North American Journal of Fisheries Management 20:328–336, 2000

Effects of Sampling Time, Intraspecific Density, and Environmental Variables on Electrofishing Catch per Effort of Largemouth Bass in Minnesota Lakes

MICHAEL C. MCINERNY* AND TIMOTHY K. CROSS

Minnesota Department of Natural Resources, 20596 Highway 7, Hutchinson, Minnesota 55350, USA

Abstract.—Effects of sampling time (day or night and fall or spring), target fish density, water clarity, water temperature, water conductivity, and lake morphometry on electrofishing catch per effort (CPUE) of largemouth bass *Micropterus salmoides* 200 mm total length (TL) and longer were determined. Electrofishing catch per hour (CPH) and catch per kilometer (CPK) were also compared to determine if each expression provided similar trends in CPUE. Correlations between day CPH and day CPK ($r = 0.99$; $P < 0.0001$) and night CPH and night CPK ($r = 0.97$; $P < 0.0001$) suggested that both measures provided similar trends in CPUE. Night CPH significantly exceeded day CPH, and spring CPH significantly exceeded fall CPH. Catchability (q) decreased with increasing density; therefore, CPH increased nonlinearly with density. Day CPH in fall decreased with increasing Secchi depth and water temperature but was unrelated to largemouth bass density. Day CPH in spring decreased with increasing Secchi depth and water temperature and increased with increasing density of largemouth bass and water conductivity. Night CPH in fall increased with increasing density and decreased with decreasing water conductivity, and night CPH in spring increased with increasing density and decreasing percent littoral area (percent of lake with depth less than 4.6 m) among lakes. These variables explained 44% of day CPH in fall, 75% of day CPH in spring, 28% of night CPH in fall, and 59% of night CPH in spring. Effects of density on q must be determined and environmental conditions must be similar before CPUE can be a useful index of largemouth bass density.

Shoreline electrofishing catch per effort (CPUE) data are used to index density of largemouth bass; however, the effects of sampling time, density of largemouth bass, and environmental variables on CPUE are not fully understood. Although some effects of density (Hall 1986; Gablehouse 1987; Coble 1992; McInerny and Degan 1993; Hill and Willis 1994; Edwards et al. 1997), time of day or year (Gilliland 1987; Bettross and Willis 1988; Malvestuto and Sonski 1990; Dumont and Dennis 1997; Sammons and Bettoli 1999), and environmental variables (Bailey and Austen 1987; Hill and Willis 1994; Dumont and Dennis 1997; Edwards et al. 1997) on electrofishing CPUE have been shown, the collective effects of all of these variables on CPUE have not been determined. The expression of electrofishing effort also varies, usually being expressed as time or distance of shoreline electrofished; however, these expressions have not been compared to determine if they provide similar trends in CPUE.

Although CPUE increases with increasing density, variable densities have affected catchability (q) of several fish species captured with various fishing gears. In cases where density effects occurred, q always decreased with increasing density (Peterman and Steer 1981; Arreguin-Sanchez 1996). Decreasing q with increasing density has been caused by gear saturation, reduced searching area and time, clumping or schooling behavior of targeted fish, or nonrandom search patterns by users of fishing gear (Peterman and Steer 1981). Density effects on electrofishing q of largemouth bass have not been tested. In all published relationships between electrofishing CPUE and population density of largemouth bass, q was assumed constant (Hall 1986; Gablehouse 1987; Coble 1992; McInerny and Degan 1993; Hill and Willis 1994; Edwards et al. 1997). Because CPUE = $q \times$ density, the value of CPUE as an index of density decreases with increased variation in q (Arreguin-Sanchez 1996).

Electrofishing CPUE of largemouth bass varies dielly and seasonally, but sampling times when CPUE best reflects density have not been determined. Night CPUE usually exceeded day CPUE in Oklahoma reservoirs (Gilliland 1987), but day and night CPUE in an Alabama reservoir did not significantly differ (Malvestuto and Sonski 1990). Day and night CPUE of largemouth bass 200–380 mm total length (TL) among 16 Texas reservoirs

* Corresponding author: mike.mcinerny@dnr.state.mn.us

Received November 25, 1998; accepted October 20, 1999

did not significantly differ in spring, but night CPUE exceeded day CPUE in fall (Dumont and Dennis 1997). Electrofishing CPUE in a South Dakota impoundment and an Alabama reservoir were similar in spring and fall and were lowest in summer (Bettross and Willis 1988; Malvestuto and Sonski 1990). However, fewer and smaller largemouth bass were captured with electrofishing in a Tennessee reservoir in fall than in spring (Sammons and Bettoli 1999). Also, different portions of largemouth bass populations appear vulnerable to electrofishing in fall than in spring (Van den Avyle 1976; McInerny and Cross 1999). Night CPUE in spring was significantly correlated with density of largemouth bass (Hall 1986; Coble 1992; McInerny and Degan 1993; Hill and Willis 1994; Edwards et al. 1997), but similar analyses have not been done for day electrofishing or other times of the year.

