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Variation in Walleye Abundance with Lake Size and Recruitment Source

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Abstract.—We quantified the relationship between lake size and abundance of walleyes *Stizostedion vitreum* at two life stages, age 0 and adult, in 172 northern Wisconsin lakes. We also determined if the relationship varied with recruitment source (stocked or natural) in order to evaluate the current system of management. For adult walleyes, as estimated by mark–recapture in spring, abundance was linearly related to lake surface area. Age-0 walleye abundance estimated by fall electrofishing catch was also linearly related to the miles of shoreline surveyed. Lake surface area explained 59% of the variability in adult walleye abundance across lakes ranging in size from 93 to 15,300 acres. Lake surface area explained 61% of the variation in abundance of self-sustaining walleye populations and 65% of stocked populations. Walleye abundance was higher in lakes sustained by natural reproduction than in lakes sustained by stocking. These patterns in abundance based on recruitment source were also apparent at age 0. We conclude that differences in abundance between self-sustaining and stocked walleye populations in northern Wisconsin lakes may be established during the first year, possibly due in part to recruitment source.

Fishery management is difficult because fish stock size varies greatly in space and time in response to recruitment and survival (Hilborn et al. 1993). Although survival can be at least partly controlled through harvest regulation, recruitment often varies because of mechanisms that are unpredictable or uncontrollable (Sissenwine et al. 1988). For this reason study of the relationship between stock and recruitment is one of the most important biological questions facing fishery managers (Hilborn and Walters 1992). Prediction of fish abundance for harvest management depends on our ability to quantify recruitment variation, if recruitment overfishing is to be avoided (Hilborn and Walters 1992).

Recruitment of walleyes *Stizostedion vitreum* can be affected by a variety of biotic and abiotic factors, including parental stock size (Busch et al. 1975; Chevalier 1977; Shuter and Koonce 1977; Madenjian et al. 1996; Hansen et al. 1998), cannibalism (Chevalier 1973; Forney 1976, 1980; Hansen et al. 1998), predation and competition (Hansen et al. 1998), rate of spring warming (Busch et al. 1975; Madenjian et al. 1996), and variability of May water temperature (Serns 1982a; Hansen et al. 1998). Walleye populations in Escanaba Lake in northern Wisconsin have been shown to decline 65% in 1 year (Hansen et al. 1991), largely because of variation in recruitment (Hansen et al. 1998). Walleye population density also varies greatly among lakes due to differences in physical, chemical, and biological features (Baccante and Colby 1996).

In the northern third of Wisconsin, regression models are used to describe adult walleye abundance as a linear function of lake size, when other data are lacking or not current, for the purpose of setting harvest limits for spearing and angling (Hansen 1989; Staggs et al. 1990; Hansen et al. 1991). Different regression models are used for stocked and naturally reproducing walleye populations because it is believed that adult densities vary with recruitment source (USBIA 1991, 1995). Walleye lakes are classified into eight categories

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TABLE 1.—Walleye recruitment classifications for northern Wisconsin lakes (USBIA 1991).

Classification	Definition
NR	Natural reproduction only; consistent enough to result in multiyear-class adult populations
C-NR	Natural reproduction is adequate to sustain the population, even though the lake is being stocked
C-	Natural reproduction and stocking provide about equal recruitment to the adult population, or the relative contributions of stocking and natural reproduction are unknown
C-ST	Stocking provides the primary source of recruitment, but some natural reproduction occurs
ST	Stocking provides the major source of recruitment and is consistent enough to result in a multiyear-class adult population
NR-2	Natural reproduction only but is inconsistent, which results in missing year-classes
REM	Stocking provides the only source of recruitment but was discontinued; the stock will disappear at some time in the future
O-ST	Stocking provides the only source of recruitment but was initiated only recently and has not yet resulted in a harvestable population of adults

