INVESTIGATING INTERACTIONS BETWEEN WALLEYE AND BLACK BASS IN NORTHERN WISCONSIN LAKES

By

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ABSTRACT

Walleye and black bass are popular game fish, walleye being the most intensively stocked and harvested fish species in Wisconsin, while black bass are the most popular game fish species in the nation. Current management practices in Wisconsin often seek to simultaneously enhance populations of these species in likes where both occur. Past studies have indicated that this may not be a feasible goal, because the species may interact negatively. My objective was to determine if available evidence supported the conclusion that walleye and black bass interact in northern Wisconsin lakes. I used data collected from 1,862 northern Wisconsin lakes over 74 years to create indices of abundance, growth, population size structure, and recruitment. I used rank correlation and measurement error ratio regression to test for relationships between these population demographics to determine if black bass and walleye populations may interact. I determined whether a high abundance of one species is significantly related to any population demographic of the others. I found a significant negative relationship between largemouth bass abundance and walleye abundance, a significant positive relationship between largemouth bass abundance and walleye growth and size structure, and a significant negative relationship between largemouth abundance and walleye recruitment. These results may be indicative of largemouth bass preying on juvenile walleye. I found no clear or consistent relationship between walleye and smallmouth bass. These findings suggest that management practices for all three species may need to be changed to account for the impossibility of enhancing populations of walleye and largemouth bass in one lake simultaneously. I recommend further study to more precisely determine the extent of the interactions between walleye and largemouth bass.

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INTRODUCTION

The competitive exclusion principle states that complete competitors cannot coexist (Hardin 1960). A corollary of this principle is that partial competitors will inhibit each other, which is generally regarded as true (Zaret and Rand 1971; Armstrong and McGehee 1980). However, establishing the degree of competition between species is difficult (Tilman 1977; Chesson 1999). Evaluating competition between two species may require making fine distinctions in the niches of each species so that two competing species may appear to coexist (Ayala 1969; Gause 1970). Determining the degree of competition between two species, and therefore the degree to which they inhibit each other, would require perfect knowledge of the niches of both species. While difficult, careful and thorough observation can enable reasonable approximations (Root 1967; Underwood 1978; Human and Gordon 1996).

Collecting the necessary data for niche determination is even more difficult if the species are not readily observed. Mobile aquatic species are notably difficult to observe adequately for characterizing their niches because of physical restrictions involved in gathering relevant data (Steig and Johnston 1996; Divens et al. 1998). Further, competition is not the only possible negative interaction between species. If one species preys on the other a measurable impact on the prey species population may be evident (Werner et al. 1983; He and Kitchell 1990).

Despite such difficulties, establishing the occurrence of interactions between species offers many benefits to managers. Recognizing the presence of interactions between species could be used to increase stocking efficiency, offer insight into the success or failure of existing stocks, and give fishery managers the ability to make more informed decisions about which stocks warrant further investments.

Walleye

The native range of walleye *Sander vitreus* extends from New Hampshire south to Pennsylvania and west of the Appalachians into Alabama, Nebraska, and the Dakotas. Walleye have been introduced south into Texas and as far west as California. Walleye thrive in shallow, mesotrophic lakes with turbid environments and large littoral areas (Hartman 2009). Walleye can thrive in clear lakes, but are able to feed in darker conditions because of a special pigment layer in the eye (*tapetum lucidum*). Walleye have large home ranges within lakes, often traveling 3–5 miles during summer (Scott and Crossman 1973).

Walleye commonly reach an average length of 13–20 inches (Scott and Crossman 1973). Walleye typically have a maximum lifespan of 10–12 years, with an average lifespan around 7 years (Becker 1983). Female walleye mature at ages 5–7, while males mature at ages 2–4. Lifespan and age at maturity vary among lakes (Becker 1983). Walleye are fecund broadcast spawners, with walleye in Lake Winnebago, WI producing 43,000 eggs at 17.4 inches (Becker 1983). Walleye spawn in shallow water of lakes and rivers, and select for a habitat of cobble and gravel reefs (Hartman 2009). Spawning runs occur in spring or early summer, and are triggered by seasonal increases in water temperature. Walleye in northern populations have been known to forego spawning in years when temperatures are unfavorable. Males arrive on the spawning grounds first, and are not territorial. Eggs are broadcast and often fall into protective crevices of rock or coarse substrate (Scott and Crossman 1973). After spawning, age–0 walleye drift with the current until captured in eddies within bays (Hartman 2009).

Larval walleye feed mainly on copepods, cladocerans, and fish, and undergo an ontogenetic shift to piscivory (Becker 1983). Adult walleye feed on a variety of fish species, but most commonly on yellow perch *Perca flavescens*. Walleye predation affects density, growth, and recruitment of populations of prey species (Colby et al. 1979; Hartman and Margraf 1992). Walleye are highly cannibalistic if yellow perch or other prey species are unavailable (Scott and Crossman 1973).

Largemouth Bass

Largemouth bass *Micropterus salmoides* are native to east–central North America, with a range stretching from the lower Great Lakes to north–eastern Mexico (Brown et al. 2009a). Largemouth bass have been widely introduced outside their native range, and established nearly everywhere the species is capable of surviving because of intense angler interest (Brown et al. 2009a). Largemouth bass are adaptable to many habitats, and can reside in nearly all types of fresh water. Ideally, the species selects for lacustrine environments with shallow littoral zones and plentiful submerged vegetation (Becker 1983). Aquatic vegetation serves to both increase the ambush foraging efficiency of adult largemouth bass and to protect juveniles from predation (Brown et al. 2009a).

Largemouth bass commonly reach an average length of 8–15 inches (Scott and Crossman 1973). Females commonly reach age–9, while males commonly reach age–6 (Becker 1983). Male largemouth bass mature at ages 3–4, and females mature at ages 4–5

(Becker 1983). Males build nests in sand, gravel, and soft mud near submerged vegetation, and guard nests until fry disperse. If the male is removed from the nest while guarding, he may not return, and the brood is unlikely to survive (Becker 1983). Largemouth bass typically spawn in late spring and early summer, but may spawn later in northern latitudes (Scott and Crossman 1973; Becker 1983).

Juvenile largemouth bass consume macroinvertebrates, and undergo an ontogenetic shift to piscivory as they grow. Adult largemouth bass are primarily piscivorous, although crustaceans also form a significant part of their diet (Scott and Crossman 1973; Becker 1983). Largemouth bass are sight feeders, and feed mostly at dawn and dusk, but may feed throughout the day. Largemouth bass ambush and suck prey into the mouth (Becker 1983). While largemouth bass are known to move into deeper water in winter, they tend to remain active, and feed throughout winter (Becker 1983).

Smallmouth Bass

The native range of the smallmouth bass *Micropterus dolomieu* is east–central North America, including the Ohio, Tennessee, upper Mississippi, Saint Lawrence River, and Great Lakes systems (Scott and Crossman 1973). Smallmouth bass have been introduced outside their native range, including Africa, Europe, Russia, and most of the rest North America (Scott and Crossman 1973). Smallmouth bass live primarily in lakes, but also survive in rivers. The species prefers mesotrophic lakes larger than 0.15 square miles, with an average depth greater than 30 feet and abundant rocky structure. Smallmouth bass tend to seek out structures such as logs, rocky outcroppings, or submerged trees in deeper water for cover while resting during dormant periods. Littoral zones with a drop–off and gravel or cobble substrate are also important for spawning and rearing (Becker 1983).

