North American Journal of Fisheries Management 21:441–447, 2001

Variation of Adult Walleye Abundance in Relation to Recruitment and Limnological Variables in Northern Wisconsin Lakes

NANCY A. NATE*[1] AND MICHAEL A. BOZEK

Wisconsin Cooperative Fishery Research Unit,[2] *University of Wisconsin–Stevens Point,*
Stevens Point, Wisconsin 54481, USA

MICHAEL J. HANSEN

University of Wisconsin–Stevens Point, College of Natural Resources, 1900 Franklin Street,
Stevens Point, Wisconsin 54481, USA

STEVEN W. HEWETT

Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat
Protection, 101 South Webster Street, Madison, Wisconsin 53707-7921, USA

Abstract.—We quantified the relationship between the abundance of adult walleyes *Stizostedion vitreum* and limnological descriptors of 166 lakes in northern Wisconsin to better predict population size than was possible with lake surface area alone. Four models described adult walleye abundance from lake surface area for drainage and landlocked lakes with self-sustaining and stocked populations. For self-sustaining walleye populations, lake surface area and watershed area explained 61% of the variation in the number of adult walleyes in drainage lakes, whereas lake surface area and the percentage of sand bottom explained 71% of the variation in the number of adult walleyes in landlocked lakes. For stocked walleye populations, lake surface area, conductivity, and the percentage of muck bottom explained 98% of the variation in the number of adult walleyes in landlocked lakes, whereas lake surface area and maximum depth explained 64% of the variation in the number of adult walleyes in drainage lakes. We conclude that models for estimating adult walleye abundance based on recruitment source may be improved by incorporating limnological variables and partitioning models by water source.

Fishery managers often make management decisions with minimal fisheries assessment information (Baccante and Colby 1996). Management risk (i.e., the risk of recruitment overfishing) likely increases in the absence of accurate fish population information (Hilborn et al. 1993). Therefore, the natural variability in fish populations among lakes needs to be explained. Identifying biotic and abiotic forces that affect growth and recruitment may help to reduce management risk (Peterman and Bradford 1987). The use of previous survey information among lakes with similar physical, chemical, and biological features may provide a means for assessing fisheries with limited information to derive appropriate management actions (Baccante and Colby 1996).

Spearing quotas and angling bag limits of walleyes *Stizostedion vitreum* are set annually for 861 lakes in the ceded territory of northern Wisconsin. For most of these lakes, linear regression models based on the relationship between previous adult walleye population estimates and lake surface area are used to predict adult walleye abundance when recent population estimates are lacking (Hansen 1989; Staggs et al. 1990; Hansen et al. 1991). Because of measurement error and variability in walleye population density among same-sized lakes, population sizes are estimated from the lower 95% prediction interval of each regression model, to ensure that lakes falling below the mean regression line will not be overharvested (Hansen 1989).

Three regression models are currently used to estimate adult walleye abundance (U.S. Department of the Interior 1995). Two of the models were developed because adult walleye density varied with recruitment source among lakes of the same surface area (U.S. Department of the Interior

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* Corresponding author: naten@dnr.state.wi.us

[1] Present address: Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection, 101 South Webster Street, Madison, Wisconsin 53707-7921, USA.

[2] The Unit is jointly sponsored by the University of Wisconsin–Stevens Point, the Wisconsin Department of Natural Resources, and the U.S. Geological Survey, Biological Resources Division.

Received February 18, 2000; accepted November 7, 2000

1995). Recently, it has been shown that lakes with mostly self-sustaining walleye populations have higher adult walleye densities than do lakes with mostly stocked populations (Nate et al. 2000). A third model was developed for lakes with remnant or newly stocked walleye populations with low densities and sporadic recruitment (U.S. Department of the Interior 1995).

Separation of lakes on the basis of recruitment source increased the accuracy and precision of abundance estimates, but much of the variation in walleye densities among lakes within the three models remained unexplained. More accurate and precise harvest quotas might be set with less risk of overharvest if the factors that regulate walleye densities among lakes can be quantified. Our objective was to improve the accuracy and precision of walleye abundance estimates from regression models by the use of physical and chemical factors to explain residual variability among lakes.