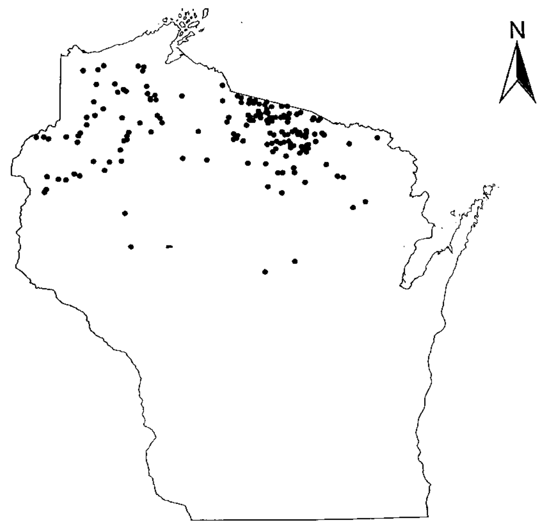

FIGURE 1.—Locations of the 172 northern Wisconsin lakes included in this analysis.

depending upon the degree to which natural reproduction and stocking contribute to recruitment (Table 1). These classes are then assigned to regression models for estimating walleye abundance. Correct classification of the recruitment source helps to ensure that appropriate quotas are set and that overharvest does not occur. Although this classification system is the basis for current walleye management in northern Wisconsin, little has been done to test the validity of the system of regression models currently in use. Our objectives were to determine (1) the adequacy of a linear fit between adult walleye abundance and lake surface area, (2) whether the relationship between adult walleye abundance and lake size varied with recruitment source, (3) the adequacy of a linear fit between age-0 walleye abundance and miles of shoreline surveyed, and (4) whether patterns in abundance among lakes with different recruitment sources were apparent at age 0.

Methods

Recruitment source was determined for 859 lakes in the northern third of Wisconsin known to have walleyes. Eight classifications were used to describe the recruitment source of walleye populations in lakes, ranging from completely self-sustaining to completely dependent on stocking, with other categories for newly stocked or remnant populations (USBIA 1991: Table 1). Classifications were assigned by state and tribal fisheries managers in northern Wisconsin based on available survey data and professional judgment. To monitor these walleye populations, approximately 25 lakes/year were randomly selected for adult population estimates and fall shoreline electrofishing surveys between 1990 and 1997.

We limited analyses to only the most recent population estimate or fall recruitment survey for each lake surveyed during 1990–1997. Hansen et al. (1991) found the accuracy of estimates of adult walleye abundance declined over time from the year the estimate was obtained to the year the estimate was used to set a harvest quota. To compare patterns in adult abundance to patterns in age-0 abundance, lakes were included only if both adult population estimates and fall recruitment surveys were available. We reasoned that age-0 catch per mile of shoreline was related to number of age 0 walleyes per acre (see Serns 1982b). Lakes with remnant (REM), highly sporadic (NR-2), and newly stocked (O-ST) classifications were eliminated from the analysis because there were few surveys done on lakes in these classifications between 1990 and 1997. In all, 172 lakes, ranging in size from 93 to 15,300 acres and representing five recruitment classifications, were included (Figure 1).

Adult abundance.—Standardized population estimates were used to evaluate walleye recruitment classifications for lakes in the northern third of Wisconsin. Adult walleye abundance was estimated by mark–recapture during spring spawning using the Chapman modification of the Petersen estimator (Ricker 1975). Adults were defined as all fish for which sex could be determined and all fish of unknown sex exceeding 15 in (Beard et al. 1997). Fish captured in fyke nets were marked by removal of a portion of one or more fins. Recapture occurred 1–2 d after the completion of the marking period by AC electroshocking of the entire lake shoreline (Beard et al. 1997).

