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[Article]

Variable Responses of Channel Catfish Populations to Stocking Rate: Density-Dependent and Lake Productivity Effects

PAUL H. MICHALETZ*

Missouri Department of Conservation, 1110 South College Avenue, Columbia, Missouri 65201, USA

Abstract.—Put–grow–take fisheries for channel catfish *Ictalurus punctatus* are popular in many small impoundments but are costly because fingerling (>175 mm total length [TL]) stockings are usually necessary to maintain these fisheries. Stocking the appropriate number of fish is important for making efficient use of these hatchery products and for creating desirable fisheries. The effect of stocking rate on channel catfish populations was evaluated by examining 60 small impoundments that had been assigned to one of three annual stocking rates (12, 37, or 74 fingerlings/ha). As channel catfish stocking rate increased, catch per unit effort (CPUE, number of fish per 3-d tandem hoop-net series) and total annual mortality increased, while proportional size distribution (PSD, formerly proportional stock density), PSD for fish 508 mm or longer, relative weight, and annual growth increments decreased; these results suggest that density-dependent processes were important. However, 10-fold differences in CPUE and threefold differences in size structure indices and growth increments were common among lakes stocked at the same rate. Further analysis revealed that CPUE and lake productivity (indexed by chlorophyll-*a* concentration) were important variables in explaining differences in size structure, condition, and growth among populations. Because of the highly variable response, appropriate stocking rates need to be determined for each lake. I propose comparing growth increments of individuals within a lake to a statewide standard to determine the relative growth rate for the lake. Stocking rates should be reduced for channel catfish populations that are growing slowly but could be increased for fast-growing populations.

Channel catfish *Ictalurus punctatus* provide popular sport fisheries in many small impoundments (hereafter termed lakes) throughout the midwestern and southern United States (Michaletz and Dillard 1999). Most populations are maintained by stocking of fingerlings (>175 mm total length [TL]) because natural recruitment is usually negligible as a result of predation (Marzolf 1957; Krummrich and Heidinger 1973; Spinelli et al. 1985; Storck and Newman 1988). These stockings represent a substantial investment of fiscal and human resources for many management agencies (Michaletz and Dillard 1999). Thus, it is important to make the most efficient use of this hatchery product. Overstocking can lead to slow growth and poor condition of channel catfish (Hill 1984; Mitzner 1999; Mosher 1999), apparently through density-dependent mechanisms, and may result in reductions in prey resources and growth of sympatric fish species (Crance and McBay 1966; Mitzner 1989; Michaletz et al. 2005; Michaletz 2006a). Conversely, stocking few fingerlings may result in fast-growing channel catfish but may not provide a viable fishery.

Channel catfish stocking rates for small lakes have varied greatly among and within resource agencies (Michaletz and Dillard 1999). Because channel catfish populations in small lakes have been difficult to sample (Michaletz and Dillard 1999), appropriate stocking rates have not been determined for individual lakes. Without population data, many agencies have used the same stocking rate for most of their small lakes; however, some agencies have adjusted stocking rates for angler harvest (Austen et al. 1997; Michaletz and Dillard 1999). In Missouri, annual channel catfish stocking rates were reduced from 74 to 124 fingerlings/ha in the 1960s and 1970s to 25–49 fingerlings/ha in the 1980s and 1990s in an effort to improve growth rates and size structure of channel catfish populations (Eder et al. 1997). However, these reductions were based on gill-net sampling in relatively few lakes; most stocked lakes had not been sampled (Eder et al. 1997).

Recent channel catfish gear evaluation studies have made more credible stocking rate evaluations possible for this species. Sullivan and Gale (1999) and Michaletz and Sullivan (2002) found that cheese-baited hoop nets fished in tandem for two or three days effectively captured channel catfish in lakes. This method enabled the collection of sufficient numbers of channel catfish for population assessment in most lakes and was not size-biased for fish larger than 250 mm TL (Michaletz and Sullivan 2002).

The objectives of this study were (1) to determine if channel catfish population characteristics were related to stocking rate and (2) to examine potential density-

* E-mail: paul.michaletz@mdc.mo.gov

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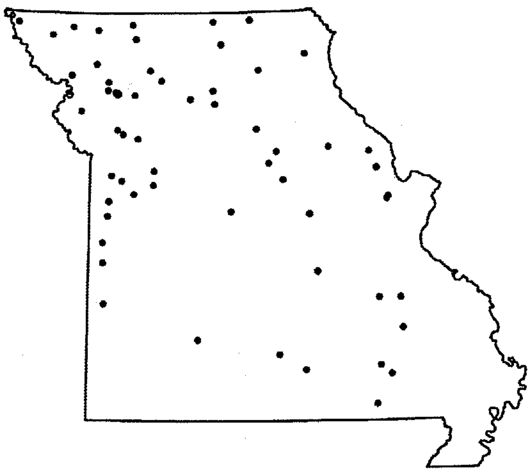

FIGURE 1.—Outline of the state of Missouri showing the locations of the 60 study lakes.

TABLE 1.—Limnological characteristics of the 60 Missouri study lakes. Mean values for water quality variables are the averages of grand means for each lake.