Variation in CPUE of largemouth bass has been linked with variation of water clarity, water conductivity, and cover, and CPUE should vary among lakes with different morphometry and substrates. Day CPUE of largemouth bass increased as water clarity decreased in Oklahoma reservoirs (Gilliland 1987), and differences between day and night CPUE of largemouth bass 200–380 mm TL among 16 Texas reservoirs increased with water clarity (Dumont and Dennis 1997). However, night CPUE of largemouth bass 200 mm TL and larger was unrelated to turbidity in Texas ponds (Edwards et al. 1997). The type, amount, and distribution of cover affects spatial distribution of largemouth bass within lakes (Annett et al. 1996), and CPUE of largemouth bass increased with increasing cover in Missouri ponds (Simpson 1978). Cover also offsets effects of clearer water on day CPUE in Illinois impoundments (Bailey and Austen 1987). Conversely, night CPUE was not affected by density of aquatic vegetation in Texas ponds (Edwards et al. 1997). Largemouth bass usually inhabit depths less than 5 m (Heidinger 1975; Carlander 1977); therefore, shoreline electofishing should sample higher portions of populations in lakes with low percentages of shallow water ($<$5 m deep) than in those with high percentages. Size and magnitude of electrical fields produced by electrofishers varies with changing substrates and water conductivity, and more electrical power is needed to elicit the desired electroshock response when differences between water and fish conductivity increase (Kolz 1989; Reynolds 1996).

Electrofishing CPUE should also vary with changing water temperature. Increased water temperature causes increases in water conductivity; therefore, CPUE will change if output power from the boat is not adjusted (Reynolds 1996). Fish activity and metabolism increase with increasing water temperature, so capture of fish is more likely in warmer water (Reynolds 1996). Spatial distribution of largemouth bass within lakes is also linked with water temperature. For example, mature ($\geq$250-mm TL) largemouth bass spawn in shallow water (usually 0.3–1.3 m deep, where electrofishing is most effective) when spring water temperatures range from 12°C to 21°C but are often found in deeper water at other times of the year (Heidinger 1975; Carlander 1977).

Catch per effort of largemouth bass is either expressed as catch per time or catch per distance, but these two measures of CPUE have not been compared. Both catch per h (CPH) or catch per km (CPK) have been significantly correlated with population density of largemouth bass 200 mm TL and longer (Hall 1986; Coble 1992; McInerny and Degan 1993; Hill and Willis 1994; Edwards et al. 1997).

Fish managers in Minnesota are developing standardized procedures for sampling largemouth bass with electrofishing; thus, identifying factors affecting CPUE are essential. Consequently, objectives of this study were to determine electrofishing CPUE and population density of largemouth bass 200 mm TL and longer in Minnesota lakes, to determine if CPH and CPK provide similar trends in CPUE, and to determine the effects of density, sampling time (day or night; fall or spring), lake morphometry, and environmental variables, such as water temperature, water clarity, and water conductivity, on electrofishing CPUE.

Methods

Largemouth bass at 12 lakes in south-central Minnesota were sampled with shoreline electrofishing (Table 1), and electrofishing CPUE and estimates of population size were determined. Lake sizes ranged from 18 to 208 ha, and percent littoral area (area of lake less than 4.6 m deep) ranged from 27% to 76% (Table 1). Each lake was electrofished during one fall and the following spring, 1992–1995.

Two sets of day and night electrofishing samples were collected at least 1 week apart at each lake within each season. All day samples except one were collected within 24 h of a night sample. In the first set, day electrofishing followed night electrofishing in one half of the lakes, and the opposite was the case for the other half. The order of day

TABLE 1.—Lake surface area (percent littoral area [<4.6 m deep]), range of water temperature, Secchi depth, and water conductivity measured during fall and spring electrofishing of largemouth bass 200 mm TL or larger at 12 Minnesota lakes.

Lake	County	Surface area (ha)	Water temp-erature (°C)	Secchi depth (m)	Water conductivity (μS/cm)
Bass	Wright	88 (45)	13–22	3.0–4.7	236–265
Camp	Wright	44 (39)	12–21	2.6–4.9	267–320
Carnelian	Stearns	66 (39)	14–20	2.7–3.3	269–319
Dog	Wright	38 (76)	14–22	0.9–3.0	193–222
Elkhorn	Kandiyohi	35 (34)	13–23	1.9–3.4	341–386
Erie	Meeker	74 (46)	16–20	1.4–3.0	278–295
Games	Kandiyohi	208 (47)	16–22	1.1–4.1	347–392
Ida	Wright	32 (75)	12–21	1.7–3.8	252–293
Little Swan	Meeker	18 (44)	12–22	1.1–1.6	313–353
Pleasant	Stearns	90 (49)	11–20	1.4–4.3	212–273
St. Anna	Stearns	48 (27)	9–16	3.1–6.0	289–332
Stahls	McLeod	57 (59)	16–19	1.1–5.0	278–322