FIGURE 1.—Locations of 166 northern Wisconsin lakes included in this study.

Methods

Walleyes occur in 861 lakes in the ceded territory of northern Wisconsin (U.S. Department of the Interior 1991). To monitor these walleye populations, approximately 25 lakes per year were randomly selected for mark–recapture surveys of adult abundance during 1990–1997. State and tribal biologists developed an eight-category classification system to place lakes along a continuum of recruitment from stocked (ST) to natural reproduction (NR); additional categories were for newly stocked or remnant populations (REM; U.S. Department of the Interior 1991). These eight classifications were then used to group lakes into three regression models (NR, ST, and REM) for estimating adult abundance (U.S. Department of the Interior 1995). Only five surveys were completed on lakes in the REM model (three classifications) during 1990–1997, so we eliminated this model from the present analysis. Adult walleye densities did not vary appreciably among the five remaining classifications within the ST and NR regression models (Nate et al. 2000), so we used only NR (mostly self-sustaining) and ST (mostly stocked) classifications in this analysis.

Adult abundance.—Standardized population surveys were used to quantify the relationship between lake surface area and numbers of adult walleyes. Adult walleye abundance was estimated by mark–recapture during spring spawning by the use of the Chapman modification of the Petersen estimator (Ricker 1975). Adults were defined as all fish whose sex could be determined and all fish of unknown sex greater than 15 in (Beard et al. 1997). Initially, fish were captured in fyke nets and marked by removal of a portion of one or more fins. Fish were recaptured by AC electroshocking 1–2 d after the marking period (Beard et al. 1997). Because the interval between marking and recapture was short, the entire lake shoreline was surveyed to ensure that marked and unmarked walleyes were equally vulnerable to recapture. For lakes with more than one population estimate between 1990 and 1997, we limited analyses to only the most recent population estimate because the accuracy of estimates of adult walleye abundance declines rapidly from one year to the next (Hansen et al. 1991). We included 166 lakes, ranging in size from 93 to 13,545 acres, in the analysis (Figure 1).

Limnological data.—We considered 14 limnological characteristics as potential explanatory variables of walleye abundance (Table 1), on the basis of surveys conducted in northern Wisconsin lakes during 1961–1983 (Wisconsin Conservation Department 1961–1966; Wisconsin Department of Natural Resources 1967–1983). We used only variables that were temporally stable. Lakes were also classified by their source of water supply (Table 2). These classifications were used to determine whether the relationship between lake surface area and adult walleye abundance in the NR and ST submodels differed for lakes that were landlocked versus lakes that had an inlet or outlet. We considered seepage and drained lakes as landlocked

TABLE 1.—Morphometric and limnological characteristics of 166 northern Wisconsin lakes. Abbreviations include the following: ft, feet; mi, miles; ppm, parts per million; in, inch, sq mi, square miles.

Variable	Mean	Minimum	Maximum
Area (acres)	926	93	13,545
Fetch (mi)	2.0	0.3	13.8
Maximum depth (ft)	42	5	117
% Littoral[a]	70	24	100
Shoreline development[b]	2.1	0.3	6.0
Secchi disk depth (ft)	10	3	38
pH	7.3	5.6	9.1
Alkalinity (ppm)[c]	36	3	117
Conductivity (0.39·mmhos/in)[d]	80	18	235
Watershed area (sq mi)	84	1	5,475
% Sand bottom	55	5	99
% Gravel bottom	19	0	70
% Rock bottom	12	0	70
% Muck bottom	14	0	80

[a] Percentage of lake surface area with a depth ≤ 20 ft.

[b] Calculated from Wetzel (1975) as [shoreline length (mi)]/{2·[π·area (sq mi)]}.

[c] Equivalent to mg/L.

[d] Equivalent to mS/cm.

TABLE 2.—Classifications for source of water (Wisconsin Department of Natural Resources 1995).