Smallmouth bass reach an average length of 8–15 inches (Scott and Crossman 1973), and have a maximum lifespan of 15 years (Becker 1983; Brown et al. 2009b). Spawning occurs in mid to late spring, but may be delayed until late July in northern latitudes (Scott and Crossman 1973). When spawning begins, males of ages 3–5 build nests in substrate of firm mud, sand, or gravel. Females will arrive to spawn, and males guard eggs and young until fry disperse. If the male is removed from the nest while guarding, he may not return, and the brood is unlikely to survive (Becker 1983). Adult smallmouth bass do not spawn each year. The mechanism to determine spawning is activated sometime in the previous year, and is poorly understood (Brown et al. 2009b).

Juvenile smallmouth bass feed primarily on insects, notably chironomids, but shift to piscivory past age–1. Adult smallmouth bass are almost entirely piscivorous, but also eat some insects and crayfish (Scott and Crossman 1973). Smallmouth bass feed almost entirely at dawn and dusk, and avoid most daylight activity. Wintering smallmouth bass lie dormant for long stretches of time, and apparently do not feed during this period (Becker 1983).

Walleye Management in Wisconsin

Walleye have been stocked across the continent, and are the most intensively stocked game fish in the state of Wisconsin (The Bureau of Fisheries Management and Habitat Protection 1999; Hartman 2009). In Wisconsin, the annual stocking goal for walleye is

6.5–million fingerlings, used largely for maintenance and supplemental stocking (The Bureau of Fisheries Management and Habitat Protection 1999). Walleye regulations in Wisconsin include a statewide 5–fish bag limit, special bag limits for the ceded territories, a reduced bag limit for certain specially designated waters, variable minimum length limits designated for individual water bodies, and seasonal closures during spawning months. Anglers expend 6.1–million angler–days of effort in Wisconsin, and 4.9–million angler–days of fishing effort on the Great Lakes alone for walleye, thereby making walleye the second most sought fish by anglers in Wisconsin (McClanahan and Hansen 2005; US Fish and Wildlife Service 2006). The estimate of the Wisconsin statewide walleye harvest is 2.2–million fish, but the species is known to be primarily caught and released, with 7.5–million fish caught (McClanahan and Hansen 2005).

Walleye populations in the Ceded Territory of Wisconsin are co-managed by tribal authorities, and so specifically restricted bag limits set by the state in the Ceded Territory are designed to accommodate tribal spearing harvest (Hansen et al. 2000; Beard et al. 2003). This added layer of management complexity in many northern portions of the state is a strong indication of the wide–ranging public and political interest in walleye harvest and management.

Bass Management in Wisconsin

Although the two species are biologically distinct, Wisconsin statewide harvest regulations do not differentiate largemouth and smallmouth bass, and instead pool the species as ‘black bass’. The justification given for this is the purported inability of anglers to distinguish between largemouth and smallmouth bass. Black bass harvest regulations in Wisconsin include a catch–and–release early season in northern portions of the state, a 14–inch statewide minimum length limit, and a combined–species bag limit of 5 fish per day. The Wisconsin annual stocking goal for black bass is 210,000 fingerlings, largely used in maintenance and supplemental stocking (The Bureau of Fisheries Management and Habitat Protection 1999). Anglers expend 4.2–million angler–days of effort in Wisconsin, and 161–million angler–days of fishing effort nationally, thereby making black bass the most sought fish by anglers in the country (McClanahan and Hansen 2005; US Fish and Wildlife Service 2006). The estimate of the Wisconsin annual statewide largemouth bass harvest is 0.5–million fish, but most black bass are caught and released, with 4.5–million fish caught (McClanahan and Hansen 2005). The estimate of the Wisconsin annual statewide smallmouth bass harvest is 0.3–million fish, but as with largemouth bass, the species is known to be primarily caught and released, with over 3–million caught (McClanahan and Hansen 2005).

Potential Interactions between Species

Past research into interactions between walleye, largemouth bass, and smallmouth bass has generally indicated that these species interact negatively. One study used fishery–dependent indices of relative abundance to test for emporal trends among popular fish species in a small northern Wisconsin lake (Inskip and Magnuson 1983). A strong negative correlation was found between indices of largemouth bass and walleye abundance. The study observed that the ascent of bass and decline of walleye coincided with climatic warming, while periods of cooling tended to favor increased walleye abundance and decreased bass abundance. However, trends were not consistent enough to explain shifts in relative abundance entirely, and the authors theorized that suppression of one species by the other, either through predation on juveniles or competition for food source, was implied by the correlation. Data available to the authors were not sufficient to isolate the mechanism responsible for this suppression.

Another study considered several factors affecting survival and growth of stocked walleye in small central Illinois impoundments dominated by Centrarchidae (Santucci and Wahl 1993). Predation by largemouth bass decreased survival of stocked juvenile walleye, although the study was unable to clearly define patterns because of data limitations.

Perhaps the most relevant and recent study considered the potential for interactions between walleye and northern pike *Esox lucius*, muskellunge *E. masquinongy*, smallmouth bass, and largemouth bass, and the impact these interactions may have had on walleye stocking (Fayram et al. 2005). This study found no evidence of smallmouth bass negatively affecting walleye. In contrast, the study found evidence that largemouth bass negatively affected walleye through predation on juveniles, and concluded that simultaneously optimizing populations of both species was an unrealistic management goal.

All of these studies agreed on certain points: each considered that interactions between walleye and black bass, while difficult to determine precisely, must be due to either predation by one species upon juveniles of the other, or competition for prey between adults of both species. As a result, I considered these mechanisms when investigating the impacts of the target species on each other.

Objective

The Wisconsin DNR published a questionnaire in spring 2010 proposing several policy changes with the intent of decreasing black bass populations in 21 lakes (Wisconsin DNR and Wisconsin Conservation Congress 2010). These proposed changes were approved, and became law in 2011. The justification offered for these changes was that black bass populations in these lakes were increasing, and were believed to be negatively affecting walleye populations. Given a lack of supporting evidence for this justification, the appropriateness of these regulations is uncertain. The decision to reduce black bass populations is especially important when considering the thriving catch and release bass fisheries on several affected lakes. These regulations may be appropriate, but the ecological basis for these policy changes should be carefully evaluated to avoid significant damage to these fisheries. Therefore, my objective was to determine if available evidence suggests that interactions occur between largemouth bass, smallmouth bass, and walleye in northern Wisconsin lakes.

METHODS

To evaluate potential interactions between walleye and black bass, one must first determine if interactions between populations of the species is plausible. If indices of abundance, growth, size structure, or recruitment are not related for populations of these species, then any potential interaction at the individual level may be ultimately insignificant to management. If population dynamics of the target species indicate that an interaction is possible, further study would be needed to step from correlation to causation and positively identify the mechanism by which one species affects the other. Finding an interaction would call for further study to determine the extent of the interaction and establish causation, whereas finding no interaction would suggest that no such interaction exists. This suggests that a false negative result would have greater consequences than a false positive result, and would call for a relatively low α, while the stochasticity inherent in fish populations means that choosing an α that is too low would drastically decrease the power of my analyses. Therefore, I decided *a priori* to use α=0.05 for all of my analyses.

Study Area

My study area encompassed northern Wisconsin, including the Ceded Territory. All lakes included in my analysis fell within the northern third of Wisconsin, and included the lakes affected by the change in walleye and black bass angling regulations (Table 1). After removal of unusable data to reduce error, my analysis was conducted using data taken during 1945-2011, on 1,074 lakes (Table 2).