and night electrofishing was reversed during the second set of electrofishing samples. Additional day or night samples, at whichever time was more efficient for capturing largemouth bass, were collected in lakes in which more recaptures were needed for estimating population size. Water temperature (°C) and specific conductance (μS/cm at 25°C) at the surface and Secchi depth (nearest 0.1 m) were measured before each day sample in fall and spring. Water temperature was also measured before all night electrofishing when not coupled with day electrofishing. Water temperature was measured with a hand-held thermometer, and specific conductance was measured with a calibrated conductivity meter.

The primary electrofishing boat was equipped with a Coffelt VVP 2E electrofisher, powered by a 3.5-kW generator. The boat was the cathode, and a single stainless steel sphere (28 cm in diameter) was the anode. About 3 kW (based on volt and amp meters on the electrofisher) of pulsed DC electricity was continuously applied from the electrofisher at each lake. The entire shoreline of each lake was electrofished each time at depths from 0.5 to 1.5 m. Only offshore ends of boat docks were electrofished because they were typically removed from lakes in fall and installed in lakes in spring. One person netted stunned largemouth bass. Ten different people netted fish during this study, but the same person netted largemouth bass in 92% of the day samples and 77% of the night samples. The same person drove the boat for 98% of the day and night samples. The boat continually moved foward, except when multiple bass were encountered and the boat was stopped to allow the netter to capture all stunned largemouth bass. Time electrofished was recorded, and distance (km) electrofished was determined by measuring the shoreline contour on the appropriate lake map. All largemouth bass captured were measured (total length in millimeters). Fall-captured largemouth bass 200 mm TL and longer were marked by an anal fin clip, and spring-captured largemouth bass 200 mm TL and longer were marked by clipping the upper lobe of the caudal fin. At three lakes, a different electrofishing boat was used to collect additional largemouth bass in June for spring estimates of population size.

Population size of largemouth bass 200 mm TL and longer was estimated at each lake in fall and the following spring. Fall population sizes were estimated with a fall marking and spring recapture design using the modified Schnabel estimator (Ricker 1975; McInerny and Cross 1999). The marked sample consisted of all largemouth bass marked in fall, and the recapture sample consisted of all largemouth bass captured in spring. Each largemouth bass was checked for an anal fin clip, and each spring recapture sample was treated as an independent capture period. Spring estimates were made with a spring marking and spring recapture design and either the modified Schnabel or Chapman–Petersen estimator (Ricker 1975; McInerny and Cross 1999). For modified Schnabel estimates, each spring electrofishing sample was treated as an independent capture period, except those collected within 24 h after some largemouth bass were marked with caudal fin clips. For Chapman–Petersen estimates, the recapture sample was the last spring capture period when at least four spring-marked largemouth bass were recaptured, and the marked sample consisted of all largemouth bass previously marked with caudal fin clips. The modified Schnabel estimator was used if both estimators could be used. For each estimate, 95% confidence intervals were approximated by using the number of recaptures as a Poisson variable (Ricker 1975).

The CPH and CPK of largemouth bass 200 mm TL and longer were calculated for each electrofishing sample collected with the primary boat. Water conductivity was calculated from specific conductance and water temperature measurements (Reynolds 1996).

To determine if CPH and CPK show similar trends of CPUE, day CPK was plotted as a function of day CPH, and night CPK was plotted as a function of night CPH. Linear associations between CPH and CPK were described with Pearson correlations, and geometric mean functional regressions were developed if associations were strongly linear ($r > 0.9$; Jensen 1986). Furthermore, if CPH and CPK plots were strongly linear, then only CPH data will be reported.

Diel and seasonal effects on CPUE and density dependence on q were determined with analysis of covariance (ANCOVA) or analysis of variance (ANOVA) and regression analysis. Diel and season effects, and effects of diel $\times$ density, season $\times$ density, season $\times$ diel, and diel $\times$ season $\times$ density interactions on CPUE were determined with ANOVA. If no significant interactions were found, diel and seasonal effects on $\log_e$ mean CPUE were determined with ANCOVA (with $\log_e$ density as the covariate). The slope of the regression would equal q. If significant interactions were found, density dependence on q would be determined for each diel-season sampling period by regressing $\log_e$ mean CPUE as a function of $\log_e$ density among lakes. Catchability is not density dependent if slopes of the regression lines do not differ from one, decreases with density if slopes are below 1, and increases with density if slopes exceed 1 (Peterman and Steer 1981). The 95% confidence intervals of slopes were calculated from standard errors. Studentized residual plots were developed for each regression; those residuals exceeding ± 2 were considered outliers (SPSS 1998).

