

Catchability of Walleyes to Fyke Netting and Electrofishing in Northern Wisconsin Lakes

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Abstract.—We quantified relationships between both fyke-net catch rates (catch/net-night) and electrofishing catch rates (catch/mi) and population densities (number/acre) of walleye *Sander vitreus* (formerly *Stizostedion vitreum*) for adult population estimates and total population estimates to determine whether catchability was density dependent. Fyke-net catch rates were modeled as a nonlinear function of adult walleye density and of four size-classes of the adult population, and electrofishing catch rates were modeled as a nonlinear function of adult and total walleye density and four size-classes of the adult and total populations. The results showed nonlinear relationships between catch rate and density for the adult and total populations. We accounted for measurement errors in catch rates and densities by estimating bias-corrected slopes by means of Monte Carlo simulations and estimated measurement-error ratios by means of an errors-in-variables model. We found that the bias-corrected slopes were higher than ordinary-least-squares regression estimates and that measurement errors were greater in catch rates than in density estimates. Lastly, we sought to explain the residual variability in the relationships between (1) fyke-net catch rates and adult walleye densities and (2) electrofishing catch rates and adult and total walleye densities. We found that the fyke-net catch rate was positively related to adult walleye density and percent littoral zone (percentage of lake surface area ≤ 20 ft deep) and negatively related to conductivity. We found that the electrofishing catch rate of adult walleyes was positively related to adult walleye density and conductivity and that the electrofishing catch rate of the total walleye population was positively related to total walleye density. We concluded that the nonlinear relationship between catch rates and walleye abundance limits the use of catch rates to index walleye abundance in northern Wisconsin lakes.

Catch rates from fishery surveys are often assumed to be related to stock abundance and are therefore commonly used as an index of abundance (Richards and Schnute 1986). A linear relationship is often assumed between catch rate (C/f) and stock density (N/A):

$$\frac{C}{f} = q \times \frac{N}{A}, \quad (1)$$

where C = catch, f = fishing effort, q = catchability, N = fish abundance, and A = area occupied by the fish stock when catchability is constant (Ricker 1975; Richards and Schnute 1986). However, catch-

ability may vary with population density, tests of density dependence in catchability are complicated by measurement errors in fish density, and catchability varies greatly among fishing gears (Palohimo and Dickie 1964; Peterman and Steer 1981; Gulland 1988). An inverse relationship between catchability and population density is especially problematical: where catch increases with declining abundance, it may lead to overexploitation in harvest fisheries (Hilborn and Walters 1992); where catch decreases with increasing abundance, it may lead to underestimates of abundance in assessment fisheries (Hilborn and Walters 1992). Catch rates and N/A are measured with error, so the slope and intercept are biased when estimated by ordinary least squares (OLS) if measurement errors are not accounted for (Ricker 1975; Fuller 1987; Quinn and Deriso 1999). The relationship between C/f and N/A is also affected by variability in catchability, which can be caused by environmental factors and fish behavior (Hilborn and Walters 1992; Borkholder and Parsons 2001; Harley et al. 2001). Con-

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sequently, the linearity of the relationship between C/f and N/A , the measurement error in C/f relative to that in N/A , and the variability in catchability must be considered when using C/f as an index of population density (Peterman and Steer 1981; Bacante 1995; Hansen et al. 2000; Harley et al. 2001; Bayley and Austen 2002).

The relationship between C/f and abundance may not always be linear, and three relationships are possible: proportional, hyperstable, and hyperdepletion (Hilborn and Walters 1992). Proportional relationships occur when catchability is constant and C/f and N/A increase at the same rate because handling time is small and the search for fish is random (Hilborn and Walters 1992). Proportional relationships between C/f in electrofishing and N/A have been shown for walleye *Sander vitreus* (formerly *Stizostedion vitreum*) fingerlings (Serns 1982), largemouth bass *Micropterus salmoides* (Hall 1986; Coble 1992; McInerny and Degan 1993), and smallmouth bass *M. dolomieu* (Milewski and Willis 1991) because sampling effort was random. Proportional relationships have also been shown for walleyes in surface gill nets (Isbell and Rawson 1989) and smallmouth bass in fyke nets (Milewski and Willis 1991) because sampling effort was randomly distributed. Hyperstability is the most common type of nonproportionality and occurs when C/f remains high while abundance declines (Hilborn and Walters 1992; Harley et al. 2001). Hyperstability is common in fisheries in which the search is efficient, handling times are long, and fish remain concentrated as abundance declines (Hilborn and Walters 1992; Harley et al. 2001). Hyperdepletion occurs when C/f decreases at a much faster rate than abundance and may be more common in fisheries in which fish exhibit differential behaviors to the gear, causing a portion of the population to be removed more rapidly than the rest (Hilborn and Walters 1992). Nonproportional relationships between catch and population density have been shown for Chinook salmon *Oncorhynchus tshawytscha* (Peterman and Steer 1981), Fortune Bay Atlantic herring *Clupea harengus harengus* (Winters and Wheeler 1985), and smallmouth bass (Sammons and Bettoli 1999) because the fish were not homogeneously distributed and fishing effort was not random.

To use catch rate as an index of abundance, the relationship between catch rate and density must be understood; however, catch per effort and density are measured with error, so estimates from OLS regression may be biased (Peterman and Steer 1981; Shardlow et al. 1985; Hilborn and Walters 1992;

Quinn and Deriso 1999; Hansen et al. 2000). Increased measurement error in the x -variable attenuates the relationship with the y -variable and leads to negatively biased parameter estimates (Fuller 1987). The ratio of measurement errors between the x - and y -variables (i.e., the measurement error ratio) determines which methods to use in the analysis. For example, if the measurement errors are much smaller in the x -variable than in the y -variable, OLS regression is appropriate (Ricker 1975). If the measurement errors are similar, geometric mean regression is appropriate (Ricker 1975). If measurement errors are greater in x than in y or the measurement error ratio is unknown, simulation methods or errors-in-variable models are appropriate (Hilborn and Walters 1992; Quinn and Deriso 1999).