Data collection

The data for my analyses were collected using various sampling procedures. For adult abundance of black bass and walleye I used data from mark–recapture surveys. For relative abundance of adult walleye, black bass, and age-0 walleye I used data collected during electrofishing surveys. For indices of growth rate and size structure I used length and age data collected during standard sampling using electrofishing, fyke nets, and trap nets.

Adult abundance. – Adult abundance for all three species was estimated by mark-recapture during spring spawning. Adults were defined as all fish for which sex was determined and all fish of unknown sex ≥15 in (Beard et al. 1977). Fish captured in fyke nets were marked by removal of a portion of one or more fins. Recapture occurred shortly after the completion of the marking period by AC electrofishing (Beard et al. 1977). Abundance was estimated using Chapman's modification of the Lincoln-Peterson single-census mark-recapture model (Ricker 1975). Total length was recorded, and age was estimated using annual growth rings on hard structures for a random subsample of captured fish. To allow for comparison between many lakes of different sizes, abundance estimates for each population were standardized to density and analyzed as number of fish per acre.

Adult relative abundance. –Standardized electrofishing surveys were used to estimate relative abundance of adult walleye and black bass (Beard et al. 1997; Schoenebeck and Hansen 2005). Catch was recorded as the total number of fish captured per mile of shoreline surveyed. Survey guidelines suggest one complete electrofishing trip around the shoreline, including islands, with two people netting fish. However, this is not always possible, and the sampling procedure was abbreviated as necessary by restricting the amount of shoreline sampled.

Age–0 relative abundance. – Standardized fall electrofishing surveys were used to estimate relative abundance of age–0 walleye and black bass (Schoenebeck and Hansen 2005). Catch was recorded as the total number of age–0 fish captured per mile of shoreline surveyed. Surveys were conducted between mid–September and late October when water temperatures ranged from 42^{0}F to 70^{0}F. Survey guidelines suggest one complete electrofishing trip around the shoreline, including islands, with two people netting fish. However, this is not always possible, and the sampling procedure was abbreviated as necessary.

Data Screening

Data were collected in the manner described above by the Wisconsin Department of Natural Resources on a total of 1,862 lakes during 1937-2011 (Table 2). Much of the data collected were unusable, and so were removed from consideration before conducting any analysis. Data were considered unusable if they were collected in a manner that differed drastically in method or sampling gear from the standard sampling protocols in Wisconsin such that they might induce sampling bias, or if they were biologically implausible from first principles (e.g. a density many times higher than the maximum found in the literature).

I restricted my analysis to surveys conducted between March and July to attempt to minimize additional error introduced by seasonal variability among populations. The sole exception was that electrofishing surveys targeting age-0 walleye were conducted in fall between August and October.

Mark-recapture data were restricted to surveys lasting less than 150 days to minimize error introduced by mortality and tag loss. In instances where multiple mark-recapture population estimates were available for one lake in the spring of the same year, one estimate was selected at random and the rest were excluded.

Electrofishing catch per effort data were restricted to surveys lasting less than 7 days to minimize error introduced by variation in catchability. In instances where multiple electrofishing surveys were conducted on one lake one year, both catch and effort were summed for all usable surveys, and catch per effort was calculated using these aggregated values. This screening procedure was applied to surveys of adult fish of all species, and to surveys of age-0 walleye.

Growth rate data were restricted to surveys lasting less than 150 days to minimize error introduced by variations in seasonal growth rates among lakes. Growth rate data were also restricted to surveys using typical sampling gear, specifically fyke nets, trap nets, boom shockers, barge shockers, and backpack shockers. Surveys using non-standard sampling gear such as poison, hook and line, or gill nets were excluded from analysis to prevent introduction of sampling-induced variation. In instances where multiple surveys were conducted on one lake in the spring of one year, number of age-3 fish caught and total length of all age-3 fish caught were summed, and mean length at age-3 was calculated using these aggregated values.

Size structure data were restricted to surveys lasting less than 150 days to minimize error introduced by variations in seasonal growth rates and seasonal mortality among lakes. Size structure data were available from surveys using both net-based gear types, specifically trap nets and fyke nets, and electrofishing gear types, specifically boom shockers, barge shockers, and backpack shockers. These gears have different size selectivity, and as proportional stock density (PSD) is a binomial proportion, there is no way to combine these gear types when measuring size structure. In light of this, size structure indices from both electrofishing-based data and net-based data were calculated and analyzed separately. Size structure data gathered using fyke nets and trap nets were included in the net-based PSD analysis, while size structure data gathered using boom shockers, barge shockers, and backpack shockers were included in the electrofishing-based PSD analysis. Size structure data gathered using any gear other than these were excluded from analysis. In instances where multiple surveys were conducted on one lake in the same spring using either net-based or electrofishing-based gear types, the numbers of stock- and quality-length fish caught were summed as appropriate, and PSD was calculated using these aggregated values.

Data Analysis

To investigate potential interactions between walleye and black bass, the first population demographic I considered was abundance. To indicate negative interactions, abundance of one species must be high while the abundance of the other must be low (MacLean and Magnuson 1977). To test for this inverse relationship, I used abundance estimates from mark–recapture studies and electrofishing catch per effort data.

I assumed that catch per effort was linearly related to abundance (Serns 1982; Cohen et al. 1993; Beard et al. 1997; Edwards et al. 1997; McInerny and Cross 2000) and therefore treated catch per effort as an index of abundance. I used catch per minute as an index of abundance fore electrofishing samples, because effort was measure in time more often than distance. To ensure that time effort and distance effort provided similar trends in electrofishing catch per effort (CPE) I calculated Pearson's correlation between catch per hour and catch per mile for all surveys where both were available, for each of my three target species. The relationships between catch per hour and catch per mile for each of my target species were strongly linear ($r>0.9$), so I concluded that using time effort instead of distance effort would not affect my analysis (Figures 1-3;McInerny and Cross 2000).

I used Spearman's rank correlation to test for a relationship between abundances of walleye and black bass in each lake and year for which data was available. Rank correlation assesses how well the relationship between two variables can be described using a monotonic function. I used rank correlation to avoid assumptions of linearity in the interaction between species implicit in Pearson's correlation. I created a measurement error ratio regression of a log-transformed power model to test for significant impacts of the abundance of each target species on the abundance of the others:

$$\log_e y = \log_e a + b * \log_e x$$

I used a power model to avoid assumptions about the form of the relationship between these species. I used measurement error ratio regression because all of the demographics tested were measured with unknown amounts of error, and so an ordinary least squares regression may have produced biased results (Fuller 1987). I used the ratio of the average of the sample coefficients of variation for the dependent and independent variables as the measurement error ratio. I calculated the CV of individual mark recapture population estimates using the formula provided by Ricker (1975)

$$CV = \frac{\sqrt{Variance}}{\mu}$$

where

$$Variance = \frac{(M+1)^2(C+1)(C-R)}{(R+1)^2(R+2)}$$

A Poisson distribution was employed in evaluating random occurrences or events in a unit of space or time when the probability of an occurrence is small (Zar 1999). I considered electrofishing to be a Poisson process, with

$$Catch = \sigma^2 = \mu = \lambda$$

and so calculated the CV of each individual electrofishing catch as

$$CV = \frac{\sqrt{Catch}}{Catch}$$

The second population demographic I considered was growth. If abundance of one species is significantly correlated with growth rate of another species, the two species may be interacting. To investigate the interactions between abundance and growth, I used mark–recapture abundance estimates and electrofishing CPE data as indices of abundance, and mean length at age–3 as an index of growth (Harley et al. 2001; Swain et al. 2007). I used Spearman's rank correlation to quantify the relationship between abundance of walleye and mean length at age–3 of largemouth bass, abundance of walleye and mean length at age–3 of smallmouth bass, abundance of smallmouth bass and mean length at age–3 of walleye, and abundance of largemouth bass and mean length at age–3 of walleye for each lake in each year that data were available. I used measurement error ratio regression of a log-transformed power model to test for significant impacts of the abundance of each target species on the growth rate of the others. I used the ratio of the average of the sample coefficients of variation for the dependent and independent variables as the measurement error ratio.