Variable	Mean ± SE	Range
Surface area (ha)	42 ± 7	5–332
Secchi depth (m)	1.1 ± 0.1	0.3–3.0
Chlorophyll *a* (mg/m^3)	30 ± 4	2–161
Total phosphorus (mg/m^3)	57 ± 5	7–183

dependent and lake productivity effects on these populations. Although, intuitively, channel catfish abundance should increase with increased stocking rate, abundance may also vary substantially as a result of differences in fishing and natural mortality. Among small lakes in Missouri, channel catfish harvest (fish/ha) varied over 100-fold (Michaletz and Stanovick 2006), and exploitation (proportion of fish harvested) varied over 10-fold (Michaletz et al. 2008). Neither was closely associated with stocking rate. In addition to fish density, lake productivity may also affect population characteristics of channel catfish because it influences macroinvertebrate community structure and biomass (Mosher 1999; Michaletz et al. 2005) and fish growth (Mosher 1999). Macroinvertebrates are common prey for channel catfish (Hubert 1999; Michaletz 2006b), and Mosher (1999) suggested that stocking rates of channel catfish could be higher in more productive lakes because these lakes supported more macroinvertebrates and faster channel catfish growth than less productive lakes. An understanding of the influences of channel catfish stocking rate, abundance, and lake productivity on population dynamics of channel catfish will enable managers to estimate appropriate stocking rates for individual lakes.

Methods

Study lakes.—The 60 study lakes were located throughout Missouri, with about one-half of them in the northwestern quarter of the state (Figure 1). The lakes varied in size from 5 to 332 ha (Table 1) and supported put–grow–take fisheries for channel catfish. The fisheries were regulated with a four-catfish (channel catfish, blue catfish *I. furcatus*, and flathead catfish *Pylodictis olivaris* combined) daily creel limit, and fishing was restricted to pole-and-line only (i.e., prohibiting trot or limb lines, jugs, etc.). Two of the study lakes had a minimum size limit of 381 mm TL on channel catfish; there was no size limit on channel catfish in the other lakes. In addition to channel catfish, bluegill *Lepomis macrochirus* and largemouth bass *Micropterus salmoides* were common in all of the study lakes and provided important sport fisheries. Crappies *Pomoxis* spp., gizzard shad *Dorosoma cepedianum,* redear sunfish *L. microlophus*, and common carp *Cyprinus carpio* were also common in some lakes.

Water quality.—Water quality data were acquired through a contract with the Limnology Laboratory, University of Missouri, Columbia. Water quality surveys were conducted mostly during 2001 and 2002, but surveys conducted in multiple years ($\geq$4 years) immediately before 2001 provided data for some lakes. Surface water samples were analyzed for total phosphorus (TP; Prepas and Rigler 1982) and chlorophyll *a* (CHLA; Knowlton 1984; Sartory and Grobbelaar 1984). Secchi depth was measured during each survey. Each lake was sampled four times per year between May and August, and data from these samples were averaged to estimate annual means for each water quality variable. These annual means were then averaged across sampling years to provide a grand mean for each lake.

Stocking.—Since 1998, each lake was stocked annually in late September to mid-October with large (mean TL > 220 mm) channel catfish fingerlings at either 12 fish/ha (low, 22 lakes), 37 fish/ha (medium, 22 lakes), or 74 fish/ha (high, 16 lakes). Prior to 1998, stocking rates varied from 0 to 74 fingerlings/ha (median = 25 fingerlings/ha) and were inconsistent among years for many lakes. For a typical stocking, 80% of the stocked fingerlings exceeded 200 mm TL (Eder et al. 1997), but fingerlings have ranged in size from 125 to 450 mm TL. The stocking rates used in this study represent the range of stocking rates currently used by the Missouri Department of Conservation (MDC), although the high stocking rate is used infrequently. With the exception of four high-stocking-rate lakes that were overstocked in the fall of 2000, the lakes consistently received the appropriate number of fish. No adjustments were made for these overstockings because they did not affect the results of this study based on preliminary analyses. Although similar in size, fingerling channel catfish stocked into lakes in the northern half of the state usually were reared for two growing seasons (age 1), whereas channel catfish stocked in lakes in the southern half usually were reared for only one growing season (age 0). However, 14 lakes received both age-0 and age-1 fish, either in different years or in the same year.

Population sampling.—The channel catfish population in each lake was sampled in either May or June with cheese-baited tandem hoop-net series in 2001, 2003, and 2005. These short-bridled series are described in detail by Michaletz and Sullivan (2002). Each series consisted of three 0.8-m-diameter hoop nets with 25-mm-bar mesh fished in tandem for 3 d before being retrieved. Each net was baited with about 4 kg of waste cheese, and sets were made on the bottom in water shallower than the thermocline. The number of series used varied with the surface area of each lake; four series were used in lakes less than 20.2 ha, six series in those 20.2–60.6 ha, and eight series were used for those 60.7 ha or larger. Sample sites were randomly chosen each year from the littoral area of each lake.

On retrieval, all fish were removed from the nets, and all channel catfish were counted and measured (TL, nearest 2.5 mm). For each lake, 5 (2001) or 10 (2003 and 2005) channel catfish per 25-mm TL were weighed (nearest 28 g or less), and their left pectoral spines were removed for aging purposes. Catches of channel catfish were recorded separately for each net within a series but were combined to calculate catch per unit effort (CPUE; number of channel catfish per 3-d tandem series) for each series. After processing, all live fish were returned to the lake. Mortality of channel catfish was negligible for most sampling events.