Regardless of the form of the relationship between C/f and N/A , catchability often varies with environmental conditions and fish behavior. The catchability of sole *Solea vulgaris* to trawls varied with water currents, depth, light, and turbidity because of gear avoidance or escapement (Dorel et al. 1985; Arreguin-Sanchez 1996). Electrofishing catch rates of largemouth bass varied with water temperature and Secchi depth because of gear avoidance, visibility to dipnetters, and the spatial distribution of the fish (McInerny and Cross 2000). The catchability of northern pike *Esox lucius* to trap nets during the spawning season varied with abundance because fishing effort was not random and some fish were more susceptible to the sampling gear (Pierce 1997). Understanding factors that affect catchability may allow fisheries managers to evaluate biases in sampling gears and the use of catch rates to index abundance.

Our objective was to evaluate the use of catch rates to predict walleye abundance in northern Wisconsin lakes by determining whether catch rates from fyke nets and electrofishing were linearly related to walleye population densities. First, we tested the linearity of the relationship between catch rates and densities. Next, we accounted for measurement errors using Monte Carlo simulations to estimate bias-corrected slopes for the relationship between C/f and N/A and an errors-in-variables model to estimate the measurement error ratio between C/f and N/A . Last, we sought to explain the residual variability in the relationship using physical, chemical, and biological attributes of the surveyed lakes.

Methods

Walleye abundance.—The Wisconsin Department of Natural Resources (WDNR) estimated the

abundance of walleyes on 22–43 lakes/year during 1990–2000. Adult walleyes were captured with 0.5-in fyke nets shortly after ice-out in late spring, usually mid-April (Hansen et al. 1991; Beard et al. 1997; Hansen et al. 2000). Fyke nets are generally set in nonrandom locations that favor high catch rates (i.e., shallow gravel bars) for 18–24 h. In northern Wisconsin, male walleyes are usually mature at a length of 12 in and females at 15 in, so adults were defined as all fish for which sex could be determined and all fish of unknown sex longer than 15 in (Beard et al. 1997; Hansen et al. 2000). Each fish was marked by the removal of a portion of one or more fins, lengths were recorded, and dorsal spines were removed from a subsample of 5–10 fish per 0.5-in length-class to estimate ages (Hansen et al. 2000). Ten percent of the mature walleyes in each lake were targeted for marking, and marking ceased when 10% of the fyke-net catches were previously marked walleyes (Hansen et al. 2000). A recapture sample was collected 1–2 d after marking (during peak walleye spawning) by electrofishing (AC output) the entire lake shoreline to estimate adult walleye abundance (Hansen et al. 2000). Marked and unmarked adult walleyes were assumed to have equal capture probabilities because of the short interval between marking and recapturing and because the entire shoreline was sampled (Hansen et al. 2000). All unmarked walleyes captured during the adult abundance sampling were marked by partial removal of one or more fins and then released for estimating total walleye abundance. A second electrofishing recapture sample was collected 14–17 d after the first, which allowed time for subadults to move inshore, to estimate total walleye abundance (Hansen et al. 2000). Electrofishing recapture samples took place at night, and electrofishing crews attempted to net all the fish they saw.

Adult and total walleye population abundances were estimated by means of the Chapman modification of the Petersen model (Ricker 1975; Hansen et al. 2000). Adult and total walleye population abundances and coefficients of variation (CV, defined as $100 \cdot \text{SD}/\text{mean}$) were estimated for the size-classes 0–11.9, 12.0–14.9, 15.0–19.9, and 20.0+ in and for males and females (Beard et al. 1997; Hansen et al. 2000).

Statistical analysis.—We used nonlinear models to test the linearity of the relationship between fyke-net catch per effort and adult walleye density, electrofishing catch per effort and adult walleye density, and electrofishing catch per effort and total walleye density. Catch rates (C/f) from fyke

nets (number/net-night) during 1997–2000 and electrofishing (number/mi) during 1990–2000 were modeled as functions of adult and total walleye densities (N/A ; number/surface acres) from mark–recapture abundance estimates:

$$\frac{C}{f} = \alpha \left(\frac{N}{A} \right)^{\beta+1}, \quad (2)$$

where α is an estimate of catchability when $\beta = 0$ and β is the degree of curvature between C/f and N/A (Peterman and Steer 1981; Hansen et al. 2000). Catch rates and densities were \log_e transformed and parameters were estimated from the linear model

$$\log_e \left(\frac{C}{f} \right) = b_0 + b_1 \log_e \left(\frac{N}{A} \right), \quad (3)$$

where the intercept b_0 ($= \log_e \alpha$) and the slope b_1 ($= \beta + 1$) were estimated by means of OLS linear regression (Peterman and Steer 1981; Hansen et al. 2000).

Measurement errors are commonly accepted as intrinsic problems in estimating fisheries parameters but are often ignored (Hilborn and Walters 1992). Population density and catch rate were both estimated with error, so we used a geometric mean functional regression to estimate a slope, assuming that the measurement errors were similar (Ricker 1975; Sokal and Rohlf 1981). We also used Monte Carlo simulations to assess the magnitude of bias in our OLS regression estimates (Peterman and Steer 1981; Shardlow et al. 1985; Hansen et al. 2000). One thousand normally distributed random values of density were generated for each lake using the estimated density and standard deviation of the estimate. Lakes with negative simulated density values were omitted from the analysis because they reflected high variability in the density estimates. Each random value of density was regressed against the catch rate with OLS to estimate a slope. The slope and intercept from each regression with simulated values was used with OLS estimates to estimate a bias-corrected slope and intercept:

$$b_{bc} = b_{ols} + (b_{ols} - b_{mc}),$$

where b_{bc} is the bias corrected slope or intercept estimate, b_{ols} is the OLS slope or intercept estimate, and b_{mc} is the estimated slope or intercept estimate from the regressions with simulated values of density. The distribution of the bias-corrected estimates was used to empirically de-

termine the median and 95% confidence intervals for the slope and intercept estimates. Bias-corrected slope estimates were tested for significant differences from 1.0 (i.e., to indicate density dependence in catchability) using the upper and lower 0.025 percentiles of the distribution of bias-corrected slopes (i.e., 95% confidence intervals). Linearity of relationships were tested between (1) fyke-net C/f and adult walleye N/A , (2) electrofishing C/f and adult walleye N/A , (3) electrofishing C/f and adult walleye N/A for the size-classes 0.0–11.9, 12.0–14.9, 15.0–19.9, and 20+ in, (4) electrofishing C/f and total walleye N/A , and (5) electrofishing C/f and total walleye N/A for the size-classes 0–11.9, 12–14.9, 15–19.9, and 20+ in.