The third population demographic I considered was size structure. I used proportional stock density as an index of size structure (PSD; Willis et al. 1993). PSD is defined as the proportion of fish of quality-length or longer that are also of stock length or longer (for stock and quality lengths of target species see Table 3):

$$\text{PSD} = \frac{\text{Number of fish} \geq \text{quality length}}{\text{Number of fish} \geq \text{stock length}} \times 100$$

To investigate the interactions between abundance and PSD, I used mark–recapture abundances and electrofishing CPE data as indices of abundance, and PSD from length measurement samples collected on my target lakes. I used Spearman's rank correlation to quantify the relationship between abundance of walleye and PSD of largemouth bass, abundance of walleye and PSD of smallmouth bass, abundance of largemouth bass and PSD of walleye, and abundance of smallmouth bass and PSD of walleye. I used measurement error ratio regression of a log-transformed power model to test for significant impacts of the abundance of each target species on the PSD of the others. I used the ratio of the average of the sample coefficients of variation for the dependent and independent variables as the measurement error ratio. I calculated the CV of individual PSD measurements using (Zar 1999)

$$Variance = \frac{(\frac{Q}{S})(1 - \frac{Q}{S})}{S - 1}$$

The final population demographic I considered was recruitment. A significant negative correlation between abundance of one species and age–0 abundance of another may indicate predation by one species on juveniles of the other. I used mark–recapture population estimates and electrofishing CPE as indices of abundance. I indexed age-0 abundance of walleye using electrofishing CPE surveys conducted along the shoreline in fall. Data for age-0 abundance of black bass in northern Wisconsin lakes were not available. I used Spearman's rank correlation to quantify the relationship between abundance of black bass and relative abundance of age-0 walleye. I used measurement error ratio regression of a log-transformed power model to test the relationship. I used the ratio of the average of the sample coefficients of variation for the dependent and independent variables as the measurement error ratio.

After performing each of the correlations and creating the functional relationships for each demographic comparison, I organized the results into tables showing the relationships between each of my target species. Calculating multiple correlations using at once may pose an increased risk of Type I error without additional screening (Cabin and Mitchell 2000). To address this, I performed the sequential Bonferroni technique to establish "table-wide" significance for each of my results (Rice 1989).

RESULTS

Electrofishing catch per mile and catch per hour provided strongly correlated indices of relative abundance for walleye, largemouth bass, and smallmouth bass in northern Wisconsin lakes (Figure 1). For walleye, electrofishing CPE increased linearly from 0.1 fish/mile and 0.0 fish/hour to 931.3 fish/mile and 0.4 fish/hour ($r = 0.963$; $df = 334$; $P < 0.001$). For largemouth bass, electrofishing CPE increased linearly from 0.1 fish/mile and 0.0 fish/hour to 391 fish/mile and 0.2 fish/hour ($r = 0.917$; $df = 347$; $P < 0.001$). For smallmouth bass, electrofishing CPE increased linearly from 0.2 fish/mile and 0.0 fish/hour to 167.2 fish/mile and 0.1 fish/hour ($r = 0.959$; $df = 149$; $P < 0.001$).

Walleye density correlated negatively with largemouth bass density in northern Wisconsin lakes (Figure 2). Walleye density decreased non-linearly with increasing largemouth bass density from 6.8 walleye/acre with 2.8 largemouth bass/acre to 0.3 walleye/acre with 12.1 largemouth bass/acre ($\rho = -0.298$, $df = 68$, $P = 0.012$; Table 4).

Walleye relative abundance correlated negatively with largemouth bass relative abundance in northern Wisconsin lakes (Figure 3). Walleye electrofishing CPE decreased non-linearly with increasing largemouth bass electrofishing CPE from 7.3

walleye/min with 0.2 largemouth bass/min to 0.0 walleye/min with 3.1 largemouth bass/min (ρ = -0.248, *df* = 341, P < 0.001; Table 4).

Walleye mean length at age-3 correlated positively with indices of largemouth bass abundance in northern Wisconsin lakes (Figure 4). Walleye mean length at age-3 increased non-linearly with largemouth bass density from 9.0 inches with 1.6 largemouth bass/acre to 18.3 inches with 16.7 largemouth bass/acre (ρ = 0.531, *df* = 46, P < 0.001). Walleye mean length at age-3 increased non-linearly with largemouth bass electrofishing CPE from 8.5 inches with 0.0 largemouth bass/min to 18.3 inches with 4.6 largemouth bass/min (ρ = 0.671, *df* =32, P < 0.001; Table 4).

Walleye size structure correlated positively with indices of largemouth bass abundance in northern Wisconsin lakes (Figure 5). Walleye PSD from net-based sampling gears increased non-linearly with largemouth bass density from 32 with 0.2 largemouth bass/acre to 100 with 26.0 largemouth bass/acre (ρ = 0.315, *df* =72, P = 0.006). Walleye PSD from electrofishing-based sampling gears increased non-linearly with largemouth bass density from 0 with 10.0 largemouth bass/acre to 100 with 22.9 largemouth bass/acre (ρ = 0.257, *df* = 82, P = 0.018). Walleye PSD from net-based sampling gears increased non-linearly with largemouth bass electrofishing CPE from 8 with 1.3 largemouth bass/min to 100 with 7.3 largemouth bass/min (ρ = 0.431, *df* =143, P = 0.004). Walleye PSD from electrofishing-based sampling gears increased non-linearly with largemouth bass electrofishing CPE from 0 with 0.0 largemouth bass/min to 100 with 3.1 largemouth bass/min (ρ = 0.337, *df* =333, P < 0.001; Table 4).

Walleye age-0 electrofishing CPE correlated negatively with indices of largemouth bass abundance in northern Wisconsin lakes (Figure 6). Walleye age-0 electrofishing CPE decreased non-linearly with increasing largemouth bass density from 134.7 walleye/mile with 0.2 largemouth bass/acre to 0.0 walleye/mile with 11.8 largemouth bass/acre (ρ = -0.350, *df* =51, P = 0.010). Walleye age-0 electrofishing CPE decreased non-linearly with increasing largemouth bass electrofishing CPE from 213.8 walleye/mile with 0.0 largemouth bass/min to 0.0 walleye/mile with 1.0 largemouth bass/min (ρ = -0.561, *df* =37, P < 0.001; Table 4).

Walleye density was not significantly related to smallmouth bass density in northern Wisconsin lakes (ρ = -0.235, *df* = 51, P = 0.090; Table 5; Figure 7). Walleye density ranged from 0.6 walleye/acre to 8.1 walleye/acre. Smallmouth bass density ranged from 0.1 smallmouth bass/acre to 8.6 smallmouth bass/acre.

Walleye relative abundance correlated positively with smallmouth bass relative abundance in northern Wisconsin lakes (Figure 8). Walleye electrofishing CPE increased non-linearly with smallmouth bass electrofishing CPE from 0.0 walleye/min with 0.3 smallmouth bass/min to 13.2 walleye/min with 0.2 smallmouth bass min (ρ = 0.231, *df* = 181, P < 0.002; Table 5).