Population variables.—Relative abundance (CPUE), size structure indices, and an index of body condition were computed for channel catfish populations for each sampling year. Proportional size distribution (PSD, formerly proportional stock density; Guy et al. 2007) was calculated according to Anderson (1980) and Gabelhouse (1984), using 280 mm TL as stock size and 410 mm TL as quality size. Proportional size distribution for fish 508 mm TL and larger (PSD_{508}) was computed instead of PSD for "preferred" size fish, because "preferred" size channel catfish of 610 mm TL or greater (Gabelhouse 1984) were uncommon or absent in most lakes. Relative weight (W_r), a body condition index, was computed for stock size and larger fish by means of the standard weight equation reported by Mitzner (1999). While it is possible that estimates of W_r may be inflated as a result of channel catfish ingesting large quantities of bait within the hoop nets, I found no differences in length–weight relationships of channel catfish caught with either cheese-baited hoop nets or gill nets (Michaletz, unpublished data).

The use of mean TL at age to compare growth rates among channel catfish populations was problematic for two reasons. First, mean TL at age was very imprecise because individual lengths were highly variable within an age-class because of the broad size range of stocked fingerlings. Second, because fish were stocked at different ages (age 0 or 1), fish of the same age would have lived in the lakes for different lengths of time. To provide a more valid comparison, the last annual growth increment was compared to the initial TL of the fish at the beginning of the growing season for each lake and year with linear regression. Only data for 2003 and 2005 were used because growth increments were not measured for 2001 samples. Comparing growth increments based on size is appropriate because fish growth is more closely related to size than to age (Gerking and Raush 1979; Gutreuter 1987). The last growth increment and the initial TL for each fish were determined from back-calculations (DISBCAL software, Missouri Department of Conservation 1989), using measurements of annuli in pectoral spine sections. Measurements were made on basal spine sections, while ages were determined from articulating process sections to ensure that all annuli were counted (Marzolf 1955; Buckmeier et al. 2002). The predicted growth increment (INC) for fish with initial lengths of 280 mm (stock size, INC_{280}) and 410 mm (quality size, INC_{410}) was estimated from these regressions and used to compare growth among lakes and years; this is similar to methods used by Putman et al. (1995) and Shoup et al. (2007). Fish from the previous fall's stocking were excluded from the analysis based on their age, because their last growth increment occurred while in the rearing ponds.

Total annual mortality (A) was computed from samples collected only in 2005 for those lakes that had been consistently stocked with the same age fish (i.e., either age-0 or age-1, but not both) each year and had a minimum sample size of 30 fish. Within each lake, fingerling channel catfish had been stocked at the same rate for seven consecutive years prior to the 2005 sample; thus, I assumed that recruitment was constant throughout that period. While natural recruitment may have occurred in some lakes, it was never documented and probably was insignificant relative to the number of fish stocked. The average mortality rate was estimated for these seven year-classes. Abundance of each age was estimated by counting annuli on pectoral spine sections (articulating process), constructing an age–length key using aged fish, and then applying this key to the entire sample to estimate CPUE for each age. Catch curves were developed by plotting the $\log_e(\text{CPUE} + 1)$ of each age versus age. In some cases, not all seven year-classes could be included in the catch curve because the youngest age-classes were not fully recruited to the sampling gear. Fish less than 250 mm TL are not fully recruited to the hoop nets (Michaletz and Sullivan 2002). Weighted linear regression using FAST software (Slipke and Maceina 2001) was conducted to estimate instantaneous mortality (Z), and A was computed as $A = 1 - e^{-Z}$ (Ricker 1975).

Analysis.—Differences in lake characteristics among the groups assigned to the three channel catfish stocking rates could confound the analysis and interpretation of the effects of stocking rate on channel catfish populations. To determine if differences in lake characteristics existed among the lakes stocked at different rates, analysis of variance (ANOVA) was used to compare surface area, TP, CHLA, and Secchi depth among the lakes stocked at the three rates. Prior to analysis, all lake variables were $\log_e(X)$-transformed to meet the assumptions of parametric analysis. Transformations were successful at normalizing the data (Shapiro–Wilk test, all $P > 0.18$, except for CHLA for the medium stocking rate where $P = 0.02$). These and all following statistical tests were considered significant at P-values ≤ 0.05.

The effect of stocking rate on population characteristics of channel catfish, other than mortality, was analyzed using repeated-measures linear mixed models (procedure MIXED, SAS Institute 2005). Mixed models are more appropriate than ordinary least-squares models for analyzing data that have a hierarchical structure and can properly handle both fixed and random effects (Wagner et al. 2006). Mixed models also appropriately handle missing data (SAS Institute 2005), which occurred for some of the models. For these models, stocking rate, year, and their interaction were fixed effects, and lake nested within stocking rate was considered a random effect. For significant models, pairwise comparisons of least-square means for fixed effects were made by means of Tukey–Kramer adjusted P-values. The first-order autoregressive covariance structure was used for all models. Preliminary analyses revealed that this structure fit the data better than four other tested covariance structures. For the CPUE model, $\log_e(X + 1)$-transformed CPUE for each tandem series was used in the analysis. Mean W_r, INC_{280}, and INC_{410} were $\log_e(X)$ transformed, and lakes were included in these models if these estimates were based on at least 10 fish for a year. Size structure indices were expressed as proportions and transformed with arcsine ($X^{0.5}$), and lakes were included in the analyses if there were at least 30 fish sampled to estimate the indices for a year. Although sample sizes exceeding 30 individuals are usually required for precise estimates of size structure indices (Gustafson 1988; Miranda 1993, 2007), sample sizes greater than 30 would have resulted in removing most of the low-stocking-rate lakes from the analysis. For example, only 13 of the 22 low-stocking-rate lakes met the 30-fish sample size criteria in 2005 (see Figure 2 for sample sizes). I chose to risk having somewhat