The measurement error ratios between catch rates and densities were estimated for adult walleye abundance and size-classes and total walleye abundance and size-classes with the errors-in-variables model with known variance:

$$\hat{\beta}_1^2 m_{XY} - \hat{\beta}_1(m_{XY} - \delta m_{XX}) - \delta m_{XY} = 0,$$

where $\hat{\beta}_1$ is the slope, m_{YY} is the variance in Y , m_{XX} is the variance in X , m_{XY} is the covariance between X and Y , and δ is the Y/X measurement-error ratio (Fuller 1987; Quinn and Deriso 1999). We substituted bias-corrected slopes for $\hat{\beta}_1$ in the errors-in-variables model to estimate δ in each relationship.

We modeled factors that affected the catchability of walleyes to fyke nets and electrofishing by incorporating physical, chemical, and biological factors in a multiple-regression equation:

$$\frac{C}{f} = \alpha \left(\frac{N}{A} \right)^{\beta+1} \cdot X_1^{b_2} \cdots X_n^{b_n}, \quad (5)$$

where the X variables were mean depth, Secchi depth, shoreline development factor, pH, conductivity, alkalinity, percent littoral zone (percentage of lake surface area ≤ 20 ft deep), and water temperature. Lake variables were obtained from the Wisconsin Surface Water Inventory database except for water temperature, which was measured during sampling (Table 1). Parameters were estimated from the \log_e transformed equation

$$\log_e \left(\frac{C}{f} \right) = b_0 + b_1 \log_e \left(\frac{N}{A} \right) + b_2 \log_e X_1 + \cdots + b_n \log_e X_n, \quad (6)$$

where $b_0 = \log_e(\alpha)$. Our previous results indicated that bias-corrected slope estimates were close to

ordinary least squares estimates, so we used OLS to estimate the parameters in the multiple-regression models. Multiple-regression models were fitted using stepwise linear regression methods. Explanatory variables were added with $P < 0.15$ to enter and $P > 0.05$ to exit, and variables were retained in the final model if $P < 0.05$. The modeling procedure was stopped when variables ceased to significantly improve the amount of variation explained by the model, and the final model was evaluated using a likelihood ratio test (Sokal and Rohlf 1981).

Results

Linearity

Fyke-net catch rates were nonlinearly related to adult walleye densities in 86 northern Wisconsin lakes during 1997–2000:

$$\frac{C}{f} = 5.37 \left(\frac{N}{A} \right)^{0.734}. \quad (7)$$

The bias-corrected slope for the relationship between number/net-night and adult walleye density was significantly less than 1.0 (95% confidence interval = 0.69–0.80), and the bias-corrected intercept was significantly different from 0 (95% confidence interval = 5.09–5.57; Figure 1).

Electrofishing catch rates were nonlinearly related to adult walleye densities in 313 northern Wisconsin lakes during 1990–2000. The bias-corrected slope for the relationship between catch rate and density for all adult walleyes was significantly less than 1.0, and the bias-corrected intercept was significantly different from 0 (Table 2; Figure 2). For the four walleye length-classes, the bias-corrected slopes generally increased with walleye size and were all significantly less than 1.0 and the bias-corrected intercepts decreased with walleye size and were all significantly greater than 0 (Table 2; Figure 3).

Electrofishing catch rates were nonlinearly related to total walleye densities in 147 northern Wisconsin lakes during 1990–2000. The bias-corrected slope for the relationship between catch rate and density for total walleyes was significantly less than 1.0, and the bias-corrected intercept was significantly different from 0 (Table 3; Figure 4). For the four walleye length-classes, the bias-corrected slopes increased with walleye size except for the 20+-in size-class and were all significantly less than 1.0, and the bias-corrected intercepts decreased with walleye size and were all

TABLE 1.—Morphometric and limnological characteristics used to relate catchability of walleye populations to fyke netting and electrofishing in northern Wisconsin lakes. Shoreline development was calculated from Wetzel (2001) as shoreline length (mi)/[2·π·area (sq mi)]. Percent littoral is defined as the percentage of lake surface area with a depth ≤20 ft.

Analysis (number of lakes)	Variable	Mean	SD	Range	
Fyke netting (86)	Adult density (number/acre)	2.85	2.07	0.07–9.72	
	Catch/net-night	13.04	11.85	0.39–50.77	
	Mean depth (ft)	15.93	6.87	3–34	
	Shoreline length (mi)	7.56	4.95	1.3–30.2	
	Secchi depth (ft)	9.38	5.95	2–38	
	Shoreline development	0.085	0.029	0.04–0.18	
	pH	7.26	0.64	6–9	
	Conductivity (0.39 μmhos/in) ^a	89.42	37.49	24–189	
	Alkalinity (ppm) ^b	39.74	20.67	8–105	
	Percent littoral	10.17	6.56	1–38	
	Adult electrofishing (194)	Adult density (number/acre)	3.26	2.54	0.21–14.82
		Catch/mile	41.14	35.83	0.49–200.39
		Mean depth (ft)	16.78	7.77	3–49
Shoreline length (mi)		10.51	18.53	2.1–232.9	
Secchi depth (ft)		9.04	4.85	2–25	
Shoreline development		0.09	0.05	0.05–0.53	
pH		7.23	0.62	5–9	
Conductivity (0.39 μmhos/in)		85.3	37.89	24–235	
Alkalinity (ppm)		39.28	21.28	4–130	
Percent littoral		9.62	5.27	1–36	
Water temperature (°F)		46.51	4.3	40–62	
Total electrofishing (147)		Total density (number/acre)	11.054	10.77	0.22–53.83
		Catch/mile	32.07	35.24	0.37–217.5
	Mean depth (ft)	17.57	8.21	3–49	
	Shoreline length (mi)	12.57	28.53	1.3–232.9	
	Secchi depth (ft)	10.31	6.13	2–38	
	Shoreline development	0.1	0.07	0.04–0.53	
	pH	7.28	0.69	5–9	
	Conductivity (0.39 μmhos/in)	88.09	38.83	17–202	
	Alkalinity (ppm)	40.47	22	3–109	
	Percent littoral	9.69	6.06	1–36	
	Water temperature (°F)	57.96	5.35	44–70	

^a Equivalent to mS/cm.