Effects of density, percent littoral area, water temperature, Secchi depth, and water conductivity on CPH and CPK among lakes were described with partial correlations when associations were linear or described with second- or third-degree polynomials when associations were nonlinear. Simple or multiple linear regressions were developed that included all variables significantly ($P < 0.05$) associated with CPH or CPK. Day and night CPH and CPK, density, and Secchi depths were lognormally distributed; therefore, they were transformed into natural logarithms. One was added to day CPH in spring before log transformation because at least one electrofishing sample contained no largemouth bass 200 mm TL or longer.

Results

Catch per h and CPK provided similar trends in CPUE of largemouth bass 200 mm TL and greater. Correlations between day CPK and day CPH ($r = 0.99$; df $= 47$; $P < 0.0001$) and night CPK and CPH ($r = 0.97$; df $= 62$; $P < 0.0001$) indicated strongly linear relationships (Figure 1). Geometric mean functional relationships were as follows: day CPK $= 0.49 \times$ day CPH $- 0.67$, and night CPK $= 0.51 \times$ night CPH $- 0.64$. Electrofishing speed averaged 2.4 km/h during the day and 2.1 km/h at night.

Electrofishing CPH and population density differed within and among lakes in both fall and spring. Night CPH exceeded day CPH in 9 of 12 lakes in fall and in all 12 lakes in spring (Table 2). Night CPH in spring exceeded night CPH in fall at all 12 lakes, but day CPH in spring exceeded day CPH in fall in 5 of 12 lakes. Estimates of population density in fall ranged from 8.0 to 48.3 fish/ha among lakes, and spring estimates ranged from 6.5 to 42.8 fish/ha (Table 2). Fall estimates exceeded spring estimates in 9 of 12 lakes; however, 95% confidence intervals of fall and spring estimates overlapped at each lake.

Mean night CPH exceeded day CPH ($F = 32.44$; df $= 1,44$; $P < 0.0001$), and mean spring CPH exceeded fall CPH ($F = 8.85$; df $= 1,44$; $P = 0.0048$). Probabilities of each interaction term exceeded 0.05. Electrofishing CPH increased nonlinearly with population density, the slope equaling 0.62 ± 0.27; thus, q decreased with increasing density. The Studentized residual of day CPH in fall from Elkhorn Lake was -3.8, which indicated that this datum was an outlier.

Environmental variables also varied within or among lakes, and these variables, along with percent littoral area and density of largemouth bass, affected day or night CPH. Water temperature ranged from 9°C to 23°C, Secchi depth ranged from 0.9 to 6.0 m, and water conductivity ranged from 193 to 392 μS/cm within and among lakes (Table 1). Day CPH in fall increased with decreasing water temperature and decreasing Secchi depth, but density did not explain a significant por-

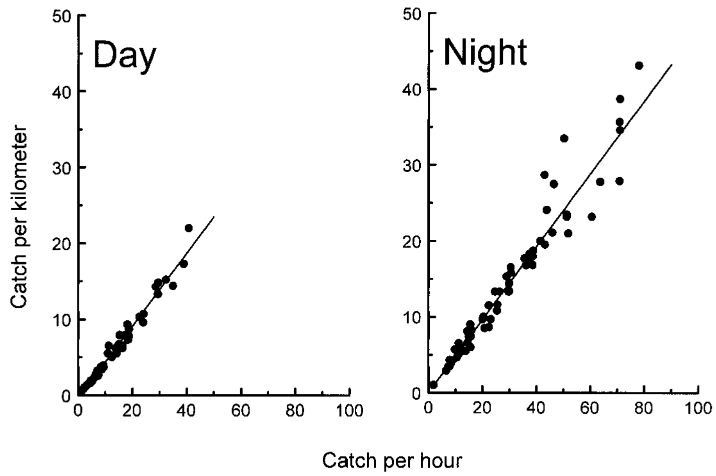

FIGURE 1.—Day electrofishing catch per kilometer (CPK) as a function of day electrofishing catch per hour (CPH) and night CPK as a function of night CPH of largemouth bass 200 mm TL and longer among 12 Minnesota lakes.

tion of day CPH in fall (Table 3). Day CPH in spring increased with increasing density and water conductivity and decreasing Secchi depth and water temperature. Night CPH in fall increased with increasing density, but unlike day CPH in spring, night CPH decreased with decreasing water conductivity. Night CPH in spring increased with increasing density and decreasing percent littoral area. These variables explained 75% of the variation in day CPH in spring; however, they explained less than 60% of the variation in night CPH in spring and day and night CPH in fall (Table 3).