Walleye mean length at age-3 was not significantly related to indices of smallmouth bass abundance in northern Wisconsin lakes (Figure 9). Walleye mean length at age-3 was not significantly related to smallmouth bass density (ρ = 0.009, *df* =30, P = 0.962). Walleye mean length at age-3 ranged from 10.4 inches to 14.8 inches. Smallmouth bass density ranged from 0.1smallmouth bass/acre to 16.0 smallmouth bass/acre. Walleye mean length at age-3 was not significantly related to smallmouth bass electrofishing CPE (ρ = -0.057, *df* = 18, P = 0.811; Table 5). Walleye mean length at age-3 ranged from 8.5 inches to 17.5 inches. Smallmouth bass electrofishing CPE ranged from 0.0 smallmouth bass/acre to 1.0 smallmouth bass/acre.

Walleye size structure showed an inconsistent relationship with indices of smallmouth bass abundance in northern Wisconsin lakes (Figure 10). Walleye PSD from net-based sampling gears increased non-linearly with smallmouth bass density from 5 with 1.0 smallmouth bass/acre to 100 with 8.6 smallmouth bass/acre ($\rho = 0.295$, $df = 53$, $P = 0.029$). Walleye PSD from electrofishing-based sampling gears increased non-linearly with smallmouth bass density from 0 with 0.2 smallmouth bass/acre to 100 with 16.0 smallmouth bass/acre ($\rho = 0.390$, $df = 82$, $P < 0.001$). Walleye PSD from net-based sampling gears was not significantly related to smallmouth bass electrofishing CPE ($\rho = -0.105$, $df = 90$, $P = 0.319$). Walleye PSD from net-based sampling gears ranged from 8 to 100. Smallmouth bass electrofishing CPE ranged from 0.0 smallmouth bass/min to 3.8 smallmouth bass/min. Walleye PSD from electrofishing-based sampling gears decreased non-linearly with increasing smallmouth bass electrofishing CPE from 100 with 0.0 smallmouth bass/min to 0 with 0.4 smallmouth bass/min ($\rho = -0.148$, $df = 179$, $P = 0.046$; Table 5).

Walleye age-0 electrofishing CPE was not significantly related to indices of smallmouth bass abundance in northern Wisconsin lakes (Figure 11). Walleye age-0 electrofishing CPE was not significantly related to smallmouth bass density ($\rho = -0.163$, $df = 40$, $P = 0.303$). Walleye age-0 electrofishing CPE ranged from 0.0 walleye/mile to 178.8 walleye/mile. Smallmouth bass density ranged from 0.1 smallmouth bass/acre to 8.6 smallmouth bass/acre. Walleye age-0 electrofishing CPE was not significantly related to smallmouth bass electrofishing CPE ($\rho = 0.228$, $df = 19$, $P = 0.320$; Table 5).

Walleye age-0 electrofishing CPE ranged from 0.0 walleye/mile to 213.8 walleye/mile. Smallmouth bass electrofishing CPE ranged from 0.0 smallmouth bass/min to 1.0 smallmouth bass/min.

Largemouth bass density correlated negatively with walleye density in northern Wisconsin lakes (Figure 12). Largemouth bass density decreased non-linearly with increasing walleye density from 38.1 largemouth bass/acre with 1.7 walleye/acre to 0.1 largemouth bass/acre with 5.2 walleye/acre (ρ = -0.298, *df* =68, P = 0.012; Table 6).

Largemouth relative abundance correlated negatively with walleye relative abundance in northern Wisconsin lakes (Figure 13). Largemouth bass electrofishing CPE decreased non-linearly with increasing walleye electrofishing CPE from 14.2 largemouth bass/min with 2.3 walleye/min to 0.0 largemouth bass/min with 3.3 walleye/min (ρ = -0.248, *df* =341, P < 0.001; Table 6).

Largemouth bass mean length at age-3 was not significantly related to indices of walleye abundance in northern Wisconsin lakes (Figure 14). Largemouth bass mean length at age-3 was not significantly related to walleye density (ρ = 0.093, *df* =52, P = 0.499). Largemouth bass mean length at age-3 ranged from 7.4 inches to 12.7 inches. Walleye density ranged from 0.3 walleye/acre to 19.9 walleye/acre. Largemouth bass mean length at age-3 was not significantly related to walleye electrofishing CPE (ρ = 0.285, *df* =44, P = 0.055; Table 6). Largemouth bass mean length at age-3 ranged from 5.4 inches to 12.7 inches. Walleye electrofishing CPE ranged from 0.0 walleye/min to 5.2 walleye/min.

Largemouth bass size structure correlated positively with indices of walleye abundance in northern Wisconsin lakes (Figure 15). Largemouth bass PSD from net-based sampling gears increased non-linearly with walleye density from 0 with 0.8 walleye/acre to 100 with 9.1 walleye/acre (ρ = 0.189, *df* = 249, P = 0.003). Largemouth bass PSD from electrofishing-based sampling gears increased non-linearly with walleye density from 0 with 0.9 walleye/acre to 100 with 9.1 walleye/acre (ρ = 0.152, *df* = 265, P = 0.007). A non-significant positive relationship was observed between largemouth bass PSD from net=based sampling gears and walleye electrofishing CPE (ρ = 0.111, *df* = 117, P = 0.227). Largemouth bass PSD from electrofishing-based sampling gears increased non-linearly with walleye electrofishing CPE from 0 with 0.0 walleye/min to 100 with 7.4 walleye/min (ρ = 0.173, *df* = 378, P = 0.001; Table 6).

Smallmouth bass density was not significantly related to walleye density in northern Wisconsin lakes (ρ = -0.235, *df* = 51, P = 0.090; Table 7; Figure 16). Smallmouth bass density ranged from 0.1 smallmouth bass/acre to 8.6 smallmouth bass/acre. Walleye density ranged from 0.1 walleye/acre to 8.1 walleye/acre.

Smallmouth bass relative abundance correlated positively with walleye relative abundance in northern Wisconsin lakes (Figure 17). Smallmouth bass electrofishing CPE increased non-linearly with walleye electrofishing CPE from 0.0 smallmouth bass/min with 0.2 walleye/min to 3.8 smallmouth bass/min with 1.4 walleye/min (ρ = 0.231, *df* = 181, P = 0.002; Table 7).

Smallmouth bass mean length at age-3 was not significantly related to indices of walleye abundance in northern Wisconsin lakes (Figure 18). Smallmouth bass mean length at age-3 was not significantly related to walleye density (ρ = 0.084, *df* = 41, P = 0.590). Smallmouth bass mean length at age-3 ranged from 7.4 inches to 12.3 inches. Walleye density ranged from 0.4 walleye/acre to 8.1 walleye/acre. Smallmouth bass mean length at age-3 was not significantly related to walleye electrofishing CPE (ρ = 0.350, *df* = 10, P = 0.263; Table 7). Smallmouth bass mean length at age-3 ranged from 7.5 inches to 10.5 inches. Walleye electrofishing CPE ranged from 0.0 walleye/min to 13.2 walleye/min.