^b Equivalent to mg/L.

significantly greater than zero except for the 20+-in size-class (Table 3; Figure 5).

Measurement Errors

The bias-corrected slopes and intercepts were close to the OLS estimates for the relationship between catch rates in fyke nets and electrofishing and walleye density (Tables 4, 5). Geometric mean functional regression overcorrected for measurement errors. For adult walleye electrofishing samples, measurement errors were higher for catch rates than for estimates of density. The measurement error ratios of catch rates to densities were lowest for the 0–11.9-in (3.46:1) and 20+-in (4.97:1) size-classes and highest for total adult abundance (28.51:1) and the 12.0–14.9-in (18.41:1) and 15.0–19.9-in (14.70:1) size-classes. For total walleye electrofishing samples, measurement errors were also higher in catch rates than in den-

sity. Measurement error ratios of catch rates to densities were lowest for total walleyes (11.20:1) and the 20+-in size-class (12.0:1) and higher for the 0–11.9-in (13.60:1), 12–14.9-in (15.20:1), and 15–19.9-in (13.29:1) size-classes.

Variability in Catchability

Adult walleye fyke-net samples.—Adult walleye density explained 47% of the variation in the catch rate of adult walleyes to fyke nets in northern Wisconsin lakes ($F = 73.11$; $df = 1, 84$; $P < 0.001$):

$$\frac{C}{f} = 5.048 \left(\frac{N}{A} \right)^{0.73} \quad (8)$$

Fyke-net catch rate was positively exponentially related to adult walleye density. The highest catch rate occurred when adult density was 2.16/acre, and the lowest catch rate occurred when adult den-

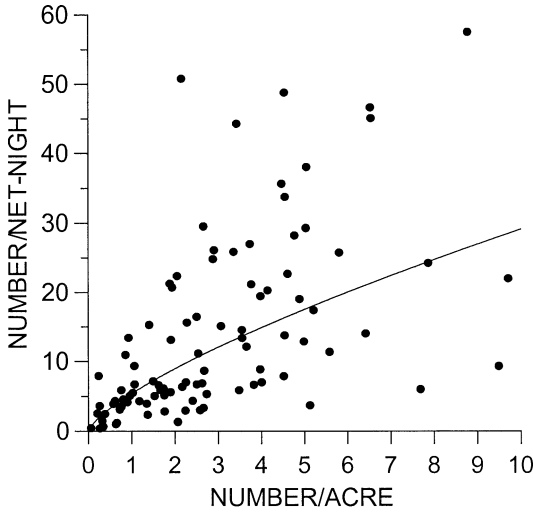


FIGURE 1.—Fyke-net catch per net-night versus adult walleye population in 86 northern Wisconsin lakes during 1997–2000.

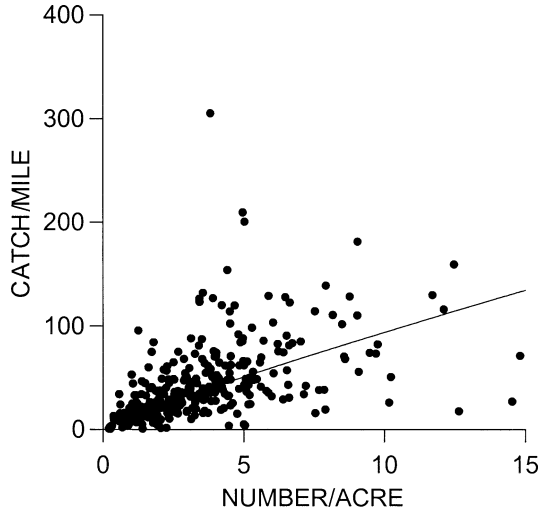


FIGURE 2.—Electrofishing catch per mile versus adult walleye population density in 313 northern Wisconsin lakes during 1990–2000.

sity was 0.27/acre. The maximum adult walleye density was 9.71 adults/acre and the lowest adult walleye density was 0.21/acre.

Lake conductivity, *K*, improved the model so that it explained 51% of the variability in the catch rate of adult walleyes in fyke nets ($F = 42.379$; $df = 2, 82$; $P < 0.007$):

$$\frac{C}{f} = 40.568 \left(\frac{N}{A}\right)^{0.704} \cdot K^{-0.471}. \quad (9)$$

Fyke-net catch rate was negatively exponentially related to conductivity. The maximum conductivity observed was 186 μ mhos and the lowest conductivity observed was 24 μ mhos.

Percent littoral zone, *L*, improved the model further so that it explained 54% of the variability in the catch rate of adult walleyes to fyke nets ($F = 31.054$; $df = 3, 81$; $P < 0.034$):

$$\frac{C}{f} = 24.656 \left(\frac{N}{A}\right)^{0.728} \cdot K^{-0.499} \cdot L^{0.282}. \quad (10)$$

TABLE 2.—Bias-corrected slope, \log_e transformed intercept, and 95% confidence intervals (CIs) and correlation coefficients for the relationship between electrofishing catch rate [$\log_e(C/f)$] and adult walleye density [$\log_e(N/A)$] in northern Wisconsin lakes during 1990–2000.

Size-class (in)	Slope estimate	95% CI		Intercept estimate	95% CI		<i>r</i>
		Upper	Lower		Upper	Lower	
0–11.9	0.75	0.78	0.72	2.837	2.850	2.824	0.68
12.0–14.9	0.70	0.72	0.67	2.586	2.589	2.582	0.71
15.0–19.9	0.81	0.85	0.77	2.290	2.300	2.279	0.63
≥ 20	0.91	0.98	0.85	1.841	1.940	1.770	0.83
All adult walleyes	0.89	0.92	0.86	2.490	2.520	2.460	0.67

Fyke-net catch rate was positively exponentially related to the percentage of littoral zone. The highest percent littoral zone was 38% and the lowest was 1%.