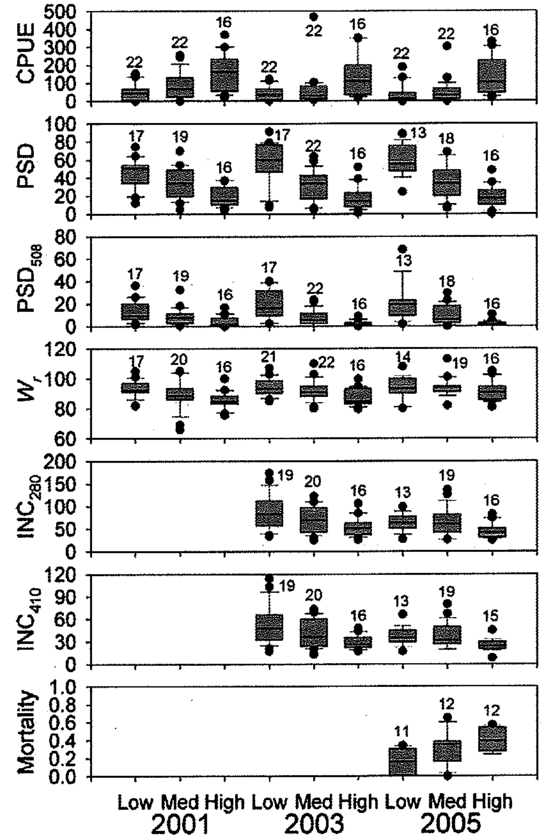

FIGURE 2.—Box plots of mean CPUE, PSD, PSD_{508}, W_r, INC_{280}, INC_{410}, and total annual mortality for channel catfish populations stocked annually at low (12 fingerlings/ha), medium (37 fingerlings/ha), or high (74 fingerlings/ha) stocking rates. Shaded boxes indicate the interquartile range, horizontal lines within the box indicate the median, the vertical lines extend from the 10th to 90th percentiles, and the individual dots indicate values outside of those percentiles. Numbers on the top of each box indicate the number of lakes included in the box plot. Growth increments were not calculated in 2001 and mortality was only estimated from 2005 samples.

less precise estimates in order to include more of the study lakes. One-way ANOVA was used to determine the relation of stocking rate to mortality. Mortality was expressed as a proportion and arcsine ($X^{0.5}$) transformed for analysis.

Other factors besides stocking rate (e.g., channel catfish density, lake productivity, and lake size) may also influence population characteristics. To examine these effects, stepwise linear regression was used to evaluate the relations between PSD, PSD_{508}, mean W_r, INC_{280}, INC_{410}, and mortality, with CPUE, TP, CHLA, Secchi depth, and lake size as potential independent variables using an entrance and exit criteria of $P = 0.10$. Except for mortality, separate regression analysis was conducted for 2003 and 2005; however, it is important to note that the same water quality and lake size data were used in the analysis for both years. Regressions were not conducted for 2001 because growth increments were not measured and populations may not have adjusted to the stocking rates implemented in 1998. Except for mortality, mean-transformed CPUE was averaged across 2001 and 2003 for the 2003 analysis and across 2003 and 2005 for the 2005 analysis in order to estimate the average conditions in which population characteristics developed. Growth estimated from 2003 and 2005 samples occurred in 2002 and 2004, respectively. For the mortality model, mean-transformed CPUE was averaged across 2001, 2003, and 2005 because mortality was estimated using all year-classes stocked since 1998. Lakes were included in regression analysis if they met the minimum sample size requirements of the mixed and ANOVA models, and data were transformed as required by those models.

Results

Lake Characteristics

Trophic state of the study lakes ranged from oligotrophic to hypereutropic based on criteria by Jones and Knowlton (1993). Although lake characteristics varied among the study lakes (Table 1), they were, overall, similar among the groups assigned to the three channel catfish stocking rates. None of the measured variables, including lake surface area ($F = 0.06$; df = 2, 57; $P = 0.94$), Secchi depth ($F = 0.35$; df = 2, 57; $P = 0.71$), TP ($F = 0.05$; df = 2, 57; $P = 0.95$), and CHLA ($F = 0.28$; df = 2, 57; $P = 0.76$) differed among the three groups of lakes.