Classification	Definition
Drainage	Lakes that have both an inlet and an outlet. The main water source is stream drainage.
Seepage	Landlocked bodies of water that have no outlet or inlet. The primary source of water is precipitation or runoff, supplemented by groundwater from the immediate drainage area.
Spring	Lakes that have an outlet but no inlet. Groundwater flow is the primary source of water.
Drained	Lakes that have an outlet but no inlet. Precipitation and direct drainage from the surrounding land are the primary source of water. Under severe conditions, the outlets from drained lakes may become intermittent.

and drainage and spring lakes as connected. We did not include lakes in the analysis if they were not classified by water source or if data were missing for any of the 14 limnological variables. To normalize their distributions, we used a natural logarithmic transformation for area, maximum depth, shoreline development factor, conductivity, and watershed area and a square-root transformation for alkalinity (Neter et al. 1996).

Statistical analysis.—We used analysis of covariance (ANCOVA) to test for the similarity of slopes and intercepts of the regression relationship between lake surface area [$\log_e$(acres)] and adult abundance [$\log_e$(number of adult walleyes)] for lakes with stocked walleye populations versus lakes with self-sustaining walleye populations (SPSS 1997). Previous research has shown that average adult and age-0 walleye densities differed between NR and ST lakes (Nate et al. 2000). However, we tested the relationship again because lakes were included in the previous analysis if both age-0 and adult survey data were available (Nate et al. 2000), whereas lakes were included in the present analysis only if limnological and water source data were available.

We used ANCOVA to test the assumption that regression slopes were homogeneous among lakes with different sources of walleye recruitment (ST and NR) via the interaction between lake surface area (covariate) and recruitment source. We then used linear regression to quantify the relationship separately for lakes with self-sustaining and stocked walleye populations (SPSS 1997). We tested for the linearity of the underlying relationship between lake surface area and adult abundance by determining whether the slopes of the relationship between $\log_e$(area) and $\log_e$(abundance) differed significantly from one (Neter et al. 1996). We used ANCOVA to test for differences in regression slopes and intercepts of the relationships between lake surface area [$\log_e$(acres)] and adult abundance [$\log_e$(number of adult walleyes)] for lakes with different water sources (landlocked or drainage) (SPSS 1997). We tested the assumption that regression slopes were homogeneous among lakes with different water sources (landlocked and drainage lakes) via the interaction between lake surface area (covariate) and water source (treatments). If regression slopes were homogeneous between two lake types, we tested for differences in average densities between the two lake types (Neter et al. 1996).

We used linear regression to quantify the relationship between lake surface area [$\log_e$(acres)] and adult abundance [$\log_e$(number of adult walleyes)] for lakes with different recruitment sources (NR or ST) and water sources (drainage or landlocked). We again tested for the linearity of the underlying relationship between lake surface area and adult abundance by determining whether the slopes of the relationships between $\log_e$(area) and $\log_e$(abundance) differed significantly from one (Neter et al. 1996). For all models, we used stepwise linear regression to test limnological variables for entry to ($P \leq 0.05$) or exit from ($P > 0.05$) the model of $\log_e$(number of adult walleyes) versus $\log_e$(acres) (SPSS 1997; Neter et al. 1996). Modeling was stopped when adding or deleting

TABLE 3.—Regression models of $\log^e$-transformed adult walleye abundance versus lake surface area (acres) for landlocked and drainage lakes with self-sustaining and stocked walleye populations in 166 lakes in northern Wisconsin, 1990–1997.

Parameter	Coefficient	SE	t^a	P
Landlocked–self-sustaining (N = 28; r^2 = 0.657)				
Intercept	2.292	0.693	3.304	0.003
Acres	0.835	0.115	−1.438	0.162
Drainage–self-sustaining (N = 97; r^2 = 0.585)				
Intercept	−0.754	0.715	−1.054	0.295
Acres	1.267	0.109	2.457	0.016
Landlocked–stocked (N = 10; r^2 = 0.789)				
Intercept	1.200	0.791	1.516	0.168
Acres	0.804	0.136	−1.436	0.189
Drainage–stocked (N = 31; r^2 = 0.480)				
Intercept	−0.085	1.279	−0.066	0.948
Acres	1.069	0.199	0.348	0.911

[a] For acres, t = (coefficient − 1)/SE.

additional variables did not significantly reduce the residual error for the equation ($P \leq 0.05$). We examined plots of residuals against predicted values to verify that errors were homogeneous and distributed normally, and there was no evidence of nonlinearity. We examined first-order autocorrelation coefficients to verify that residuals were independent.