Adult walleye electrofishing samples.—Adult walleye density explained 47% of the variability in adult walleye catch rate to electrofishing ($F = 167.163$; $df = 1, 192$; $P < 0.001$):

$$\frac{C}{f} = 14.197 \left(\frac{N}{A}\right)^{0.772}. \quad (11)$$

Electrofishing catch rates were positively exponentially related to adult walleye density. The maximum adult walleye density was 14.82 adults/acre, and the minimum adult walleye density was 0.07 adults/acre.

Conductivity, *K*, improved the model so that it explained 49% of the variability in adult walleye catch rate to electrofishing ($F = 88.071$; $df = 2, 187$; $P < 0.013$):

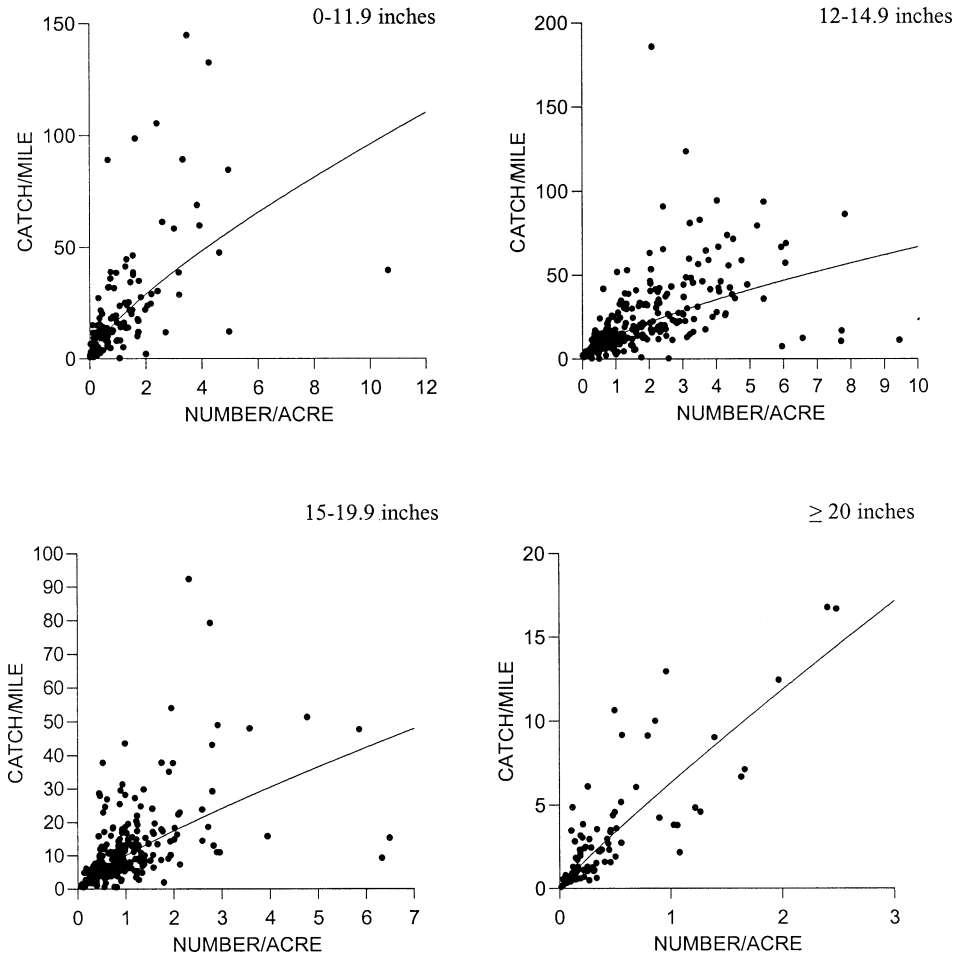


FIGURE 3.—Electrofishing catch per mile versus adult walleye population density for the following length-classes of walleyes in northern Wisconsin lakes during 1990–2000: 0–11.9 in ($N = 133$), 12.0–14.9 in ($N = 248$), 15.0–19.9 in ($N = 241$), and 20+ in ($N = 84$).

$$\frac{C}{f} = 4.162 \left(\frac{N}{A} \right)^{0.78} \cdot K^{0.281}. \quad (12)$$

Catch rates were positively exponentially related to conductivity. The highest conductivity was 235 μmhos and the lowest conductivity was 24 μmhos .

Total walleye electrofishing samples.—Total walleye density explained 31% of the variability in adult walleye catch rate to electrofishing ($F = 81.315$; $df = 1, 179$; $P < 0.001$):

$$\frac{C}{f} = 6.013 \left(\frac{N}{A} \right)^{0.507}. \quad (13)$$

Biological and environmental variables did not increase the model's ability to explain the variability in electrofishing catch rates of the total walleye population.

Discussion

We found that catch rates of adult walleyes in fyke nets were nonlinearly related to adult walleye densities, which suggests that gear saturation increased at high densities. As adult walleye density increased, catchability decreased, thereby leading to hyperstability, as has been shown for other passive gears, including longlines, crab pots, gill nets, and lobster traps (Bennett 1974; Hamley 1975; Miller 1990; Somerton and Kikkawa 1995; Miller and Rodger 1996; Zhou and Shirley 1997; Hansen et al. 1998; Rugolo et al. 1998). In our analysis, fyke nets were set in areas of high abundance to capture fish for marking, which may have led to gear saturation. The fyke nets were checked daily, which reduces the likelihood of physical limitations causing gear saturation (Hamley and Howley

TABLE 3.—Bias-corrected slope, \log_e transformed intercept, 95% confidence intervals (CIs) and correlation coefficients for the relationship between electrofishing catch rate [$\log_e(C/f)$] and total walleye density [$\log_e(N/A)$] in northern Wisconsin lakes during 1990–2000.