Population Variables

About 79,000 channel catfish were collected during this study. On average, 436 (SE = 39) channel catfish were collected from each lake during a year, but this number varied from 0 to 2,757 fish. Population variables also differed substantially among the lake–year combinations. For example, mean CPUE ranged from 0 to 469 fish/tandem hoop-net series, PSD ranged from 0.3% to 91%, PSD_{508} ranged from 0% to 68%, and mean W_r ranged from 66 to 113 (Figure 2). Growth increments varied sevenfold or more, with INC_{280} ranging from 25 to 174 mm and INC_{410} ranging from 8 to 114 mm (Figure 2). Of the 103 regression equations used to estimate growth increments, 97 were significant ($P \leq 0.05$) and another two were marginally significant ($P \leq 0.10$). Initial TL explained from 0% to 93% of the variation in growth increments, with a median value of 57%. Mortality ranged from 0% to 65% among lakes (Figure 2). Of the 35 regressions equations used to estimate mortality, 18 were significant ($P \leq 0.05$) and another nine were marginally significant ($P \leq 0.10$). The median r^2 for all equations was 0.70, with a range of 0.02–0.97.

Stocking Rate Effects

As channel catfish stocking rate increased, CPUE and mortality increased, while PSD, PSD_{508}, W_r, INC_{280}, and INC_{410} decreased (Figure 2). Stocking rate was significant in mixed models for all population characteristics (Table 2). There were also differences among years for CPUE, W_r, INC_{280}, and INC_{410} but not for PSD and PSD_{508}. In general, values were most different between 2001 and 2005 and were intermediate for 2003. For growth models, increments were larger for 2003 samples than for 2005 samples. The interaction term between stocking rate and year was significant for PSD and PSD_{508} because the magnitude of stocking rate effect varied across years. Mortality increased with stocking rate ($F = 6.00$; df = 2, 32; $P = 0.006$), with values for the low stocking rate being significantly lower than those for the medium stocking rate (pairwise comparison of least-square means, $P = 0.04$) and the high stocking rate ($P = 0.002$); values for the medium and high stocking rate were not significantly different ($P = 0.18$).

While the stocking rate for channel catfish influenced population characteristics on a broad scale, there was considerable variability in these characteristics among lakes stocked at the same rate. Tenfold differences in CPUE and threefold differences in growth increments and size structure indices were common among lakes within a stocking rate. While most channel catfish populations in lakes stocked at the low rate exhibited low abundance and fast growth, such as in Deer Ridge Lake (Figure 3), others had moderately high abundance and moderate growth (e.g., Indian Creek Lake), and some had low abundance and slow growth (e.g., DiSalvo Lake). Populations in Brookfield and Willowbrook lakes

TABLE 2.—Results of repeated-measures linear mixed models for the effects of channel catfish stocking rate, year, and their interaction on catch-per-unit-effort (CPUE), proportional size distribution (PSD), PSD for 508-mm and larger fish (PSD_{508}), mean relative weight (W_r), and growth increments for 280-mm (INC_{280}) and 410-mm (INC_{410}) channel catfish. All variables were transformed (see text for details). Numerator degrees of freedom were two for rate and year and four for the interaction term, except for growth increment models where degrees of freedom equaled one for year and two for the interaction term because estimates were not made for 2001. Denominator degrees of freedom (df) are listed. For post-hoc tests, rates or years with no letters in common indicate significant differences at $P \leq 0.05$.

Variable	Effect	df	*F*	*P*	Post-hoc tests		
CPUE	Rate	57	11.91	<0.0001	Low z	Med z	High y
	Year	919	15.41	<0.0001	2001 z	2003 y	2005 x
	Rate × year	919	1.44	0.22			
PSD	Rate	53	22.42	<0.0001	Low z	Med y	High x
	Year	92	2.21	0.12	2001 z	2003 z	2005 z
	Rate × year	92	2.55	0.04			
PSD_{508}	Rate	53	20.75	<0.0001	Low x	Med y	High z
	Year	92	0.64	0.53	2001 z	2003 z	2005 z
	Rate × year	92	2.49	0.05			
W_r	Rate	56	6.55	0.003	Low z	Med zy	High y
	Year	96	3.74	0.03	2001 z	2003 zy	2005 y
	Rate × year	96	0.89	0.47			
INC_{280}	Rate	53	6.10	0.004	Low z	Med zy	High y
	Year	44	10.05	0.003		2003 z	2005 y
	Rate × year	44	0.23	0.79			
INC_{410}	Rate	53	8.36	0.0007	Low z	Med z	High y
	Year	43	6.42	0.02		2003 z	2005 y
	Rate × year	43	0.78	0.46			

exhibited characteristics typical of high-stocking-rate lakes with high CPUE and slow growth (Figure 3). However, some populations in high-stocking-rate lakes were less abundant and grew relatively fast (e.g., Rothwell Park Lake). Similar variation occurred among populations stocked at the medium rate.

Density-Dependent and Lake Productivity Effects

Population characteristics of channel catfish were influenced by density-dependent and lake productivity effects. Stepwise regression equations revealed that both CPUE and CHLA commonly explained significant portions of the variance in population characteristics (Table 3), except for mortality. No independent variable was significant in explaining variation in mortality. For other characteristics, CPUE usually explained a higher proportion of the variation than did CHLA. Size structure, condition, and growth decreased with increasing CPUE and increased with increasing CHLA. However, except for growth increments, these variables explained only about one-third or less of the variation in these characteristics. For growth increment models, CPUE, CHLA, and sometimes lake size explained about one-half of the variation. Secchi depth and TP did not enter any of the models except for the 2005 INC_{410} model. However, because TP and Secchi depth were both highly correlated with CHLA ($P < 0.0001$) and CHLA explained more variation, TP and Secchi depth were excluded from the final model.