Age-0 relative abundance.—Standardized fall electrofishing surveys were used to determine if recruitment classifications evident at the adult life stage were also evident at age 0. Catch was recorded as the total number of age-0 walleyes captured per mile of shoreline surveyed. Surveys were conducted between mid-September and late October when water temperatures ranged from 42°F to 70°F. The survey guidelines suggest one complete electrofishing trip around the shoreline, including islands, with two people netting fish. However, this was not possible in some years for some lakes. For most surveys (83% across all years), at least 75% of the entire shoreline, including islands, was surveyed once, with two people netting fish. The collective mean of the percent of shoreline surveyed for each year ranged from 69% in 1990 to 99% in 1991 and 1992. The entire shoreline (100%) was surveyed in 110 of 172 lakes. Fish scales were collected to verify the length cutoffs between age-0 and age-1 walleyes from the length-frequency distribution.

Statistical analysis.—We modeled adult walleye abundance as a function of lake size to test for differences in recruitment classifications with

$$N = \alpha A^{\beta},$$

which describes numbers of adult walleyes (N) as a function of lake size in acres (A), the rate of change in numbers with lake size (α), and the degree of curvature in the relationship (β; Goddard et al. 1987). We transformed the model to a linear form to estimate parameters and to normalize the distribution of the errors (Neter et al. 1996):

$$\log_e N = \log_e \alpha + \beta \log_e A,$$

where, in the linear form, the intercept ($\log_e \alpha$) describes the natural logarithm of the average density (number per acre) of adult walleyes and the slope (β) describes the rate of change in number of adult walleyes as a function of lake size. This coefficient will be close to 1 if density is constant at all lake sizes.

Analysis of covariance (ANCOVA) was used to test for differences in regression slopes and intercepts among lakes in each recruitment classification (SPSS 1997). We tested the assumption that regression slopes were homogeneous among the five recruitment classifications through the interaction between lake surface area (covariate) and recruitment classification (treatments). If regression slopes were homogeneous among recruitment classes, differences in average densities (means adjusted for the effect of lake size) among recruitment classifications were tested.

Recruitment classifications describe a continuum of walleye recruitment, from entirely self-sustaining to entirely sustained by stocking. Groups of recruitment classifications were tested starting with all five classifications and eliminating one classification at a time to determine which classifications were similar. For example, if the intercept of at least one classification was significantly different in the model with five classifications (NR, C-NR, C-, C-ST, ST), then the ST category was dropped, and the model was tested again with the remaining four classifications. This process of elimination continued until remaining intercepts were not significantly different from one another. All of the dropped classifications were included in an additional ANCOVA to determine whether the line intercepts were significantly different among the various dropped classifications. If there were no significant differences in intercepts among the dropped classifications, we concluded there were two groups among the five classifications tested: those that were not dropped and those that were dropped from the original group. We then performed an additional ANCOVA, with group as the main effect and surface area as the covariate, to determine whether the mean number of adult walleyes (adjusted for lake size) for the first group was significantly different than the mean number for the second group.

An ANCOVA was similarly used to test for differences in numbers of age-0 walleyes among the five recruitment classifications, shoreline miles serving as the covariate. Slopes and intercepts were tested in a similar manner to determine differences in catch per effort among the five recruitment classifications. An additional ANCOVA was also used to determine if mean numbers of age-0 walleyes caught (adjusted for shoreline miles surveyed) in the first group were significantly different among the resulting group(s) of recruitment classifications.

Linear regression was used to quantify the relationships between lake size ($\log_e$[area in acres]) and adult abundance ($\log_e$[number of adults]) and

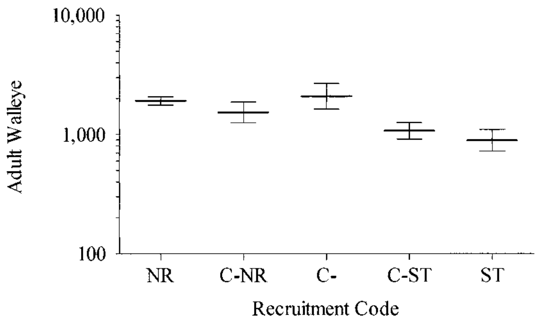

FIGURE 2.—Adjusted mean (±SE) number of adult walleyes for five recruitment classifications in 172 northern Wisconsin lakes, 1990–1997. Classification abbreviations are defined in Table 1. Means are adjusted for the effect of lake surface area.