Smallmouth bass size structure showed an inconsistent relationship with indices of walleye abundance in northern Wisconsin lakes (Figure 19). Smallmouth bass PSD from net-based sampling gears decreased non-linearly with increasing walleye density from 100 with 0.0 walleye/acre to 0 with 5.6 walleye/acre (ρ = -0.164, *df* = 186, P = 0.025). Smallmouth bass PSD from electrofishing-based sampling gears was not significantly related to walleye density (ρ = 0.111, *df* = 230, P = 0.091). Smallmouth bass PSD from electrofishing-based sampling gears ranged from 0 to 100. Walleye density ranged from 0.0 walleye/acre to 19.9 walleye/acre. Smallmouth bass PSD from net-based sampling gears was not significantly related to walleye electrofishing CPE (ρ = 0.072, *df* = 66, P = 0.562). Smallmouth bass PSD from net-based sampling gears ranged from 0 to 100. Walleye electrofishing CPE ranged from 0.1 walleye/acre to 15.6 walleye/acre. Smallmouth bass PSD from electrofishing-based sampling gears increased non-linearly with walleye electrofishing CPE from 0 with 0.0 walleye/min to 100 with 13.2 walleye/min (ρ = 0.220, *df* = 203, P = 0.001; Table 7).

DISCUSSION

Time effort and distance effort provide similar trends in electrofishing CPE, which is consistent with with previous research (McInerny and Cross 2000). Either metric may be used for walleye, largemouth bass, and smallmouth bass in northern Wisconsin lakes. This corroborates the results of research on the effect of time effort and distance effort on electrofishing CPE of largemouth bass in Minnesota lakes (McInerny and Cross 2000). Time effort can be more precisely recorded than distance effort, is often easier to replicate, and has almost no chance of unit conversion error. For these reasons, and because it was more often recorded in the available data, I chose to use time effort for calculating electrofishing CPE in all of my analyses except those involving age-0 walleye. When recording time effort it is necessary to closely follow established protocols to avoid introducing sampling error (Hubert and Fabrizio 2007).

Finding a significant negative relationship between all indices of walleye and largemouth bass abundance and relative abundance is consistent with previous research on the relationship between these species (Inskip and Magnuson 1983, Santucci and Wahl 1993, Fayram et al. 2005). To establish negative interaction between species, abundance of one species must correlate negatively with abundance of another (MacLean and Magnuson 1977). My results suggest that there may be some negative interaction between walleye and largemouth bass. However, considering only the relationship between abundance of these species does not fully explain the nature of the interaction. To achieve a more complete understanding, it is necessary to look at the relationships between abundance of one species and several demographics of the others.

Finding a significant positive relationship between walleye growth rate and both abundance and relative abundance of largemouth bass suggests that largemouth bass may be preying on walleye, which corresponds with findings from previous studies (Santucci and Wahl 1993, Fayram et al. 2005). A negative relationship between growth rate of one species and indices of abundance of another might indicate that the species compete for resources such as food or habitat, and so have less energy to devote to somatic growth (Mittelbach 1988). A positive relationship might indicate that one species is experiencing less intra-specific competition for resources, because of lower densities caused by predation by the other species (Peterson 1982; Mittelbach 1988; Hixon and Carr 1997). A similar relationship between these demographics could be caused by several combinations of complex habitat and food web interactions in certain ecosystems that contain other apex predators (Rahel and Stein 1988).

Finding a positive relationship between walleye size structure, indexed by PSD, and largemouth bass abundance suggests that largemouth bass may be preying on juvenile walleye, which corroborates other studies on intra- and inter-specific competition that have shown changes in growth rate and size structure in the presence of predation on juveniles (Mittelbach 1988; Rice et al. 1993; Fayram et al. 2005). PSD is the proportion of large fish in a population, and so is closely tied to both growth rate and recruitment. If a population is experiencing high growth rates, more fish will reach larger sizes and increase the size structure of the population. If a population is experiencing low recruitment, there will be few small fish, and PSD will be higher. Conversely, if a population is experiencing slower growth rates, fewer fish will reach larger sizes, and so PSD will be lower. Similarly, if a population is experiencing high recruitment, there will be more small fish and PSD will be lower (Carline et al. 1984). In analyzing potential interactions between species, a comparison of PSD of one species and abundance of another serves to reinforce the comparisons involving growth rate and recruitment. If the relationship found between PSD of one species and abundance of another matches the relationship between growth rate and abundance of those species, it helps to support the conclusion that the observed relationship actually exists, and is not merely an artifact of the methods used in collecting the data. Similarly, calculating separate indices of size structure based on gear type, because there is no way to aggregate PSD among gear types with different size selectivity, can help to reinforce the conclusions being drawn. If separate measures of PSD show the same relationship with indices of abundance, the results are more robust. Finding a positive relationship between all indices of walleye size structure and largemouth bass abundance and relative abundance reinforces the conclusions drawn from the comparisons of growth rate and abundance: largemouth bass may be preying on walleye. Further, the comparison of PSD and abundance suggests that largemouth bass may be preying specifically on juvenile walleye, as this would have a greater impact on walleye size structure. Predation on juvenile walleye would result in fewer small fish to lower walleye PSD, and could also cause walleye to experience less intra-specific competition at young ages, allowing for greater increases in growth rate.

Finding a negative relationship between walleye recruitment and largemouth bass abundance suggests that largemouth bass may prey on juvenile walleye, and agrees with previous research on the relationship between the two species as well as with research on the impact of predation on recruitment (Santucci and Wahl 1993; Post et al 1998; Fayram et al. 2005). This result also corroborates the results of the comparisons between walleye growth rate and size structure and largemouth bass abundance. A positive relationship between recruitment of one species and abundance of another may indicate a complex ecosystem interaction, such as the second species serving as a substitute prey item for an apex predator that preys on both target species (Ostman 2004). A negative relationship may indicate the second species preying on juvenile members of the first species (Rieman et al. 1991; Rice et al. 1993; Walters and Kitchell 2001).

The relationship between walleye abundance and smallmouth bass abundance is unclear, which agrees with previous research on these species showing varying relationships between abundances of these species and differing degrees of diet and habitat overlap under a range of conditions (Fedoruk 1966; Johnson and Hale 1977; Frey et al. 2003; Fayram et al. 2005; Wuellner et al. 2010). Comparing mark-recapture abundances of each species shows no significant relationship, while comparing relative abundance of each species shows a significant positive relationship. Given that both mark-recapture surveys and electrofishing CPE have been shown to provide reliable measures of abundance and relative abundance, the fact that these metrics do not show the same relationship implies that the interactions between walleye and smallmouth bass may be insignificant (Peterson and Cederholm 1984; Schoenebeck and Hansen 2005). Alternatively, it is possible that sampling error or bias introduced by sampling protocols may have caused either or both of the indices of smallmouth bass abundance to deviate from an accurate representation of the populations being observed.

Finding no significant relationship between walleye growth rate and smallmouth bass abundance and relative abundance supports the conclusion that there may be no significant interaction between these species, which agrees with previous research (Fedoruk 1966; Johnson and Hale 1977; Wuellner et al. 2010). Previous studies have found either no overlap in diet between these species (Fedoruk 1966; Johnson and Hale 1977), or diet overlap centered on non-limiting forage species (Wuellner et al. 2010).

Finding an inconsistent relationship between walleye size structure and indices of smallmouth bass abundance suggests that there may be no significant relationship between them, and agrees with previous research (Fedoruk 1966; Johnson and Hale 1977; Wuellner et al. 2010). When comparing walleye size structure to smallmouth bass abundance and relative abundance, I was again forced to separate PSD based on the types of sampling gear used to collect the data. The results of each of these comparisons, all four of which ostensibly measure the same population demographics, should agree with each other for any positive conclusion to be drawn. The fact that walleye PSD showed a positive relationship to mark-recapture abundance of smallmouth bass, but mixed results when compared to smallmouth bass electrofishing CPE, again supports the conclusion that either the interaction between these species is insignificant or sampling error may have been introduced during data collection.