Discussion

Overall, as stocking rate increased the relative abundance and mortality of channel catfish increased, and condition, growth, and size structure decreased. However, population responses to stocking rate were quite variable, probably because of differing mortality rates and lake productivity. Exploitation was highly variable and unrelated to stocking rates in small lakes in Missouri (Michaletz et al. 2008), which contributed to differences in population density among lakes stocked at the same rate. Differences in density led to varying degrees of density dependency on growth and condition. At low densities, channel catfish grew well in most lakes, even though some, such as Rothwell Park Lake (Figure 3), were stocked at the high rate. At high densities, channel catfish grew slowly in most lakes similar to results from previous studies (Hubert 1999; Mitzner 1999; Mosher 1999), possibly because they depleted their food supply (Michaletz et al. 2005). In this study, CPUE explained more of the variation in population characteristics than any other measured variable, suggesting that density was an important determinant of population characteristics. However, lake productivity, as indexed by CHLA, also influenced channel catfish populations. Channel catfish tended to grow faster, were in better condition, and exhibited better size structure in more productive lakes at a given level of CPUE. For example, fish grew faster in more-productive Rothwell Park Lake (CHLA = 33 mg/m^3) than in less-productive DiSalvo Lake (CHLA =

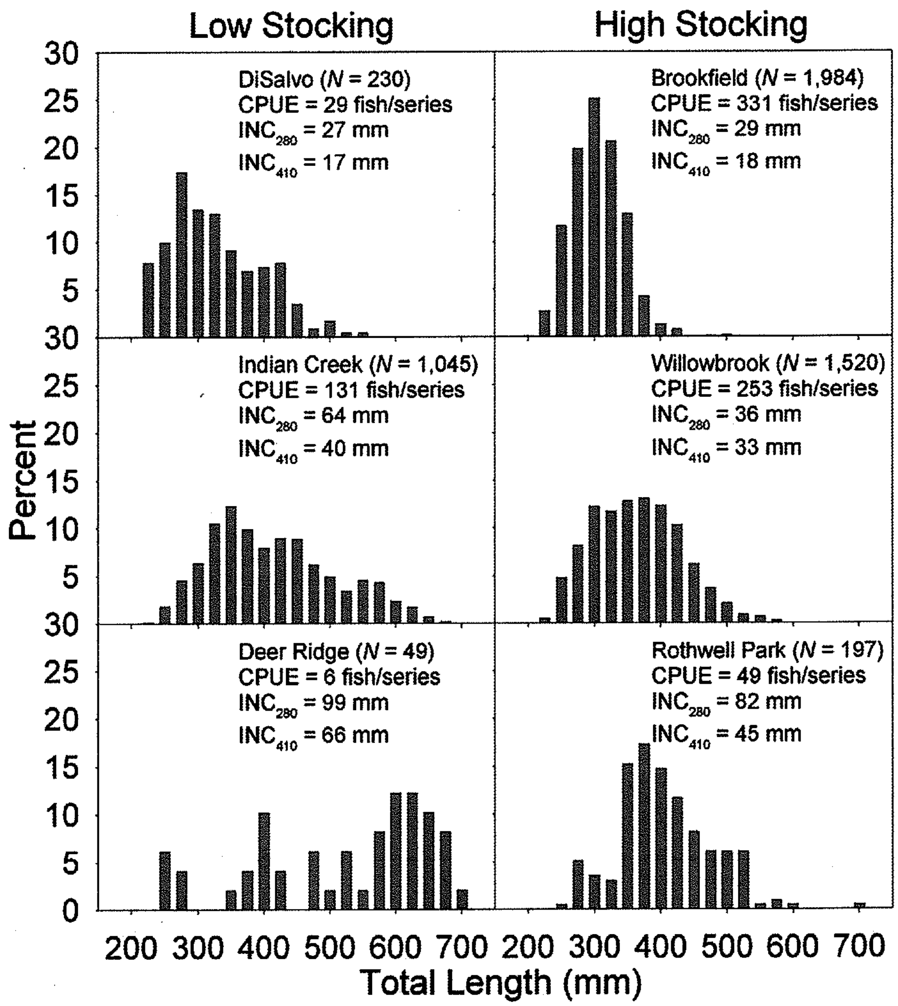

FIGURE 3.—Examples of length frequencies of channel catfish in lakes stocked at the low (12 fingerlings/ha) and high (74 fingerlings/ha) stocking rate sampled in 2005. Sample size (*N*), CPUE, INC_{280}, and INC_{410} are also indicated.

7 mg/m^3), even though CPUE was somewhat higher for Rothwell Park Lake (Figure 3). Previous studies have also documented improved growth and size structure with increasing fertility (Cole et al. 1991; Mosher 1999; Shephard and Jackson 2006). In contrast, Durham et al. (2005) did not find a relationship between growth and the morphoedaphic index, a measure of lake productivity, for channel catfish in Texas reservoirs.

Increasing growth and condition of channel catfish with increasing water fertility is probable because food abundance may increase with fertility (Mosher 1999). Michaletz et al. (2005) found that biomass of soft-bodied macroinvertebrates (excluding mollusks) increased with CHLA for a subset of lakes used in this study. Using data collected during 2002 from Michaletz et al. (2005), I found a positive relationship between soft-bodied macroinvertebrate biomass and channel catfish growth during that year (INC_{280}, Pearson's $r = 0.62$, $P = 0.002$, $N = 23$ lakes; INC_{410}, $r = 0.67$, $P = 0.0005$, $N = 23$ lakes). Thus, change in prey abundance with lake productivity is probably the underlying cause of the positive relationship between channel catfish growth and lake productivity.