between miles of shoreline ($\log_e$[shoreline miles]) and number of age-0 walleyes ($\log_e$[number of age 0 + 1]) for the resulting groups. Prediction intervals, rather than confidence intervals, were estimated for each model because the models were used to estimate walleye abundance for individual lakes, rather than to estimate mean abundance for all lakes of a given surface area (Neter et al. 1996). The adequacy of the linear fit was tested for all models by determining if the slope (β) was significantly different from 1 ($P \leq 0.05$). Residual errors were examined for normality, homogeneity, independence, and linearity (Neter et al. 1996).

Results

Adult Abundance

The relationship (slope) between $\log_e$(area) and $\log_e$(number of adults) did not differ among recruitment classifications ($F = 1.50$; df = 4, 162; $P = 0.204$), but average levels of $\log_e$(number of adults), when corrected for $\log_e$(area), did vary among recruitment classes ($F = 5.05$; df = 4, 166; $P \leq 0.001$; Figure 2). Average numbers of adult walleyes, when corrected for lake surface area, were not different for the three recruitment classifications (NR, C-NR, and C-) representing lakes with natural reproduction ($F = 0.60$; df = 2, 127; $P = 0.548$) or for two recruitment classifications (ST and C-ST) representing lakes that were mostly stocked ($F = 0.87$; df = 1, 38; $P = 0.356$). Average levels of adult walleye abundance were higher in lakes with natural reproduction than in stocked lakes ($F = 18.56$; df = 1, 169; $P \leq 0.001$).

Based on the ANCOVA, all recruitment classifications were categorized into two linear regression models, one for lakes with natural reproduction (NR, C-NR, C-) and another for stocked

TABLE 2.—Regression parameters for $\log_e$ (adult walleye population estimates) versus $\log_e$ (lake surface area) and $\log_e$ (age-0 [+1] walleye catch) versus $\log_e$ (miles of shoreline surveyed) for 172 lakes in northern Wisconsin, 1990–1997.

Lake type and parameter	Coefficient	SE	t^a	P
Adult, all lakes (N = 172; R^2 = 0.599)				
Intercept	0.618	0.429	1.439	0.152
Acres	1.049	0.066	0.742	0.459
Adult, natural lakes (N = 131; R^2 = 0.608)				
Intercept	0.807	0.484	1.667	0.098
Acres	1.042	0.074	0.568	0.571
Adult, stocked lakes (N = 41; R^2 = 0.650)				
Intercept	0.538	0.742	0.726	0.472
Acres	0.987	0.116	0.112	0.911
Age 0, all lakes (N = 172; R^2 = 0.166)				
Intercept	1.761	0.408	4.320	<0.001
Miles	1.184	0.204	0.902	0.368
Age 0, natural lakes (N = 131; R^2 = 0.185)				
Intercept	2.539	0.394	6.438	<0.001
Miles	1.049	0.194	0.253	0.801
Age 0, stocked lakes (N = 41; R^2 = 0.190)				
Intercept	−0.441	0.793	−0.056	0.956
Miles	1.260	0.417	0.624	0.534

[a] For acres (adults) and miles (age 0), t = (coefficient − 1) /SE

lakes (ST and C-ST). A linear fit was adequate for both models (slopes were not significantly different from 1; Table 2). Lake size accounted for 61% of the variation in adult walleye abundance in lakes with natural reproduction and 65% of the variation in stocked lakes (Figure 3; Table 2). Average density of adult walleyes was 2.24 fish/acre in lakes with natural reproduction and 1.71 fish/acre in stocked lakes (back-transformed y-intercepts; Table 2). In all lakes, lake size accounted for 60% of the variation in adult walleye abundance (Table 2).