Size-class (in)	Slope estimate	95% CI		Intercept estimate	95% CI		r
		Upper	Lower		Upper	Lower	
0–11.9	0.59	0.69	0.51	2.04	2.24	1.80	0.48
12.0–14.9	0.62	0.68	0.58	1.14	1.19	1.09	0.62
15.0–19.9	0.70	0.78	0.64	0.94	0.95	0.93	0.55
≥ 20	0.37	0.47	0.28	-0.15	0.02	-0.30	0.35
All walleyes	0.85	0.89	0.82	1.31	1.37	1.23	0.78

1985; Dauk and Schwarz 2001); but as densities increased, nets exhibited decreased ability to catch additional fish, leading to lower catches. Catches of American lobster *Homarus americanus* increased when traps were hauled twice per day rather than once per day in Nova Scotia, Canada (Miller and Rodger 1996). Lobster catches decreased by 54% when traps were stocked with one lobster and fished for 24 h (Addison 1995). Decreased catches of adult walleyes due to gear saturation limits the ability to use C/f as a reliable index of abundance (Beverton and Holt 1957). However, correcting fyke-net catches for soak time may allow the use of C/f to index abundance (Zhou and Shirley 1997).

We also found a nonlinear relationship between electrofishing catch rate and density, which suggests that handling time limited catch rates at high densities; that is, as more fish were encountered at higher densities, netters may have been limited

in the number of fish that they could handle. Handling-time problems may be caused by the inability of electrofishing units (assuming the boat is moving) to stun fish long enough for crews to net all the fish in high-density patches (McInerny and Cross 2000; Bayley and Austen 2002). Handling-time problems may also be caused by the preferential behavior of netters, as when netters target some fish over others (e.g., netting bigger fish in higher proportions than smaller fish). Catch rates of largemouth bass, bluegill *Lepomis macrochirus*, and redear sunfish *L. microlophus* differed among sampling crews in Florida (Hardin and Connor 1992) and efforts have been made in other studies to control for variability in sampling crew efficiency (Buynak and Mitchell 1993; McInerny and Cross 2000). Handling time may also be related to boat speed. A boat traveling at high speed does not allow netters to see and net all fish, which would decrease catch rates at higher abundances. Conversely, a boat traveling at low speed may allow netters to see and capture all fish, which would lead to catches that are proportional to abundance (McInerny and Cross 2000). Bayley and Austen (2002) described the variability in catchability due to boat speed when more time was spent near productive fish habitat and crews circled back to collect stunned fish behind the boat and concluded that boat speed should be consistent with the crew's ability to net fish. Other studies have controlled for boat speed by using the same driver (Edwards et al. 1997; McInerny and Cross 2000); however, use of the same boat driver to monitor walleye populations in northern Wisconsin is not possible because of the large number of lakes that are sampled each year.

Catchability may be affected if individual fish or size-classes in the population react differently to the electrical field and thereby allow themselves to be more easily netted than others. Bayley and Austen (2002) hypothesized that larger fish may be less vulnerable to electrofishing gears because

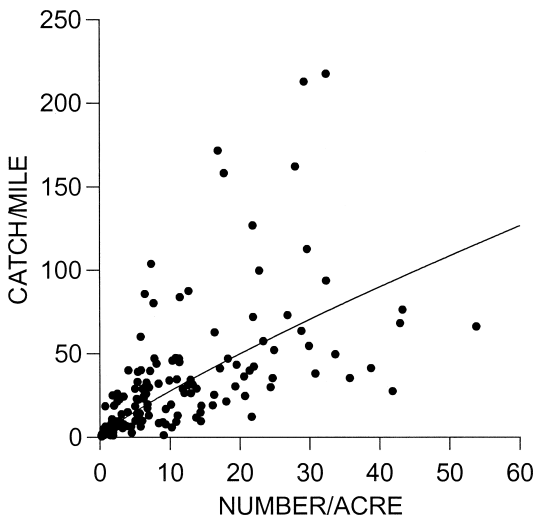


FIGURE 4.—Electrofishing catch per mile versus total walleye population density in 147 northern Wisconsin lakes during 1990–2000.

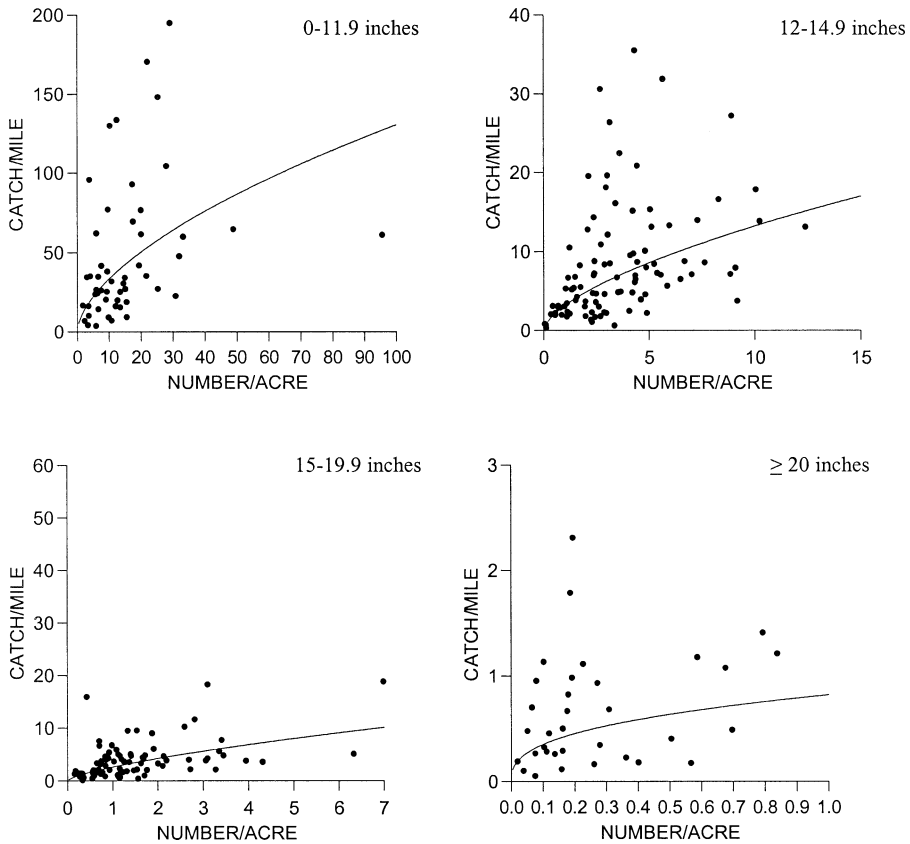


FIGURE 5.—Electrofishing catch per mile versus total walleye population density for the following length-classes of walleyes in northern Wisconsin lakes during 1990–2000: 0–11.9 in ($N = 51$), 12.0–14.9 in ($N = 98$), 15.0–19.9 in ($N = 86$), and 20+ in ($N = 84$).