Finding no significant relationship between walleye recruitment and smallmouth bass abundance and relative abundance supports the conclusion that there may be no significant interaction between these species, which agrees with previous research (Johnson and Hale 1977; Frey et al. 2003; Wuellner et al. 2010). Past studies have found inconsistent or unclear relationships between walleye and smallmouth bass, as well as a lack of predation on walleye by smallmouth bass (Johnson and Hale 1977; Frey et al. 2003; Wuellner et al. 2010).

Largemouth bass growth rates were not related to walleye abundance and relative abundance, which corroborates previous research (Fayram et al. 2005). Given that abundances of these species are negatively related, this suggests that walleye are not driving the interaction between them. This fits with the previous conclusion that largemouth bass may be preying on juvenile walleye, and agrees with previous research that found no predation by walleye on largemouth bass (Fayram et al. 2005).

Comparing largemouth bass size structure to walleye abundance and relative abundance showed no consistent relationship, which agrees with previous research that suggests that largemouth bass do not prey on walleye (Fayram et al. 2005). Again, these indices all ostensibly measure the same population demographics, and so should show the same relationship if interaction occurs. This suggests that the impact of walleye abundance on largemouth bass size structure is not completely understood, and may not be significant at the population level.

Finding no significant relationship between smallmouth bass growth rate and walleye abundance and relative abundance supports the conclusion that there may be no significant interaction between these species, which agrees with previous research (Johnson and Hale 1977; Frey et al. 2003; Wuellner et al. 2010). Finding no consistent relationship between smallmouth bass size structure and either walleye abundance or relative abundance suggests that the impact of walleye abundance on smallmouth bass size structure, if any, is unclear and may not be significant at the population level. This agrees with previous research that found no diet overlap or predator-prey relationship between walleye and smallmouth bass (Johnson and Hale 1977; Frey et al. 2003), as well as with research that found significant but non-limiting diet overlap between these species (Wuellner et al. 2010).

The relationships between walleye demographics and largemouth bass abundance are consistent with what we described *a priori* as indicative of largemouth bass preying on juvenile walleye, and closely agree with previous research (Inskip and Magnuson

1983; Santucci and Wahl 1993; Fayram et al. 2005). A study on Big Pine Lake, Wisconsin examined sport catches of largemouth bass and walleye from 1897-1977, found a negative relationship between these species, and concluded that interpsecies interaction most likely contributed to the relationship (Inskip and Magnuson 1983). A study on Ridge Lake, Illinois examined survival and growth of juvenile walleye in the presence of largemouth bass and found that predation by largemouth bass had severe negative impacts on juvenile walleye (Santucci and Wahl 1993). A study of several datasets from northern Wisconsin lakes, coupled with diet analysis and bioenergetic modeling, found evidence that largemouth bass prey on juvenile walleye (Fayram et al. 2005).

The lack of clear or consistent relationships between walleye demographics and smallmouth bass abundance suggests that in northern Wisconsin lakes there may be no interaction between these species, which agrees with research previously conducted on the relationship between these species (Fedoruk 1966; Johnson Hale 1977; Frey et al. 2003; Fayram et al. 2005; Wuellner et al. 2010). A study on Falcon Lake, Manitoba compared the stomach contents of walleye and smallmouth bass and found no competitive food interaction (Fedoruk 1966). A study on four Minnesota lakes from 1945-1948 introduced smallmouth bass in the presence of established walleye populations and found that interspecific competition did not appear to be a factor in fluctuations of abundance (Johnson and Hale 1977). A study on Big Crooked Lake, Wisconsin examined the stomach contents of walleye and smallmouth bass and found no significant indications of competition or diet overlap (Frey et al. 2003). A study of several datasets from northern Wisconsin lakes, coupled with diet analyses and bioenergetic modeling, found no significant relationship between walleye and smallmouth bass (Fayram et al. 2005). A study on Lake Sharpe, South Dakota compared the stomach contents of walleye and smallmouth bass and found a significant overlap in the consumption of gizzard shad, a non-limiting prey species (Wuellner et al. 2010). Given the lack of consistent sampling methods for smallmouth bass in Wisconsin, however, the lack of a relationship may also be due to limitations of the data. Conducting further sampling and analysis on smallmouth bass populations would be prudent.

MANAGEMENT IMPLICATIONS

This study was correlative, and makes use of pre-existing data collected without this analysis in mind. The lack of readily available diet and habitat data to accompany this analysis limits the strength of my conclusions. This project offers insight into the relationships between the target species, and can guide future research. Dismissing these results out of hand because of their correlative nature would be imprudent, but taking drastic management action on the strength of the available data alone would likely be premature. Further study, including diet analysis, bioenergetic modeling, ecosystem modeling, and manipulative field experiments, will be necessary to strengthen my findings and conclusions.

If largemouth bass prey on juvenile walleye, attempting to optimize both species in the same water is likely counterproductive. Many of the primary tools to manage and enhance recreational angling fisheries rely on benefits to the managed species to accrue for anglers. If enhancing the population of walleye in a lake through stocking or stricter angling regulations does not provide any benefit to angling, then such management efforts is a waste of time and resources.

In lakes with both largemouth bass and walleye populations, special rules for one species or the other may need to be considered because restrictive regulations seeking to manage for both species are impractical. Given the prevalence of harvest-oriented walleye fisheries in Wisconsin, permissive largemouth bass regulations might be considered prudent if anglers could be encouraged to reduce largemouth bass populations through harvest.

If largemouth bass negatively interact with walleye but smallmouth bass do not, this makes a strong case for managing these species separately to avoid unnecessarily restricting the management options for smallmouth bass fisheries where walleye are present. Currently largemouth bass and smallmouth bass in Wisconsin are managed collectively as ‘black bass’.

TABLES

TABLE 1. Northern Wisconsin lakes where walleye and black bass angling regulations were changed in 2010.

Lake	**County**	**Acres**
Bear Lake	Barron	1,348
Horseshoe Lake	Barron	115
Lower Turtle Lake	Barron	286
Upper Turtle Lake	Barron	427
Lake Owen	Bayfield	1,250
Big McKenzie Lake	Burnett	1,129
Middle McKenzie Lake	Burnett	527
Big Butternut Lake	Polk	384
Half Moon Lake	Polk	550
Pipe Lake	Polk	293
Ward Lake	Polk	82
Chain Lake	Rusk	454
Clear Lake	Rusk	94
Island Lake	Rusk	534
McCann Lake	Rusk	126
Nelson Lake	Sawyer	2,716
Whitefish Lake	Sawyer	800
Sissabagama Lake	Sawyer	805
Long Lake	Washburn	3,478
Nancy Lake	Washburn	757

TABLE 2. Parameters of Wisconsin DNR sampling dataset used for analysis before and after screening.

	All Analyses	
	Before Screening	**After Screening**
N (lake/year)	7,672	3,346
Years	1937-2011	1945-2011
Number of Lakes	1,862	1,074

TABLE 3. Stock– and quality–lengths used to calculate proportional stock density (PSD) for walleye, largemouth bass, and smallmouth bass, as reported by Willis et al. (1993).

	Length Class	
Species	**Stock**	**Quality**
Walleye	10 in	15 in
Largemouth Bass	8 in	12 in
Smallmouth Bass	7 in	11 in

TABLE 4. Parameters of Spearman's rank correlations and measurement error ratio power models comparing walleye population demographics to largemouth bass abundance in northern Wisconsin lakes.