Age-0 Relative Abundance

The relationship (slope) between $\log_e$(shoreline miles shocked) and $\log_e$(number of age-0 + 1) did not differ among recruitment classifications ($F = 0.90$; df = 4, 162; $P = 0.463$), but average levels of $\log_e$(number of age-0 + 1), when corrected for $\log_e$(shoreline miles shocked), did vary among recruitment classes ($F = 15.72$; df = 4, 166; $P \leq 0.001$; Figure 4). Age-0 relative abundances for lakes with natural reproduction (NR, C-NR, C-) were not significantly different ($F = 0.28$; df = 2, 127; $P = 0.756$). Likewise, age-0 relative abundances for stocked lakes (C-ST and ST) were not significantly different ($F = 2.74$; df = 1, 38; $P =$

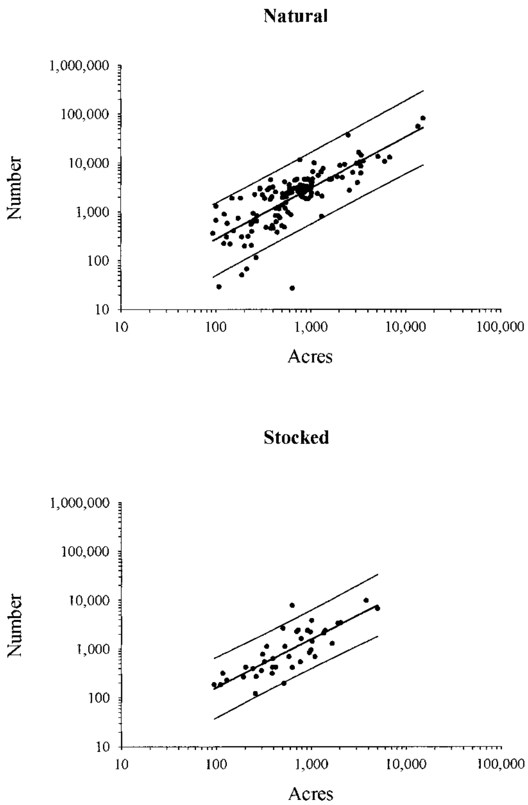

FIGURE 3.—Number of adult walleyes as a function of lake surface area (acres) for 172 lakes in northern Wisconsin sustained by natural reproduction and stocking, 1990–1997. Upper and lower lines depict 95% prediction intervals for individual lakes. Adult walleye abundance was estimated in each lake by mark–recapture using the Chapman modification of the Petersen estimator.

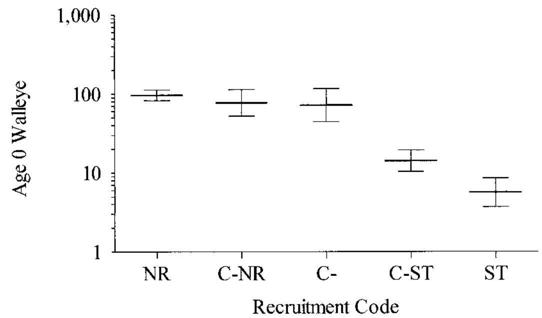

FIGURE 4.—Adjusted mean (±SE) number of age-0 walleyes for five recruitment classifications in 172 northern Wisconsin lakes, 1990–1997. Classification abbreviations are defined in Table 1. Means are adjusted for the effect of miles of shoreline surveyed.