of their increased ability to avoid electrofishing gears, which may bias the use of C/f as an index of fish density. Size-dependent catchability will occur if fish of different size-classes exhibit differing vulnerability to capture because of behavioral differences. Bayley and Austen (2002) reported unimodal relationships between catchabil-

ity and fish length for largemouth bass, common carp *Cyprinus carpio*, and bluegills and proposed that size-dependent catchability may be due to behavioral responses. Similarly, our results indicate that size-dependent catchability may be due to differing behaviors among size-classes. During our adult population estimates mature adults were ac-

TABLE 4.—Ordinary least squares (OLS), geometric mean functional regression (GM), Monte Carlo (MC), and bias-corrected (BC) estimates of the slope and \log_e transformed intercept for the relationship between fyke-net and electrofishing catch rates and adult walleye density in northern Wisconsin lakes during 1990–2000.

Gear and size-class	OLS		GM		MC		BC	
	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope
Fyke net	1.698	0.711	1.389	1.094	1.724	0.688	1.680	0.734
Electro-fishing								
0–11.9	2.800	0.658	2.921	0.963	2.713	0.565	2.837	0.751
12–14.9	2.588	0.679	2.550	0.959	2.599	0.662	2.586	0.696
15–19.9	2.283	0.764	2.376	1.209	2.285	0.719	2.292	0.809
≥ 20	1.770	0.856	1.997	1.033	1.726	0.803	1.839	0.909
Total	2.521	0.862	2.099	1.285	2.557	0.834	2.493	0.890

TABLE 5.—Ordinary least squares (OLS), geometric mean functional regression (GM), Monte Carlo (MC), and bias-corrected (BC) estimates of the slope and \log_e transformed intercept for the relationship between electrofishing catch rate and total walleye density in northern Wisconsin lakes during 1990–2000.

Size-class	OLS		GM		MC		BC	
	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope
0–11.9	2.144	0.550	2.068	1.136	2.262	0.508	2.042	0.592
12–14.9	1.167	0.599	2.282	0.965	1.204	0.575	1.145	0.623
15–19.9	0.948	0.652	2.411	1.179	0.972	0.603	0.942	0.701
≥20	–0.195	0.343	2.441	0.994	–0.232	0.316	–0.150	0.370
Total	1.364	0.819	2.579	1.045	1.440	0.789	1.308	0.849

tively seeking mates, and shortly after spawning adults tended to move offshore rapidly, which may have affected their vulnerability to electrofishing gears. In contrast, immature walleyes tend to remain offshore until waters begin to warm, and vulnerability to electrofishing may have differed among size-classes because of movement patterns. Sex-related behavioral differences in large walleyes may also have affected our catchability analyses because males tend to remain in spawning areas longer than females, thereby increasing their vulnerability to electrofishing gears.

We found that geometric mean (GM) functional regression overcorrected for measurement errors because the GM regression assumes a 1:1 ratio of measurement errors (Ricker 1975) and measurement errors were greater in the dependent variable in our models. Ordinary least squares regression estimates were close to bias-corrected slopes because measurement errors were smaller in our x -variable than our y -variable (Ricker 1975). Lower measurement errors in density than in catch per effort may be a reflection of the greater precision of the density estimates as a result of excluding estimates with CVs greater than 0.40; however, walleye abundance estimates for northern Wisconsin lakes generally have CVs less than 0.2. Measurement error in catch rate was highest in the most abundant size-classes (12.0–19.9-in walleyes during the adult sample and 0.0–14.9-in walleyes during the total sample), which suggests that measurement error in catch per effort increased with abundance. Increased measurement error in catch rate may be due to multiple factors, such as variations in crew behavior, gear efficiency, fish behaviors, or environmental variables.

We found that conductivity and percent littoral zone helped to explain the variability in fyke-net catch rates of adult walleyes in northern Wisconsin lakes. A positive relationship between fyke-net catch rates and adult walleye density is consistent with the results of other studies of passive gears

because catch rate increased with fish density (Ryan 1984; Hamley and Howley 1985; Milewski and Willis 1991). A negative relationship between catch rate and conductivity is probably caused by the relationship between conductivity and adult walleye abundance. Nate et al. (2001) found an inverse relationship between conductivity and walleye abundance in stocked Wisconsin lakes and attributed it to water quality limitations to walleye populations. In our analyses, the lower catch rates associated with increased conductivity could be a function of lower walleye abundance in lakes with increased conductivity. Our negative relationship between catch rate and conductivity may also be due to the relationship between conductivity and water clarity (Wetzel 2001). In clear waters, with low conductivities, walleyes might seek fyke nets as cover and thereby increase their catchability. Cover-oriented species, such as white crappies *Pomoxis annularis*, are caught at higher rates in fyke nets than species that are not cover oriented (Hubert and Schmitt 1982; Holland and Peters 1992). Clear water may also allow field crews to more easily locate potential spawning areas to set nets in, which would increase catch rates in clear water. The positive relationship between percent littoral zone and adult walleye catchability that we found is consistent with the behavior of the species and most common deployment techniques. Walleyes move into shallow areas (between 12 and 30 in deep) to spawn, so fyke nets are set in areas where high abundance is expected (Becker 1983). Fyke nets are also generally set in shallow water, so that the floats on the lead are on the surface and the weighted line is on the bottom, to prevent fish from swimming over or under the lead line. Lakes with higher percentages of littoral zone also have a greater number of sites where nets can be set than lakes with lower percentages of littoral zone, where nets may need to be set along steep banks, drop-offs, or other potentially less efficient locations.

