walleye abundance in lakes with walleye populations representative of five of eight recruitment classifications was not statistically differentiable, and that the recruitment classification scheme could be simplified to two recruitment classifications: “NR” for lakes in which walleyes reproduce, and “ST” for lakes in which walleyes do not reproduce (Nate et al. 2000). Therefore, for our second objective—predicting the presence of self-sustaining versus stocked walleye populations—lakes designated as having some natural reproduction were considered self-sustaining, while lakes with populations where stocking was the major source of walleye recruitment were considered stocked.

Lake data.—For our first two objectives, limnological data (Table 1) obtained from the Wisconsin Department of Natural Resources Surface Water Inventory File were used to discriminate walleye from nonwalleye lakes and self-sustaining from stocked walleye lakes. The Surface Water Inventory File contains data from limnological surveys conducted on most northern Wisconsin lakes during 1961–1983 (Wisconsin Conservation Department 1961–1966; Wisconsin Department of Natural Resources 1967–1983). Gaps in the data were supplemented with data from Surface Water Resources publications (Wisconsin Conservation Department 1961–1966; Wisconsin Department of Natural Resources 1967–1983). Six physical lake

variables were selected based on their potential importance for walleye survival and reproduction, and thus their potential to discriminate walleye from nonwalleye lakes and stocked from self-sustaining walleye lakes. Lake area, depth, and fetch are descriptive of the thermal habitat in the lake, while substrate measures are indicators of potential spawning habitat.

The data set was limited to include only those lakes with surface areas greater than 13 acres (the smallest lake known to have walleyes in the data set). Lakes were also eliminated from the analysis if data were missing for any of the six physical variables of interest, reducing the number of lakes from 13,417 to 2,657. In the resulting data set, walleyes were present in 585 lakes and absent in 2,072. For the first objective, a balanced, randomly selected subsample of 120 lakes (60 walleye, 60 nonwalleye) was selected for building the linear discriminant function (LDF). An additional independent data set of 100 lakes (40 walleye, 60 non-walleye) was used to validate the resulting classification. The initial model building and validation data sets were also used for the next two objectives. Of the 60 walleye lakes used to build the first model, 30 were lakes with stocked walleye populations and 30 were lakes with self-sustaining walleye populations, and all lakes had creel survey information available for the third objective. Because there were fewer stocked walleye lakes with creel surveys, the sample size of stocked walleye lakes in the validation data set for our second objective differed (10 versus 30). We included stocked lakes because our first objective was to classify lakes based on the physical features of the lakes where walleyes presently exist. Walleyes may be stocked into lakes for many reasons, not always to establish a self-sustaining population.

An LDF (Morrison 1990) was used to determine if physical lake variables could be used to classify lakes into groups based on known group membership. Linear discriminant analysis was selected be-

TABLE 2.—Linear discriminant functions (LDFs) for determining lakes where walleyes were absent (≥ 10.64) from lakes where walleyes were present (< 10.64) and lakes with stocked walleye populations (≥ 2.60) from lakes with self-sustaining walleye populations (< 2.60) using six physical characteristics for 120 northern Wisconsin lakes.

Variable	Coefficient			Coefficient		
	Absent	Present	Difference	Stocked	Self-sustaining	Difference
Constant						
Area (acres)	-60.55	-71.19	10.64	-85.15	-87.75	2.60
Fetch (mi)	8.55	10.94	-2.39	13.00	13.68	-0.67
Maximum depth (ft)	-28.59	-28.73	0.14	-35.06	-37.77	2.70
Bottom sand (%)	8.98	9.57	-0.59	15.43	15.52	-0.09
Bottom gravel (%)	44.30	41.44	2.86	48.40	48.65	-0.25
Bottom muck (%)	39.48	39.69	-0.21	38.12	37.55	0.57
Bottom muck (%)	51.37	48.11	3.26	36.56	39.40	-2.83