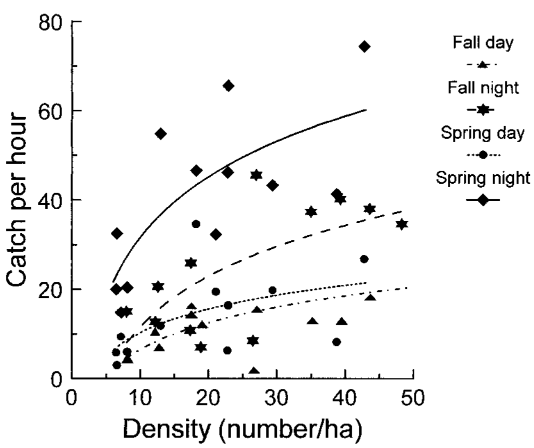

FIGURE 2.—Mean day and night electrofishing catch per hour of largemouth bass 200 mm TL and longer during fall and spring as a function of population density of largemouth bass 200 mm TL and longer among 12 Minnesota lakes.

Discussion

Catch per hour and CPK provided similar measures of CPUE because boat speeds changed little among samples, encounter rates of largemouth bass were not excessive, and electroshock response was marginally adequate. Besides being affected by density, seasonal and diel CPH was affected by gear saturation, temporal and spatial distribution patterns of largemouth bass, relative amounts of shallow water habitat, and avoidance behavior of largemouth bass. Density explained little variation in CPH because the range of densities among study lakes was narrow, and samples came from a diverse set of lakes. Data were not available to explain the variable and contradictory effects of water conductivity on CPH and the very low day CPH in fall at Elkhorn lake.

Linear relationships between CPH and CPK occurred because the same person drove the boat in a similar manner, numbers of largemouth bass encountered were usually not overwhelming, and the power applied was marginally adequate. Encounter rates averaged less than 1.3 largemouth bass/min; thus, the boat usually moved forward at a constant speed. Narcosis was minimally adequate because netters had to quickly react to capture largemouth bass stunned near the anode or they would recover and escape. Furthermore, stunned largemouth bass were not observed along the sides of the boat near the stern or behind the boat; thus, backing the boat to capture bass was not done. Power could not be increased to improve electroshock response because the generator was oper-

TABLE 2.—Day and night electrofishing catch per hour (CPH) ± standard error and population density estimates (95% confidence intervals in parentheses) of largemouth bass 200 mm TL and longer in fall and spring in 12 Minnesota lakes.

Lake	Day CPH	Night CPH	Population density (number/ha)
Fall			
Bass	4.6 ± 1.4	15.0 ± 2.7	8.0 (5.0–13.4)
Camp	18.2 ± 5.8	38.0 ± 4.8	43.6 (26.2–77.3)
Carnelian	7.0 ± 0.4	20.6 ± 5.0	12.6 (8.8–18.6)
Dog	10.6 ± 3.4	12.7 ± 1.1	12.2 (7.8–20.2)
Elkhorn	1.9 ± 0.6	8.5 ± 2.0	26.5 (14.6–53.0)
Erie	12.9 ± 5.9	37.4 ± 1.2	35.0 (24.2–52.4)
Games	12.2 ± 2.8	7.0 ± 0.4	18.9 (8.9–43.7)
Ida	34.2 ± 4.7	34.6 ± 4.0	48.3 (29.0–85.6)
Little Swan	16.3 ± 1.0	25.9 ± 2.4	17.4 (12.2–25.6)
Pleasant	13.0 ± 3.4	40.2 ± 3.0	39.3 (26.5–61.1)
St. Anna	15.6 ± 7.0	45.6 ± 16.5	27.0 (20.1–36.9)
Stahls	14.8 ± 3.4	10.8 ± 0.6	17.3 (10.0–32.4)
Spring			
Bass	3.0 ± 1.0	32.5 ± 6.1	6.6 (3.3–14.5)
Camp	8.2 ± 0.7	41.3 ± 2.5	38.8 (17.3–97.1)
Carnelian	11.8 ± 4.6	54.8 ± 8.8	13.0 (8.3–21.5)
Dog	9.4 ± 9.4	14.8 ± 3.7	7.2 (4.1–13.8)
Elkhorn	34.6 ± 6.0	46.6 ± 3.6	18.2 (11.3–30.9)
Erie	16.4 ± 2.2	65.6 ± 5.2	22.9 (14.2–39.0)
Games	5.8 ± 0.7	20.0 ± 3.4	6.5 (3.5–13.2)
Ida	19.8 ± 15.2	43.3 ± 13.8	29.4 (16.2–58.7)
Little Swan	19.5 ± 6.5	32.3 ± 9.2	21.1 (11.3–43.1)
Pleasant	6.3 ± 3.2	46.2 ± 5.3	22.8 (14.8–37.1)
St. Anna	26.8 ± 2.6	74.4 ± 3.6	42.8 (21.3–93.8)
Stahls	6.0 ± 1.3	20.4 ± 4.6	8.1 (4.2–17.1)

TABLE 3.—The strongest regression models using $\log_e$ density of largemouth bass 200 mm TL or longer, water temperature, $\log_e$ Secchi depth, water conductivity, and percent littoral area (depth < 4.6 m) to explain $\log_e$ electrofishing catch per hour of largemouth bass 200 mm TL and longer during the day or night in fall or spring among 12 Minnesota lakes (R^2 = adjusted R^2).