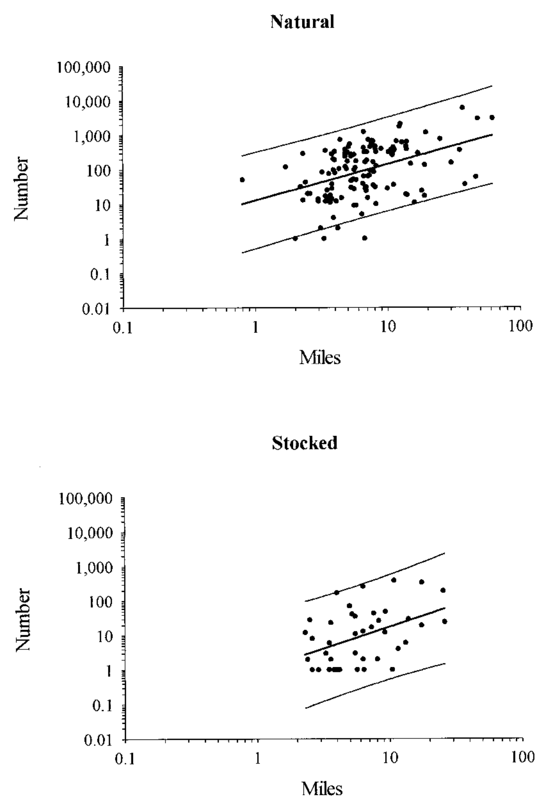

FIGURE 5.—Number of age-0 walleyes as a function of shoreline miles surveyed for 172 lakes in northern Wisconsin sustained by natural reproduction and stocking, 1990–1997. Upper and lower lines depict 95% prediction intervals for individual lakes. Age-0 walleyes in each lake were sampled during fall by electrofishing.

0.106). Higher numbers of age-0 walleyes per mile were found in lakes with natural reproduction than in stocked lakes (F = 58.93; df = 1, 169; $P \leq 0.001$).

Based on the ANCOVA, we categorized all recruitment classifications into two separate linear regression models in which recruitment was primarily from either natural reproduction (NR, C-NR, C-) or from stocking (ST and C-ST). For both models, slopes were significantly higher than 1 (Table 2). Miles of shoreline surveyed accounted for 18.5% of the variation in numbers of age-0 walleyes in lakes with natural reproduction and 19.0% of the variation in numbers of age-0 walleyes in stocked lakes (Figure 5; Table 2). On average, there were 11.67 age-0 walleyes caught per mile of shoreline in lakes with natural reproduction and near zero age-0 walleyes caught per mile of shoreline in stocked lakes (back-transformed *y*-intercepts: Table 2). In all lakes, miles of shoreline surveyed accounted for 16.6% of the variation in age-0 relative abundance (Table 2).

Discussion

The average density of walleyes in northern Wisconsin lakes differed according to recruitment source. This result was expected because recruitment source is the basis for the current walleye lake classification system. Similarly, data from Li et al. (1996) indicated that gill-net catch per effort (CPE) in lakes with naturally reproducing walleye populations was higher than in stocked lakes in Minnesota. However, the five separate classifications defining recruitment status currently used in Wisconsin were not all significantly different descriptors of the relationship between lake size and adult walleye abundance. Rather, two general classifications emerged, one for self-sustaining walleye populations and another for those maintained by stocking.

Differences in abundance between our classifications (stocked and natural walleye lakes), based on fall electrofishing surveys, were also apparent at age 0, although the proportion of unexplained variability in CPE estimates was greater than for adult population estimates. Serns (1982b) found that fingerling CPE was a strong predictor of fingerling population abundance in 13 northern Wisconsin lakes. Of the 13 lakes Serns (1982b) analyzed, 10 were included in our analysis. Patterns in age-0 walleye CPE that mirrored adult walleye abundance in our study suggests that differences in abundance may have been established in the first year and were closely tied to recruitment source.

We believe that poor survival of walleyes between stocking and fall may contribute to consistently lower recruitment and, thus, lower adult abundance in lakes maintained by stocking. Examining 125 water bodies, Laarman (1978) reported walleye stocking was successful for 48% of introductory stocking (lakes where walleyes were absent), 32% of maintenance stocking (lakes with populations maintained by stocking), and 5% of supplemental stocking (lakes with natural reproduction). Many factors may influence survival of stocked walleyes and contribution to year-class strength, including temperature (Fielder 1992a; Paragamian and Kingery 1992), pH (Bergerhouse 1992), zooplankton density (Fielder 1992a; Jennings and Philipp 1992), predation (Santucci and Wahl 1993), cannibalism (Chevalier 1973; Forney 1976, 1980; Hansen et al. 1998), transportation and handling time (McWilliams and Larscheid 1992), and length at stocking and stocking density (Fielder 1992b; Koppelman et al. 1992; Santucci and Wahl 1993).