Even after accounting for differences in density and lake productivity among lakes, there was a considerable amount of unexplained variation in population characteristics. Other lake characteristics that were unmeasured in this study (i.e., dissolved oxygen and temperature regimes, substrate type, morphology, prey community composition and abundance, and watershed variables) have been shown to affect channel catfish

TABLE 3.—Stepwise regression models explaining variance in channel catfish PSD, PSD_{508}, W_r, INC_{280}, and INC_{410}, using CPUE, chlorophyll-*a* concentration (CHLA), total phosphorus, Secchi depth, and lake surface area (ha) as potential independent variables. All variables were transformed prior to analysis (see text for details).

Model	R^2	N	Parameter	Estimate	Partial r^2	P
			2003			
PSD	0.15	55	Intercept	0.499		0.006
			CHLA	0.103	0.100	0.02
			CPUE	−0.057	0.047	0.09
PSD_{508}	0.19	55	Intercept	0.230		0.04
			CHLA	0.071	0.106	0.02
			CPUE	−0.050	0.086	0.02
W_r	0.34	59	Intercept	4.639		<0.0001
			CPUE	−0.036	0.342	<0.0001
INC_{280}	0.57	55	Intercept	4.776		<0.0001
			CPUE	−0.311	0.472	<0.0001
			CHLA	0.165	0.094	0.002
INC_{410}	0.45	55	Intercept	3.910		<0.0001
			CPUE	−0.265	0.307	<0.0001
			CHLA	0.209	0.140	0.0007
			2005			
PSD	0.29	47	Intercept	0.733		<0.0001
			CPUE	−0.123	0.197	0.002
			CHLA	0.108	0.086	0.03
PSD_{508}	0.34	47	Intercept	0.346		0.008
			CPUE	−0.103	0.232	0.0006
			CHLA	0.094	0.111	0.009
W_r	0.13	49	Intercept	4.524		<0.0001
			CPUE	−0.019	0.075	0.06
			CHLA	0.023	0.059	0.08
INC_{280}	0.58	48	Intercept	4.942		<0.0001
			CPUE	−0.277	0.485	<0.0001
			ha	−0.106	0.059	0.02
			CHLA	0.113	0.035	0.06
INC_{410}	0.42	47	Intercept	3.357		<0.0001
			CPUE	−0.214	0.235	0.0005
			CHLA	0.259	0.187	0.0005

(Hill 1984; Hubert 1999; Mosher 1999; Durham et al. 2005) and may account for additional variation among these populations. Temporal variation in population parameters may also be explained by these variables. For example, the slower growth that occurred in 2004, relative to 2002, may have been a result of the exceptionally cool summer temperatures in 2004. Optimum temperature for growth of channel catfish is about 30–32°C (Kilambi et al. 1971; Andrews and Stickney 1972), and water temperatures were probably below optimum for much of the growing season in 2004, when air temperatures in Missouri averaged only 21.9°C from June through September, compared to 24.2°C in 2002 (computed from data in NOAA 2005a, 2005b).

The positive relationship between annual mortality and stocking rate was unexpected, because channel catfish harvest and exploitation were previously not strongly related to stocking rate (Michaletz and Stanovick 2006; Michaletz et al. 2008). Fishing mortality is often a larger component of total mortality than is natural mortality for put-grow-take fisheries (Hanson 1986; Eder and McDannold 1987; Santucci et al. 1994). One possible explanation is that natural mortality increased with stocking rate because of density-dependent effects, such as depleted prey resources, reduced growth, and poor body condition, which may have led to increased susceptibility to disease and predation (Biro et al. 2003; Miranda and Bettoli 2007). However, no independent variable, including CPUE, was significantly related to mortality in regression models, so it is uncertain if density-dependent mortality existed. Alternatively, high mortality may have occurred in some low-stocking-rate lakes, but these lakes were not included in the analysis because of low sample sizes of fish resulting from a combination of low stocking rate and high mortality. Thus, the conclusion that mortality rate was lower in low-stocking-rate lakes may be inaccurate. Further study is needed to determine if mortality is density dependent, and if so, to identify the mechanisms causing this dependency.

Variation in population characteristics of channel catfish among the study lakes covered the range for these characteristics reported in other studies. For example, PSD ranged from 0.3% to 91% in this study, compared with values ranging from about 12%–96% in other midwestern lakes (Parrett et al. 1999; Flammang and Schultz 2007). Relative weight ranged from 66 to 113, which is similar to the range of 73–111 reported for other small lakes (Mitzner 1999; Mosher 1999; Parrett et al. 1999). Because I used growth increments instead of mean TL at age to compare growth among populations, I found only two studies using similar methods (Putman et al. 1995; Shoup et al. 2007), and only one (Shoup et al. 2007) that determined growth in lakes. Shoup et al. (2007) used initial lengths of 300 and 450 mm for Illinois lakes instead of the 280 and 410 mm used in this study. I computed growth increments for initial lengths of 300 and 450 mm by using my regression equations for the slowest and fastest growing populations. Based on these calculations, growth increments for a 300-mm fish ranged from 24 to 165 mm for my study lakes, compared with 41–105 mm for Illinois lakes, and growth increments for a 450-mm fish ranged from 0 to 96 mm for my lakes, compared with 0–105 mm for Illinois lakes (Shoup et al. 2007). Annual total mortality estimates ranged from 0% to 65% among the study lakes, compared with 13%–88% for other populations (Hubert 1999). While no mortality is highly improbable and likely the result of sampling bias, several populations in Missouri lakes exhibited very low mortality, similar to that of unexploited or lightly exploited populations (Gerhardt and Hubert 1991).