Independent variable	Coefficient	SE	*t*	*P*	Regression statistics	
					R^2	*P*
Fall day						
Constant	5.6155	0.7754	7.24	<0.0001	0.44	0.0009
Water temperature	−0.1563	0.0404	−3.87	0.0009		
Log_e Secchi depth	−0.9192	0.2807	−3.27	0.0036		
Fall night						
Constant	2.9330	1.5555	2.54	0.0191	0.28	0.0114
Log_e density	0.6837	0.2567	2.66	0.0146		
Water conductivity	−0.0073	0.0032	−2.29	0.0328		
Spring day						
Constant	1.0259	0.7728	1.33	0.2001	0.75	<0.0001
Log_e density	0.6814	0.1453	4.69	0.0002		
Water conductivity	0.0098	0.0021	4.69	0.0002		
Log_e Secchi depth	−0.8880	0.1947	−4.56	0.0002		
Water temperature	−0.1510	0.0398	−3.79	0.0012		
Spring night						
Constant	2.8546	0.4683	6.10	<0.0001	0.59	<0.0001
Log_e density	0.5128	0.1132	4.53	0.0001		
Percent littoral area	−1.4749	0.4959	−2.97	0.0061		

ating at maximum capacity. When electroshock responses are ideal, the relationship between CPH and CPK could deviate from linear if excessive numbers of largemouth bass forced the driver to stop the boat and allow the netter to catch all stunned fish. In these cases, effort expressed as time would increase, but effort expressed as distance would not. Boat speed during the day exceeded boat speed at night because fewer largemouth bass were usually encountered during the day and because the boat was driven more cautiously at night. Error in time measurements was probably less than error in distance measurements. Error in time measurements was low because power was continuously applied; however, distance measurements of lake contours did not include changes in distance caused by navigating around shallow bays, underwater bars, boat docks, emergent aquatic vegetation, and fallen trees.

Catchability decreased with increasing density of largemouth bass because narcosis of largemouth bass varied and netters were unable to capture all fish when multiple largemouth bass were encountered. Gear saturation causes density dependent *q* as fish densities increase (Peterman and Steer 1981). Other factors linked with density dependency of *q*, including limited searching area and time, schooling of fish, and nonrandom searching patterns, occur when fish densities are low and fisheries are being exploited (Peterman and Steer 1981; Arreguin-Sanchez 1996). Although schooling could have influenced *q* in this study, our sampling methodology remained the same regardless of catch.

Decreased *q* with increasing density of largemouth bass at least 200 mm TL occurred elsewhere but only when CPUE or population densities were similar or higher than in this study. Slopes ($\pm$95% confidence intervals) of $\log_e$ CPH–$\log_e$ population density or $\log_e$ CPK–$\log_e$ population density (spring mark and spring recapture designs) relationships among Ohio reservoirs (0.70 $\pm$ 0.15; Hall 1986), among zones in North and South Carolina (0.77 $\pm$ 0.15; McInerny and Degan 1993), and among South Dakota impoundments (0.75 $\pm$ 0.24; pulsed AC electrofishing; Hill and Willis 1994) were significantly below one; thus *q* decreased with increasing density. However, slopes of the same relationships were 1.24 $\pm$ 0.86 in a Wisconsin lake (Coble 1992), 0.91 $\pm$ 0.32 among South Dakota impoundments (pulsed DC electrofishing; Hill and Willis 1994), and 1.12 $\pm$ 0.50 among Texas ponds (Edwards et al. 1997); thus *q* was not density dependent. Using ANCOVA with $\log_e$ density as the covariate, $\log_e$ CPK in our study lakes was significantly lower than $\log_e$ CPK in North and South Carolina reservoirs. Log_e CPH in our study lakes did not differ from $\log_e$ CPH in Ohio reservoirs or a Wisconsin lake, but significantly exceeded $\log_e$ CPH in South Dakota impoundments and experimental ponds in Texas. Catch per h with pulsed AC electrofishing exceeded CPH with pulsed DC electrofishing in South Dakota impoundments (Hill and Willis 1994). The highest density observed in the South Dakota study was 34 times greater than the highest density in our study, and the highest density in the Ohio and Texas studies was 4–9 times higher than in our study. However, the highest density in our study was similar to that found in North and South Carolina reservoirs and exceeded the highest density in the Wisconsin study.