We found that conductivity helped to explain the variability in electrofishing catch rates of adult walleyes in northern Wisconsin lakes. A positive relationship between adult walleye density and electrofishing catch rate is consistent with the results of other studies of fingerling and yearling walleyes (Serns 1982, 1983) and other species (Hall 1986; Coble 1992; McInerny and Degan 1993). The influence of conductivity on electrofishing efficiency and increases in electrofishing efficiency with increased conductivity have been well documented (Reynolds 1996; Bayley and Austen 2002). Hill and Willis (1994) found that conductivity influenced AC electrofishing catch rates of largemouth bass in Midwestern lakes; however, they were dealing with much higher conductivities (410–1,700 $\mu\text{S}/\text{cm}$) than occurred in northern Wisconsin lakes (24–235 $\mu\text{S}/\text{cm}$). Conductivity increases with water temperature (Reynolds 1996), which may explain why we found that conductivity affected catchability during the adult electrofishing sample but not the total electrofishing sample. In Wisconsin surveys, adult walleye sampling takes place soon after ice-out and water conductivity may play an important role in electrofishing efficiency at that time; later, during the total population sampling, water temperatures were probably higher and conductivity may not have significantly affected the catchability of walleyes to electrofishing. Serns (1982) also found no effect of conductivity on the electrofishing efficiency of walleye fingerlings when sampling was done from mid-September to October. In fall, the electrofishing catch rates of age-0 walleyes vary with water temperature (Borkholder and Parsons 2001), but water temperature did not explain the variability in catch rates in our analysis. The inability of water temperature to explain the variation in electrofishing catchability may be due to a lack of variability in water temperatures, as electrofishing sampling took place in early spring before water warmed. The inability of environmental variables to explain more variability in catchability is compatible with Serns's (1982) findings that electrofishing efficiency for fingerling walleyes was not affected by conductivity or shoreline complexity. Serns (1982) also found that electrofishing efficiency was negatively affected by lake surface area and shoreline length. Shoreline length (mi) was incorporated into electrofishing catch rates (catch/mi) and surface area (acres) was incorporated into total walleye density (number/acre), implicitly incorporating much of the variability in catchability in these variables.

Management Implications

The relationship between catchability and population density must be recognized to correctly manage fisheries (Peterman and Steer 1981; Hansen et al. 2000). Our results suggest that the catchability of walleyes to fyke nets and electrofishing changes with density and that catch rates should be used cautiously to index walleye abundance in northern Wisconsin lakes. Although hyperstable relationships are common in harvest fisheries, where attempts are made to maximize catch per effort, such relationships may be less expected in assessment fisheries, where attempts are made to randomly sample populations in order to understand the dynamics of the fishery (Hilborn and Walters 1992). The problems created by hyperstable relationships in harvest fisheries occur at low population densities and are due to nonrandom searching, whereas the problems created by hyperstable relationships in assessment fisheries occur at high densities and are due to gear saturation and handling time. Regardless of the type of fishery, fisheries managers need to recognize hyperstable relationships to correctly manage stocks. A hyperstable relationship in fyke-net and electrofishing assessment fishery catch rates decreases the sensitivity of catch rates to changes in walleye density because density increases at a faster rate than catch rates. A hyperstable relationship limits the use of C/f in predicting density at high catch rates and decreases the precision of density estimates as catch rates increase. The variability in the relationship between catch rate and population density may also be problematic in using catch rates to predict density. The multiplicative error structure in the relationship indicates that relatively high catch rates may reflect a wide range of population densities. Based on our analyses, electrofishing catch rates of 100 adult walleyes per mile are possible at densities ranging from less than 5 adults per acre to more than 10 adults per acre. Catch rates may be useful in monitoring lakes with historically low walleye densities because hyperstability becomes more problematic at high densities and the variability in the relationship increases with density. Similarly, catch rates may also be useful in monitoring lakes with high walleye densities if fisheries managers only need a qualitative index of fish densities rather than an accurate estimate of abundance; however, the variability in the relationship should be considered. Using C/f to index walleye densities in northern Wisconsin may be problematic for setting harvest

limits based on abundance estimates because the sensitivity of C/f to changes in abundance decreases with walleye density. However, if fisheries managers are less concerned about harvests in lakes with high densities, then C/f may be useful in indexing walleye abundance. Although the variability in catch rates may limit the ability of catches to index abundance in northern Wisconsin lakes, long-term catch rate data are still valuable for monitoring trends and changes in walleye populations within lakes over time.

To understand the true relationship between C/f and N/A , measurement errors need to be assessed (Quinn and Deriso 1999). In our analysis, measurement errors in walleye density led to attenuated OLS regression estimates of the slope of the relationships between survey catch rate and walleye density, but because these errors were greater in survey catch rates our bias-corrected slopes were close to OLS estimates. Serns (1982) used C/f as the independent variable to predict walleye density, but our analysis suggests that that would have increased the errors in the x -axis and led to biased regression estimates because the slope becomes attenuated with increased errors in the x -axis (Quinn and Deriso 1999). In our analysis, predicting walleye densities from catch rates would have led to underestimates of abundance at high catch rates.

Understanding the factors that affect the catchability of walleyes to fyke nets and electrofishing could help managers to index walleye abundance more precisely using catch rates. Including physical, chemical, and biological factors helped to explain the variability in catch rates, but the inability to explain more than 54% of that variability limited the use of C/f in indexing walleye abundance. Our data were limited due to unrecorded or unquantified measurements of weather conditions (e.g., cool, cloudy), water clarity (e.g., clear, stained), and water temperatures during some sampling events. In some cases, those factors may be useful in explaining the variability in walleye catchability to fyke nets and electrofishing. Other factors, such as barometric pressure and habitat features, that have been shown to affect fish behavior may also be useful for explaining the variability in fyke-net and electrofishing catch rates but were beyond the scope of our study. Further research into the factors that affect catchability may lead to predictive models based on catch rates that would enable monitoring of important fisheries with less effort (Buynak and Mitchell 1993).

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