cause our first two objectives were to discriminate between two known groups (walleye versus non-walleye lakes and stocked versus self-sustaining walleye lakes) for the purpose of developing a classification scheme for new observations. Linear discriminant analysis is a useful technique for classifying new, unknown observations and has been used in previous analyses linking fish populations to their habitat (e.g., Johnson et al. 1977; Tonn and Magnuson 1982). Linear discriminant analysis requires independent unbiased samples from known populations (in this case walleye and nonwalleye lakes, and stocked and self-sustaining walleye lakes). The samples should be multivariate normal and the populations should have equal covariance structure (Morrison 1990). Lake surface area, fetch, and maximum depth were transformed into natural logarithms and percent sand, gravel, and muck were transformed into arcsines to meet assumptions of multivariate normality (Neter et al. 1996). We assumed an equal a priori probability of walleye and nonwalleye lakes (i.e., 50% in each class).

Fish data.—Principal components analysis (PCA; Morrison 1990) was used to describe patterns in relative abundance (as indexed by angling catch rates from creel surveys) for five fish species, including smallmouth bass, largemouth bass, muskellunge *E. masquinongy*, northern pike, and walleyes, in lakes with self-sustaining and stocked walleye populations. Angling catch rates are linearly related to walleye population density (Beard et al. 1997; Hansen et al. 2000; Newby et al. 2000). Creel survey data were available only for walleye lakes, so PCA was not used to explore fish community differences for walleye and nonwalleye lakes, and an LDF could not be developed using both physical and biological variables. PCA has been used to examine data structure and ordination

in fisheries (Claramunt and Wahl 2000; Willis and Magnuson 2000). The 60 walleye lakes used to build the LDF in the first analysis were also used for the principal components analysis, of which 30 had self-sustaining walleye populations and 30 had stocked walleye populations.

Creel surveys for each of the 60 walleye lakes were conducted during the angling season (first Saturday in May through March 1 of the following year) as part of a larger study of northern Wisconsin lakes during 1990–2001 (Beard et al. 1997). A stratified random roving access design was used (Pollack et al. 1994), and sampling was stratified by weekend days (holidays included) and weekdays. We used general catch rates (total number caught per hour fished) of smallmouth bass, largemouth bass, muskellunge, northern pike, and walleyes estimated from complete-trip interviews of anglers as indices of relative abundance (Beard et al. 1997). The catch rates were summarized by month and day type (weekend or weekday), and a yearly mean catch rate for each lake was estimated as a weighted mean of the monthly estimates. The catch rates were transformed into natural logarithms (+1) to normalize their distributions. PCA was used on the correlation matrix because the catch rates of the various species varied over two orders of magnitude.

Results

Lakes with walleyes were larger, deeper, and had more sand and gravel bottom than lakes without walleyes, which were smaller, shallower, and had more muck bottom (Table 1). An LDF that included lake surface area, fetch, mean depth, percent sand, percent gravel, and percent muck (Table 2) discriminated lakes without walleye populations from lakes with walleye populations (Table 3). Bottom muck (%), bottom sand (%), and area

TABLE 3.—Classification with cross-validation summary for LDF using lake surface area, fetch, maximum depth, percent sand, percent gravel, and percent muck to discriminate 120 northern Wisconsin lakes with and without walleye populations and 60 northern Wisconsin lakes with stocked and self-sustaining walleye populations. The table shows the number of observations classified into each group.

	Model building			Model validation		
	A	B	Total	A	B	Total
Walleye present (A) versus absent (B)						
A	51	9	60	56	4	60
B	6	54	60	4	36	40
Total	57	63	120	60	40	100
Priors	0.5	0.5		0.5	0.5	
Stocked (A) versus self-sustaining (B)						
A	15	15	30	3	7	10
B	12	18	30	8	22	30
Total	27	33	60	11	29	40
Priors	0.5	0.5		0.5	0.5	

(acres) contributed the most to the LDF, based on differences in their respective coefficients. Of the 120 lakes used to construct the LDF, the model correctly classified 85% of lakes without walleye populations and 90% of lakes with walleye populations. Of the 100 lakes used to validate the LDF, the model correctly classified 93% of lakes without walleye populations and 90% of lakes with walleye populations. The low error rates suggest that the LDF of lake surface area, fetch, mean depth, percent sand, percent gravel, and percent muck may be used to predict whether a lake has the physical features conducive for walleyes.