Spawning behavior caused largemouth bass to concentrate in shallow water in spring, which caused higher CPH in spring than in fall. Most (81%) spring samples were collected at water temperatures within the range (12–20°C) at which largemouth bass spawn. Furthermore, largemouth bass usually spawn at depths between 0.3 and 1.3 m (Heidinger 1975; Carlander 1977) where electrofishing is most effective. Largemouth bass often inhabit deeper (up to 5 m), more offshore habitats at other times of the year (Heidinger 1975; Warden and Lorio 1975; Carlander 1977; Kwak and Henry 1993). Spring concentrations of largemouth bass were also lower in lakes with relatively low amounts of shallow water habitat than in lakes with high amounts of shallow water habitat, which was suggested by the negative relationship between spring CPH and percent littoral area.

Seasonal differences in CPH could not be caused by changes in largemouth bass density because spring densities could not exceed fall densities. No recruitment of largemouth bass occurred between fall and spring because growth ceased during winter (Minnesota Department of Natural Resources, unpublished data). Furthermore, all except Stahls and Games lakes are closed systems; thus emigration or immigration of largemouth bass was impossible in 10 lakes. Differences between fall and spring density equaled natural overwinter mortality, which was unknown, because winter fishing mortality of largemouth bass among Minnesota lakes is negligible (median harvest = 0/ha; range = 0.0–0.7 per ha; Minnesota Department of Natural Resources, unpublished data). Relatively low numbers of recaptured largemouth bass (5–43 for fall estimates and 4–18 for spring estimates) prevented calculation of estimates precise enough to detect actual seasonal differences in density.

Night CPH exceeded day CPH, and day CPH increased with decreasing water clarity because largemouth bass were less likely to avoid the electrofishing boat. Furthermore, day CPH increased as water temperature decreased because cold water probably impeded avoidance behavior. In clear water (i.e., when netters could see the lake bottom), netters observed largemouth bass and other fish actively avoiding the boat, but behavior of largemouth bass in turbid waters or at night was not observable. Avoidance responses were probably reduced in colder water because metabolism in fish decreases with decreasing water temperature (Reynolds 1996). Although water clarity did not affect night CPH, water clarity less than that measured in this study could reduce the ability of netters to see and capture stunned largemouth bass at night (Reynolds 1996).

Diel differences in CPH were probably not associated with diel spatial distribution patterns of largemouth bass. Offshore to inshore migrations of largemouth bass occur just as frequently during the day as night (Miller 1975; Warden and Lorio 1975).

Density explained low amounts of CPH in this study because the range of densities was low and samples came from a morphologically diverse set of lakes. In this study, $\log_e$ density explained 48% of variation in $\log_e$ night CPH in spring, despite a sixfold difference in densities among lakes. In the Ohio, North Carolina, South Carolina, and South Dakota studies, the highest densities of largemouth bass 200 mm TL and larger were 11–67 times greater than the lowest densities (Hall 1986; McInerny and Degan 1993; Hill and Willis 1994). Consequently, $\log_e$ density explained 72–95% of the variation in $\log_e$ night CPH in spring of largemouth bass at least 200 mm TL. Log_e density explained 57% to 66% of variation in $\log_e$ night CPH in spring of largemouth bass at least 200 mm TL in the Wisconsin and Texas studies even though the highest densities were only 2–4 times greater than the lowest densities. Size, depth, and percent littoral area differed more among our study lakes than in either the Wisconsin or Texas studies. A single water body was sampled in Wisconsin, and all Texas ponds were of similar area (0.15–0.58 ha) and had similar depths (<1.2 m deep). Adjusting for differences in littoral area improved the relationship between density and night CPH in Minnesota lakes by 11%. Furthermore, coarse woody debris, emergent and submergent macrophyte composition and coverages, and substrates differed among the study lakes (Minnesota Department of Natural Resources, unpublished data).

Management Implications

Density dependency of *q* must be determined because if *q* greatly decreases with increasing density, large changes in densities may not be detectable with CPUE (Peterman and Steer 1981). In lakes similar to ours, CPUE determined with electrofishing during spring when largemouth bass are spawning provides the best index of density. Night electrofishing would be preferable over day electrofishing because CPH is higher and affected by fewer environmental variables.

Acknowledgments

We thank R. Binder, B. Brouillet, B. Carlson, D. Coahran, R. Hogg, B. Koenen, S. Roepke, K. Stauffer, and P. Wingate of the Minnesota Department of Natural Resources for assisting in electrofishing. Suggestions made by C. Anderson, J. Boxrucker, M. Allen, M.J. Hansen, and two anonymous reviewers improved this manuscript. This study was funded in part by the Federal Aid in Sport Fish Restoration, study 650, F-26-R, Minnesota.

References

Annett, C., J. Hunt, and E. D. Dibble. 1996. The complete bass: habitat use patterns of all stages of the life cycle of largemouth bass. Pages 306–314 *in* L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society, Symposium 16, Bethesda, Maryland.