Results

The slope of the relationship between $\log_e$(number of adult walleyes) and $\log_e$(acres) did not differ between lakes with self-sustaining and stocked populations (F = 0.238; df = 1, 162; P = 0.627), but lakes with self-sustaining populations had higher levels of walleye abundance than lakes with stocked populations (F = 22.4; df = 1, 163; $P \leq 0.001$). Lake size accounted for 56% of the variation in adult walleye abundance in stocked lakes (F = 52.59; df = 1, 39; $P \leq 0.001$) and 57% of the variation in adult walleye abundance in lakes with self-sustaining populations (F = 163.49; df = 1, 123; $P \leq 0.001$).

The slope of the relationship between $\log_e$(number of adult walleyes) and $\log_e$(acres) differed between drainage and landlocked lakes for all NR and ST lakes combined (F = 3.88; df = 1, 162; $P \leq 0.05$). For drainage lakes, the slope of the relationship between $\log_e$(number of adult walleyes) and $\log_e$(acres) differed significantly from one (t = 2.54; df = 126; P = 0.012), which suggests that the underlying relationship between the number of adult walleyes and lake surface area was not linear. Lake surface area accounted for 55% of the variation in adult walleye abundance in landlocked lakes (F = 46.11; df = 1, 36; $P \leq$ 0.001) and 56% of the variation in adult walleye abundance in drainage lakes (F = 162.38; df = 1, 126; $P \leq 0.001$).

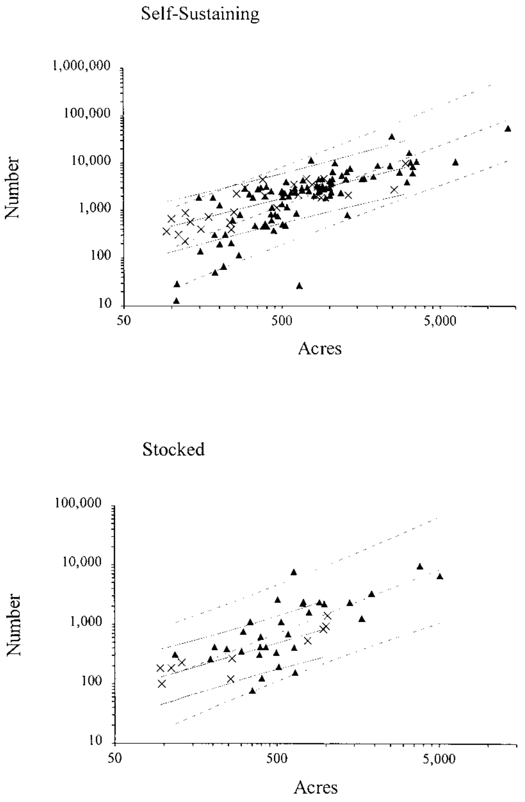

FIGURE 2.—Number of adult walleyes as a function of lake size for self-sustaining populations (top panel) in drainage lakes (N = 97; dashed lines and triangles) and landlocked lakes (N = 28; solid lines and x symbols) and for stocked populations (bottom panel) in drainage lakes (N = 31; dashed lines and triangles) and landlocked lakes (N = 10; solid lines and x symbols) in northern Wisconsin during 1990–1997. Top and bottom lines depict 95% prediction intervals for individual lakes.

Three of the four models based on different recruitment and water sources explained more variation than did models based on only recruitment or water source alone (Table 3; Figure 2). The fit of each model increased with the addition of limnological variables, although none of the four models shared a common additional variable (Table 4). For landlocked lakes with self-sustaining populations, the best model included the percentage of sand bottom. However, its coefficient was negative. For drainage lakes with self-sustaining populations, the overall relationship was not linear

TABLE 4.—Regression models of $\log_e$-transformed adult walleye abundance versus lake surface area (acres) for landlocked and drainage lakes with self-sustaining and stocked walleye populations with added limnological variables in 166 lakes in northern Wisconsin, 1990–1997.