In northern Wisconsin lakes, stocking density alone did not account for low walleye abundance in stocked lakes because more walleyes were stocked than were produced by self-sustaining populations. In unpublished investigations during 1990–1995 (Wisconsin Department of Natural Resources, unpublished data), average stocking rates of walleye fingerlings were higher in lakes sustained by stocking (31.3 fish/acre) than were average densities of native age-0 walleyes in lakes sustained by natural reproduction that were not stocked (5.3 fish/acre), as estimated from fall recruitment-survey CPE with the Serns index (Serns 1982b), $Y = 0.234$ (fingerling CPE). Li et al. (1996), in a review of 4,470 Minnesota lake surveys, also found that walleye population abundance was not linearly related to stocking density.

Several factors have been shown to influence natural recruitment, including lack of spawning habitat (Moyle 1946; Kitchell et al. 1977), inability to locate spawning habitat for stocked fish (Jennings et al. 1996), extremes (low or high) in parental stock size (Busch et al. 1975; Chevalier 1977; Shuter and Koonce 1977; Madenjian et al. 1996), predation and competition (Johnson and Hale 1977), inadequate lipid reserves for maturing females (Henderson and Nepszy 1994; Madenjian et al. 1996), and upper lethal temperatures (Hokanson 1977). Li et al. (1996) concluded that stocking is most likely to increase walleye abundance in lakes where natural reproduction is limited but food is not. In addition, Marshall and Ryan (1987) found that walleyes tend to inhabit lakes with surface areas greater than 781 acres. Lakes in both of our regression models were similar in size. Therefore, lake size cannot account for differences in abundance between the two general models (stocked or natural).

The positive linear relationship between lake surface area and adult walleye abundance in northern Wisconsin lakes was similar to other findings linking surface area to fish abundance and yield (Youngs and Heimbuch 1982; Goddard et al. 1987; Hansen 1989; Rempel and Colby 1991; Baccante and Colby 1996). In the 172 northern Wisconsin lakes in this study, large lakes produced more walleyes than small lakes. Youngs and Heimbuch (1982) demonstrated that lake surface area was a more accurate predictor of fish yield than the ratio of total dissolved solids to mean depth (MEI).

Rempel and Colby (1991) also found that lake surface area was a strong predictor of fish yield, but suggested that harvest from atypical lakes could be more accurately predicted by including the MEI. Therefore, adding another descriptor of lake shape to a multiple-regression model, in addition to accounting for recruitment source, may explain more of the variability in numbers of walleyes in northern Wisconsin lakes.

Management Implications and Recommendations

We found that the relationship between adult walleye abundance and lake size in northern Wisconsin lakes differed for populations largely maintained by natural reproduction versus those largely maintained by stocking. Further, five of the eight classifications currently used to describe adult walleye recruitment were not statistically differentiable. Only two recruitment classifications resulted. Although these two lake types differed, independent recruitment surveys would be required to quantify the relative contribution from stocking and natural reproduction of walleyes for use in more detailed classification schemes. Therefore, current management may be simplified by collapsing the five classifications into two general classifications.

The accuracy of population estimates derived from the lower 95% prediction interval of the regression equation may be improved if further study can identify mechanisms that affect walleye abundance and recruitment. For example, it is important to identify characteristics of lakes that favor survival of stocked walleyes to optimize their survival after stocking. Likewise, it is important to identify physical, chemical, and biological characteristics of lakes that favor natural reproduction of walleyes to enhance their preservation and management. A lake classification system based on easy-to-measure variables would reduce the need for intensive lake-by-lake monitoring.

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