Arreguin-Sanchez, F. 1996. Catchability: a key parameter for fish stock assessment. Reviews in Fish Biology 6:221–242.

Bailey, P. B., and D. J. Austen. 1987. Comparative analysis of fish populations in Illinois impoundments: gear efficiencies and standards for condition factors. Illinois Natural History Survey, Aquatic Biology Section Technical Report 87/14, Champaign.

Bettross, E. A., and D. W. Willis. 1988. Seasonal patterns in sampling data for largemouth bass and bluegills in a northern Great Plains impoundment. Prairie Naturalist 20:193–202.

Carlander, K. D. 1977. Handbook of freshwater fishery biology, volume 2. Iowa State University Press, Ames.

Coble, D. W. 1992. Predicting population density of largemouth bass from electrofishing catch per effort. North American Journal of Fisheries Management 12:650–652.

Dumont, S. C., and J. A. Dennis. 1997. Comparison of day and night electrofishing in Texas reservoirs.

North American Journal of Fisheries Management 17:939–946.

Edwards, C. M., R. W. Drenner, K. L. Gallo, and K. E. Rieger. 1997. Estimation of population density of largemouth bass density in ponds by using mark–recapture and electrofishing catch per effort. North American Journal of Fisheries Management 17: 719–725.

Gablehouse, D. W. 1987. Responses of largemouth bass and bluegills to removal of surplus largemouth bass from a Kansas pond. North American Journal of Fisheries Management 7:81–90.

Gilliland, E. 1987. Evaluation of Oklahoma's standardized electrofishing in calculating population structure indices. Proceedings of the Annual Conference Southeastern Association Fish and Wildlife Agencies 39(1985):277–287.

Hall, T. J. 1986. Electrofishing catch per hour as an indicator of largemouth bass density in Ohio impoundments. North American Journal of Fisheries Management 6:397–400.

Heidinger, R. C. 1975. Life history and biology of the largemouth bass. Pages 11–20 *in* H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Hill, T. D., and D. W. Willis. 1994. Influence of water conductivity on pulsed AC and pulsed DC electrofishing catch rates for largemouth bass. North American Journal of Fisheries Management 14:202–207.

Jensen, A. L. 1986. Functional regression and correlation analysis. Canadian Journal of Fisheries and Aquatic Sciences 43:1742–1745.

Kolz, A. L. 1989. A power transfer theory for electrofishing. U.S. Fish and Wildlife Service Fish and Wildlife Technical Report 22:1–11.

Kwak, T. J., and M. G. Henry. 1993. Fish mortality and behavioral impacts associated with largemouth bass fishing tournaments on Lake Minnetonka, Minnesota. University of Minnesota, Minnesota Cooperative Fish and Wildlife Research Unit, Final Report, St. Paul.

Malvestuto, S. P., and B. J. Sonski. 1990. Catch rate and stock structure: a comparison of daytime versus nighttime electric fishing on West Point Reservoir, Georgia–Alabama. Pages 210–218 *in* I. G. Cowx, editor. Developments in electric fishing. Cambridge University Press, Cambridge, UK.

McInerny, M. C., and T. K. Cross. 1999. Comparison of three mark–recapture designs for estimation population size of largemouth bass in Minnesota lakes. North American Journal of Fisheries Management 19:758–764.

McInerny, M. C., and D. J. Degan. 1993. Electrofishing catch rates as an index of largemouth bass population density in two large reservoirs. North American Journal of Fisheries Management 13:223–228.

Miller, R. J. 1975. Comparative behavior of centrarchid basses. Pages 85–94 *in* H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Peterman, R. M., and G. J. Steer. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Transactions of the American Fisheries Society 110:585–593.

Reynolds, J. B. 1996. Electrofishing. Pages 221–253 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Ricker, W. E. 1975. Computations and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Sammons, S. M., and P. W. Bettoli. 1999. Spatial and temporal variation in electrofishing catch rates of three species of black bass (*Micropterus* spp.) from Normandy Reservoir, Tennessee. North American Journal of Fisheries Management 19:454–461.

Simpson, D. E. 1978. Evaluation of electrofishing efficiency for largemouth bass and bluegill populations. Master's thesis. University of Missouri, Columbia.

SPSS 1998. SYSTAT 80 statistics. SPSS Chicago.

Van den Avyle, M. J. 1976. Analysis of seasonal distribution patterns of young largemouth bass (*Micropterus salmoides*) by use of frequency-of-capture data. Journal of the Fisheries Research Board of Canada 33:2427–2432.

Warden, R. L., Jr., and W. J. Lorio. 1975. Movements of largemouth bass (*Micropterus salmoides*) in impounded waters as determined by underwater telemetry. Transactions of the American Fisheries Society 104:696–702.