Parameter	Coefficient	SE	t	P
Landlocked–self-sustaining ($N = 28$; $R^2 = 0.705$)				
Intercept	2.787	0.679	4.104	<0.001
Acres	0.885	0.109	8.130	<0.001
% Sand bottom	−0.014	0.006	−2.282	0.031
Drainage–self-sustaining ($N = 97$; $R^2 = 0.607$)				
Intercept	−0.957	0.700	−1.368	0.175
Acres	1.370	0.113	12.102	<0.001
$\log_e$(watershed area)	−0.148	0.058	−2.536	0.013
Landlocked–stocked ($N = 10$; $R^2 = 0.978$)				
Intercept	4.312	0.791	9.232	<0.001
Acres	0.958	0.081	11.882	<0.001
$\log_e$ (conductivity)	−0.900	0.129	−6.971	<0.001
% Muck bottom	−0.047	0.008	−6.116	<0.001
Drainage–stocked ($N = 31$; $R^2 = 0.641$)				
Intercept	−0.976	1.090	−0.895	0.378
Acres	0.831	0.178	4.674	<0.001
$\log_e$(maximum depth)	0.694	0.186	3.734	<0.001

(Table 3), and the best model included $\log_e$(watershed area) (Table 4). However, the coefficient for $\log_e$(watershed area) was negative. For landlocked lakes with stocked walleye populations, the best model included $\log_e$(conductivity) and the percentage of muck bottom. The coefficients for both $\log_e$(conductivity) and the percentage of muck bottom were negative. For drainage lakes with stocked walleye populations, the best model included $\log_e$(maximum depth). The coefficient was positive.

Discussion

Our results suggest that the accuracy and precision of estimated walleye abundance could be improved by subdividing models on the basis of water source and by incorporating limnological variables into the models. The accuracy of regression models, as indicated by the slope and intercept, was improved by subdividing two models for stocked and self-sustaining populations into four models for stocked and self-sustaining populations in landlocked and drainage lakes. For both self-sustaining and stocked walleye populations, slopes of regression models were lower and intercepts were higher for landlocked lakes than for drainage lakes. The precision of the regression models, as indicated by the coefficient of determination, was improved by 2.2–18.9% (depending on the model) with the addition of limnological variables. The models presented herein explained 71% (self-sustaining populations in landlocked lakes) to 98% (stocked populations in landlocked lakes) of the variation in adult walleye numbers, whereas the models presented by Nate et al. (2000) explained 61% (self-sustaining populations) to 65% (stocked populations) of the variation in adult walleye numbers.

Numbers of adult walleyes increased with lake surface area at a higher rate for drainage lakes than for landlocked lakes in northern Wisconsin, regardless of recruitment source. Walleye abundance estimated from regression models, without considering drainage type, may therefore overestimate walleye abundance in small drainage lakes with self-sustaining populations. Walleye abundance could be overestimated by mark–recapture in drainage lakes if marked fish are underrepresented in the recapture sample via immigration of unmarked fish into the recapture sample (Van Den Avyle 1993). Immigration of unmarked fish into drainage lakes is possible because these lakes have inlets and outlets but would have to occur consistently to affect the slope of the relationship for 97 lakes with self-sustaining populations and 31 lakes with stocked populations. Thus, this potential bias seems unlikely.