For walleye lakes, an LDF that included lake surface area, fetch, mean depth, percent sand, percent gravel, and percent muck (Table 2) did not effectively discriminate lakes with stocked walleye populations from lakes with self-sustaining walleye populations (Table 3). Bottom muck (%) and fetch (miles) contributed the most to the LDF, based on differences in their respective coefficients. Of the 60 lakes used to construct the LDF, the model only correctly classified 50% of the lakes with stocked walleye populations and 60% of the lakes with self-sustaining walleye populations. Of the 40 lakes used to validate the LDF, the model correctly classified only 30% of the lakes with stocked walleye populations and 73% of the lakes with self-sustaining walleye populations. The higher error rates suggest that the LDF of lake surface area, fetch, mean depth, percent sand, percent gravel, and percent muck cannot be

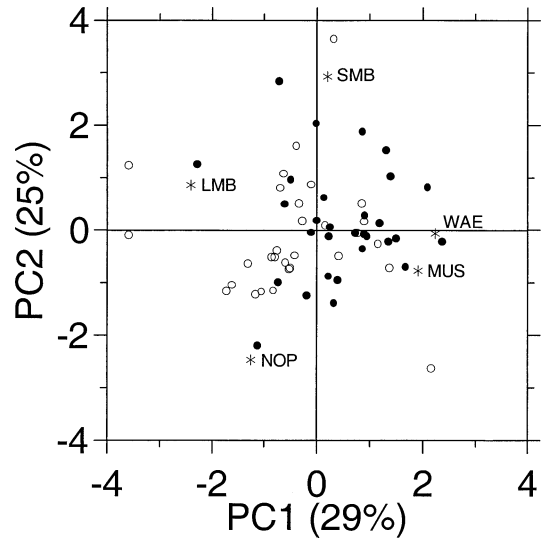


FIGURE 2.—First (PC1) and second (PC2) principal components of angler catch rates (number/h of fishing) for five game fish species from 60 northern Wisconsin lakes with self-sustaining (closed dots) and stocked (open dots) walleye populations during 1990–2001. Asterisks indicate scaled eigenvectors ($4\times$) for muskellunge (MUS), northern pike (NOP), smallmouth bass (SMB), largemouth bass (LMB), and walleyes (WAE).

used to predict whether a lake has the physical features conducive to walleye reproduction.

PCA indicated that different densities of game fish species characterized the lakes with stocked and self-sustaining walleye populations (Figure 2). The first principal component explained 29% of the variation in the data, and represented a contrast between the relative abundances of walleyes and muskellunge and the relative abundance of largemouth bass. The second principal component explained 25% of the variation in the data and represented a contrast between the relative abundances of northern pike and smallmouth bass. Lakes with stocked walleye populations generally grouped to the left of center along the first principal component, while lakes with self-sustaining walleye populations generally grouped to the right of center along the first principal component axis. High largemouth bass and northern pike densities often characterized lakes with stocked walleye populations, whereas high walleye and muskellunge densities often characterized lakes with self-sustaining walleye populations.

Discussion

Our results identified the physical features of lakes that are related to the presence of walleyes

and the biological features of lakes that are related to the presence of self-sustaining walleye populations, which clarify the findings of our previous analyses (Nate et al. 2000, 2001). Nate et al. (2000) showed that lakes with walleye populations could be classified into two broad groups: those with self-sustaining populations, and those with stocked populations. Our present findings clarified the idea that interactions with other species (such as northern pike and largemouth bass) may determine the likelihood that a lake will support a self-sustaining walleye population. Nate et al. (2001) further showed that the limnological characteristics of lakes (such as area, depth, and substrate) were useful for describing the abundance of stocked and self-sustaining walleye populations. Our present findings showed that such variables, combined and used as the basis for lake classification, were important descriptors of walleye presence, but were less useful as predictors of a lake's ability to support a self-sustaining population.