Recently, Buckmeier et al. (2002) recommended that otoliths be used instead of pectoral spines to age channel catfish. They reported that ages estimated from otoliths were more accurate and precise than those estimated from pectoral spines. In this study, pectoral spines were used because they have been commonly used to age channel catfish and do not require sacrificing fish. Aging errors in this study, if any, would have only affected estimates of mortality. Because mortality estimates included only fish up to age 7 or 8, it is doubtful that serious aging errors existed; older fish are usually more difficult to age. Spine sections were examined by a reader with more than 15 years of experience in aging channel catfish. In blind tests (actual age of fish unknown to the reader), this reader has accurately aged known-aged fish. During this study, a second reader examined some of the spine sections and his age estimates were in complete agreement with those of the first reader. Annuli were very distinct on spine sections, and by examining articulating process sections, annuli were not missed because of the enlargement of the central lumen (Marzolf 1955; Buckmeier et al. 2002). Thus, aging errors probably were small and did not affect the conclusions of this study.

Management Implications

Clearly, a single stocking rate is not appropriate for all small lakes. Stocking rate will need to be tailored to each lake because of differences in lake productivity, prey resources, fishing and natural mortality, and a host of other factors. While most lakes that received the low stocking rate appeared to be understocked, which resulted in very low abundances of fast-growing channel catfish, some lakes, such as Indian Creek Lake (Figure 3), contained desirable populations with moderately high abundances and growth. In other low-stocking-rate lakes, such as DiSalvo Lake (Figure 3), channel catfish exhibited slow growth even though their abundance was low. These lakes may have been overstocked even at the low rate, although it may not be possible for channel catfish to grow well at any stocking rate in these lakes because of low lake productivity. Most lakes stocked at the high rate showed signs of overstocking, with high abundances of slow-growing fish (e.g., Brookfield and Willowbrook lakes). Conversely, a few, such as Rothwell Park Lake, contained populations with moderate abundance and relatively fast growth (Figure 3). Variability in populations also occurred for lakes stocked at the medium rate, but most exhibited moderate abundance and growth.

For most Missouri lakes, an annual stocking rate of about 25–37 fingerlings/ha should provide a channel catfish population with moderate level of abundance and growth. Others may need to be stocked at a rate less than 12 fingerlings/ha, or at a rate of 74 fingerlings/ha or more. With the exception of the high stocking rate (74 fingerlings/ha), these rates are low compared to stocking rates used in the 1990s by many agencies (Shaner et al. 1996; Michaletz and Dillard 1999). However, as in Missouri, biologists in other states have found that overstocking has occurred in some lakes and have recommended reducing stocking rates in those lakes (Shaner et al. 1996; Mitzner 1999; Mosher 1999).

Criteria for determining appropriate stocking rates need to be developed. Mitzner (1999) suggested that mean length and W_r could be used to track populations. If these variables decreased over time to undesirable levels then stocking rates should be reduced. Mosher (1999) suggested that stocking density be reduced if the mean length of stocked channel catfish after 1 year was less than 300 mm. While these approaches have merit, using mean length is problematic when fish of varying sizes are stocked into the populations. Additionally, mean length is not a good measure of growth because it could be small because of poor growth or high exploitation. Using W_r to track populations is complicated by the difficulty of accurately weighing fish in the field (Gutreuter and Krzoska 1994) and this index may not accurately reflect growth rates (Gutreuter and Childress 1990). For this study, W_r was correlated with growth increments for 2003 (INC_{280}, $r = 0.50$, $P = 0.0001$, $N = 55$ lakes; INC_{410}, $r = 0.50$, $P = 0.0001$, $N = 55$ lakes) but not for 2005 (INC_{280}, $r = 0.26$, $P = 0.08$, $N = 48$ lakes; INC_{410}, $r = 0.28$, $P = 0.06$, $N = 47$ lakes). However, even for 2003, it accounted for only 25% of the variation in growth increments.

I propose that growth increments be used to determine stocking rates for individual lakes. The last growth increment of a given-size fish could be compared to a statewide standard to determine the relative growth rate for individuals in a population. For populations with much slower than average growth, stocking rates should be reduced. Conversely, for populations with exceptional growth, opportunities to increase stocking rates exist. A major advantage of using growth is that it is responsive to the many density-dependent and density-independent variables that exist in lakes. Comparing growth increments of fish with the same initial length avoids the previously mentioned problems of comparing mean lengths at age of hatchery-reared fish. After a single population sampling, the relative growth rate could be determined, and stocking rates could be adjusted as needed. Subsequent sampling could be done periodically to determine the response of the population to stocking rate adjustments, and further adjustments could be made if necessary. Biologists are cautioned to be aware of and account for major climatic events, such as occurred in 2004, that may cause atypical growth in populations over a large geographic area.

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