The percentage of sand bottom was inversely related to the number of adult walleyes in landlocked lakes with self-sustaining populations in northern Wisconsin, which suggests that large amounts of sand may restrict walleye abundance by limiting recruitment. Walleyes typically spawn on rocky, wave-washed shallows in lakes without inlets (Becker 1983). In Lake Winnibigoshish, Minnesota, walleye egg survival was lowest on soft muck and detritus, moderate on fine sand, and highest on gravel and rubble (Johnson 1961). Walleye eggs require oxygen during incubation, and because walleyes do not provide parental care for their eggs, physical forces such as waves must oxygenate the eggs (Daykin 1965). Eggs deposited on rocky substrate will settle into cracks and crevices where they are protected from predation. If crevices become filled with sediment, protection is no longer afforded, and sedimentation may interfere with gas exchange (Daykin 1965). The spawning habitat may be the primary factor limiting reproduction in eutrophic systems (Moyle 1954).

Conductivity and the percentage of muck bottom were inversely related to numbers of adult walleyes in landlocked lakes with stocked populations in northern Wisconsin, which suggests that substrate type may also limit walleye abundance in stocked lakes. Muck substrate and high conductivity characterize shallow eutrophic lakes, in which temperature and oxygen may limit walleye abundance. Further, eutrophication reduces transparency and hypolimnetic volume and increases nutrients and total dissolved solids (Leach et al. 1977). Percids initially respond to eutrophication with increased growth and production but later respond with decreased growth and increased susceptibility to parasites (Leach et al. 1977).

Walleye abundance was not related to substrate in drainage lakes with self-sustaining populations in northern Wisconsin. Drainage lakes are components of larger systems, so walleyes might spawn in inlet streams on gravel substrate (Becker 1983). In contrast, our results suggest that the watershed area may be inversely related to walleye abundance. Lakes lower in a chain tend to have higher ionic concentrations (Kratz et al. 1997; Soranno et al. 1999) and higher species richness (Kratz et al. 1997) than do lakes higher in a chain. Consequently, productivity or fish community diversity may limit the abundance of self-sustaining walleye populations in drainage lakes.

Walleye abundance was also not related to substrate in drainage lakes with stocked walleye populations in northern Wisconsin. Rather, walleye abundance was positively related to maximum depth. Shallow lakes may be symptomatic of advanced stages of eutrophication (Lampert and Sommer 1997) or may lack the range of temperatures optimal for walleye growth and development (Hokanson 1977).

Management Implications

The accuracy of walleye abundance estimated from regression models may be increased by separation based on recruitment source and water source. Regression models presented by Nate et al. (2000) generally underestimated walleye abundance for small landlocked lakes and overestimated walleye abundance for small drainage lakes. For example, adult walleye abundance estimated from the NR model in Nate et al. (2000) for a 100-acre lake is 272 fish (95% prediction interval = 50–1,498 fish). In contrast, adult walleye abundance estimated from models presented herein that were based on water source (Table 3) is 462 fish (133–1,611 fish) for landlocked lakes and 161 fish (23–1,106 fish) for drainage lakes. Therefore, safe harvest levels could be increased in 100-acre landlocked lakes but should be decreased in 100-acre drainage lakes. Because most lakes with self-sustaining walleye populations were drainage lakes, walleye abundance in this large group of lakes is generally overestimated, and the resulting harvest may be higher than anticipated on the basis of current regression models.

The precision of estimates of walleye abundance from regression models may also be increased by incorporation of limnological variables into the models. Regression models of the relationship between lake surface area and adult abundance that did not include other variables, presented by Nate et al. (2000), explained 61–65% of the variation in numbers of adult walleyes. In contrast, multiple regression models that included limnological variables, presented herein (Table 4), explained 61–98% of the variation in numbers of adult walleyes. In general, increased model precision would result in higher harvest quotas, because quotas are generated from the lower 95% prediction interval of the regression models (Hansen 1989). Other factors such as the density of other fish species may explain some of the remaining variation in numbers of adult walleyes, but data are currently lacking for developing such models. Such improvements in model precision would lead to less uncertainty in estimated abundance and, subsequently, to higher allowable harvest levels for spearing and angling fisheries in northern Wisconsin lakes.

Acknowledgments

We thank the many previous and present Wisconsin Department of Natural Resources personnel who gathered the data used in this analysis. Neal Niemuth reviewed a previous draft of the manuscript. This research was completed in partial fulfillment of the requirements for a Master of Science degree at the University of Wisconsin–Stevens Point.

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