Our results demonstrate that the physical features of lakes (such as lake surface area, fetch, maximum depth, and substrate composition) are related to walleye presence in northern Wisconsin lakes, which has also been suggested by others. Surface area and some measure of depth were previously found to be useful variables for predicting species associations (Johnson et al. 1977; Schneider 1981; Tonn et al. 1983; Marshall and Ryan 1987). A large surface area may correspond to more habitat area or volume for fish (Christie and Regier 1988), and depth and area describe lake morphometry, which affects most physical, chemical, and biological processes within lakes (Wetzel 1975). For example, the quantity, density, and composition of submerged macrophytes (which are largely a function of depth and area) have been linked to fish abundance and species richness (Keast and Harker 1977; Randall et al. 1996).

Our results show that walleyes are less likely to be present in small shallow lakes in northern Wisconsin. Surface area and depth affect solar radiation input and circulation patterns within lakes, and thus thermal stratification (Wetzel 1975; Lampert and Sommer 1997). The optimal range of temperatures for walleye growth and development is 20–28°C (Hokanson 1977). Temperatures outside the preferred range may negatively affect growth and metabolism, and ultimately production (Magnuson et al. 1979; Christie and Regier 1988). Christie and Regier (1988) quantified thermal habitat space (defined as the amount of lake bottom and pelagic volume with temperatures within a

species' optimal thermal niche) for four species (including walleyes) during summer and found a strong correlation with yield for all species. However, the lakes used in our study were smaller in size and shallower in depth than those studied by Christie and Regier (1988), so the relationship between thermal habitat volume and walleye population characteristics in northern Wisconsin lakes may be a fruitful focus of future investigations.

Our results suggest that interactions with northern pike and largemouth bass, rather than differences in the physical characteristics of lakes, may hinder the presence of self-sustaining walleye populations in northern Wisconsin lakes. For example, competition between introduced northern pike and walleyes for yellow perch may have caused walleye populations to decline in two Minnesota lakes (Colby et al. 1987), and predation by largemouth bass on stocked walleyes limited walleye survival in a centrarchid-dominated Illinois impoundment (Santucci and Wahl 1993). Our findings cannot determine the type of interaction between walleyes, northern pike, and largemouth bass, but they do suggest that some type of interaction occurs which hinders walleye populations from being self-sustaining.

Our finding of a negative association between the relative abundance of walleyes and the relative abundance of northern pike may reflect differences among lakes in the physical features related to spawning site characteristics. Northern pike spawn on areas of flooded emergent vegetation (Becker 1983), which may be more prevalent in certain lake types, and thereby allow the successful reproduction of northern pike. In contrast, walleyes spawn on coarse rubble substrates (Becker 1983). The substrate variables used in our analysis were measured during a different time period than the relative abundance estimates and, therefore, may not reflect current conditions, but the relationship between coarse substrates and self-sustaining walleye populations is reasonable.

Management Implications

Stocking guidelines for walleyes in Wisconsin do not presently account for the physical features of lakes or attributes of the fish community. Our results suggest that the success of walleye stocking could be improved by only stocking lakes with physical features that are likely to support walleyes (i.e., large and deep, with gravel bottom) and with fish communities that are likely to support walleye reproduction (i.e., muskellunge, but not northern pike or largemouth bass). More explicitly, our LDF

could be used to classify lakes that are likely to support walleyes based on readily available physical characteristics in the absence of more current information. Stocking could be prohibited in lakes that do not have appropriate physical characteristics based on the LDF. Further, our PCA suggests that fish community attributes could be useful for predicting the potential for establishing a self-sustaining walleye population. Therefore, lakes should be surveyed to assess the fish community before stocking with walleyes. If high densities of northern pike and largemouth bass are present, the probability of establishing a self-sustaining walleye population may be low and thus walleye stocking, for the purpose of establishing a self-sustaining population, may not be effective. Creel surveys are relatively expensive for use as indices of species densities, so less expensive survey methods should be developed for use in models that predict the likelihood of successfully establishing a walleye population. Our research was correlative, so more research is needed to identify the mechanisms by which the physical and biological characteristics of lakes determine walleye presence and reproduction status in lakes. In addition, similar studies should be conducted in other regions of North America to determine if our findings are generally applicable to other parts of the walleye range.

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