Walleye (Y) vs. Largemouth Bass (X)										
Comparison (Y vs. X)	**Spearman's ρ**	**N**	**T**	**P (two-tailed)**	**Significant α=0.05?**	**Sequential Bonferroni Value**	**Bonferroni Significant?**	**Alpha**	**Beta**	**R^2**
Walleye Density vs. Largemouth Bass Density	-0.2983	70	2.5771	0.0061	Yes	0.0250	Yes	1.8926	-0.2240	0.1359
Walleye CPE vs. Largemouth Bass CPE	-0.2482	343	4.7314	0.0000	Yes	0.0063	Yes	0.0280	-1.0560	0.2299
Walleye MLA3 vs. Largemouth Bass Density	0.5315	48	4.2555	0.0000	Yes	0.0083	Yes	12.4304	0.0433	0.2522
Walleye MLA3 vs. Largemouth Bass CPE	0.6712	34	5.1221	0.0000	Yes	0.0071	Yes	14.6810	0.1009	0.5218
Walleye PSD Net vs. Largemouth Bass Density	0.3150	74	2.8166	0.0031	Yes	0.0125	Yes	79.9875	0.0534	0.1146
Walleye PSD EF vs. Largemouth Bass Density	0.2573	84	2.4110	0.0091	Yes	0.0500	Yes	73.1207	0.0522	0.0852
Walleye PSD Net vs. Largemouth Bass CPE	0.4306	145	5.7056	0.0000	Yes	0.0056	Yes	91.1415	0.0683	0.1674
Walleye PSD EF vs. Largemouth Bass CPE	0.3370	335	6.5309	0.0000	Yes	0.0050	Yes	76.8528	0.1527	0.1110
Walleye YoY CPE vs. Largemouth Bass Density	-0.3495	53	2.6641	0.0051	Yes	0.0167	Yes	5.4357	-0.7313	0.3566
Walleye YoY CPE vs. Largemouth Bass CPE	-0.5608	39	4.1205	0.0001	Yes	0.0100	Yes	0.5571	-1.0953	0.6962

TABLE 5. Parameters of Spearman's rank correlations and measurement error ratio power models comparing walleye population demographics to smallmouth bass abundance in northern Wisconsin lakes.

Walleye (Y) vs. Smallmouth Bass (X)										
Comparison (Y vs. X)	Spearman's ρ	N	T	P (two-tailed)	Significant α=0.05?	Sequential Bonferroni Value	Bonferroni Significant?	Alpha	Beta	R^2
Walleye Density vs. Smallmouth Bass Density	-0.2350	53	1.7269	0.0451	No	0.0083	No	2.0828	-0.6038	0.1970
Walleye CPE vs. Smallmouth Bass CPE	0.2311	183	3.1959	0.0008	Yes	0.0056	Yes	79.4410	2.0169	0.5114
Walleye MLA3 vs. Smallmouth Bass Density	0.0088	32	0.0482	0.4809	No	0.0500	No	12.0735	0.0087	0.0116
Walleye MLA3 vs. Smallmouth Bass CPE	-0.0571	20	0.2428	0.4054	No	0.0250	No	13.2140	0.0246	0.0225
Walleye PSD Net vs. Smallmouth Bass Density	0.2952	55	2.2489	0.0143	Yes	0.0063	No	67.3583	0.1114	0.0737
Walleye PSD EF vs. Smallmouth Bass Density	0.3905	84	3.8406	0.0001	Yes	0.0050	Yes	48.8915	0.2693	0.2462
Walleye PSD Net vs. Smallmouth Bass CPE	-0.1050	92	1.0013	0.1597	No	0.0125	No	66.5820	-0.0237	0.0049
Walleye PSD EF vs. Smallmouth Bass CPE	-0.1482	181	2.0056	0.0232	Yes	0.0071	No	35.9972	-0.0797	0.0178
Walleye YoY CPE vs. Smallmouth Bass Density	-0.1629	42	1.0440	0.1513	No	0.0100	No	1.8234	-6.8947	0.7946
Walleye YoY CPE vs. Smallmouth Bass CPE	0.2279	21	1.0201	0.1599	No	0.0167	No	1.0373E+11	9.8621	0.7632

TABLE 6. Parameters of Spearman's rank correlations and measurement error ratio power models comparing largemouth bass population demographics to walleye abundance in northern Wisconsin lakes.

Largemouth Bass (Y) vs. Walleye (X)										
Comparison (Y vs. X)	**Spearman's ρ**	**N**	**T**	**P (two-tailed)**	**Significant α=0.05?**	**Sequential Bonferroni Value**	**Bonferroni Significant?**	**Alpha**	**Beta**	**R^2**
Largemouth Bass Density vs. Walleye Density	-0.2983	70	2.5771	0.0061	Yes	0.0125	Yes	17.2587	-4.4648	0.6209
Largemouth Bass CPE vs Walleye CPE	-0.2482	343	4.7314	0.0000	Yes	0.0071	Yes	0.0339	-0.9469	0.1952
Largemouth Bass MLA3 vs. Walleye Density	0.0930	55	0.6800	0.2497	No	0.0500	No	9.0733	0.0175	0.0181
Largemouth Bass MLA3 vs. Walleye CPE	0.2852	46	1.9735	0.0273	No	0.0167	No	9.3314	0.0198	0.0497
Largemouth Bass PSD Net vs. Walleye Density	0.1890	251	3.0372	0.0013	Yes	0.0100	Yes	76.2485	0.0689	0.0104
Largemouth Bass PSD EF vs. Walleye Density	0.1515	267	2.4955	0.0066	Yes	0.0063	Yes	68.1045	0.0573	0.0088
Largemouth Bass PSD Net vs. Walleye CPE	0.1115	119	1.2133	0.1137	No	0.0250	No	82.1053	0.0370	0.0174
Largemouth Bass PSD EF vs. Walleye CPE	0.1730	380	3.4158	0.0004	Yes	0.0083	Yes	67.1542	0.0504	0.0180

TABLE 7. Parameters of Spearman's rank correlations and measurement error ratio power models comparing smallmouth bass population demographics to walleye abundance in northern Wisconsin lakes.

Smallmouth Bass (Y) vs. Walleye (X)										
Comparison (Y vs. X)	**Spearman's ρ**	**N**	**T**	**P (two-tailed)**	**Significant α=0.05?**	**Sequential Bonferroni Value**	**Bonferroni Significant?**	**Alpha**	**Beta**	**R^2**
Smallmouth Bass Density vs. Walleye Density	-0.2350	53	1.7269	0.0451	No	0.0083	No	3.3710	-1.6562	0.2014
Smallmouth Bass CPE vs Walleye CPE	0.2311	183	3.1959	0.0008	Yes	0.0071	Yes	0.1143	0.4958	0.0958
Smallmouth Bass MLA3 vs. Walleye Density	0.0845	43	0.5429	0.2950	No	0.0500	No	9.6564	0.0120	0.0052
Smallmouth Bass MLA3 vs. Walleye CPE	0.3497	12	1.1802	0.1314	No	0.0167	No	9.1934	0.0241	0.2625
Smallmouth Bass PSD Net vs. Walleye Density	-0.1637	188	2.2630	0.0124	Yes	0.0083	No	92.0997	-0.0463	0.0065
Smallmouth Bass PSD EF vs. Walleye Density	0.1113	232	1.6991	0.0453	No	0.0125	No	73.1207	0.0522	0.0168
Smallmouth Bass PSD Net vs. Walleye CPE	0.0716	68	0.5829	0.2810	No	0.0250	No	89.2385	0.0203	0.0092
Smallmouth Bass PSD EF vs. Walleye CPE	0.2204	205	3.2189	0.0007	Yes	0.0063	Yes	69.2494	0.1248	0.0819

FIGURES

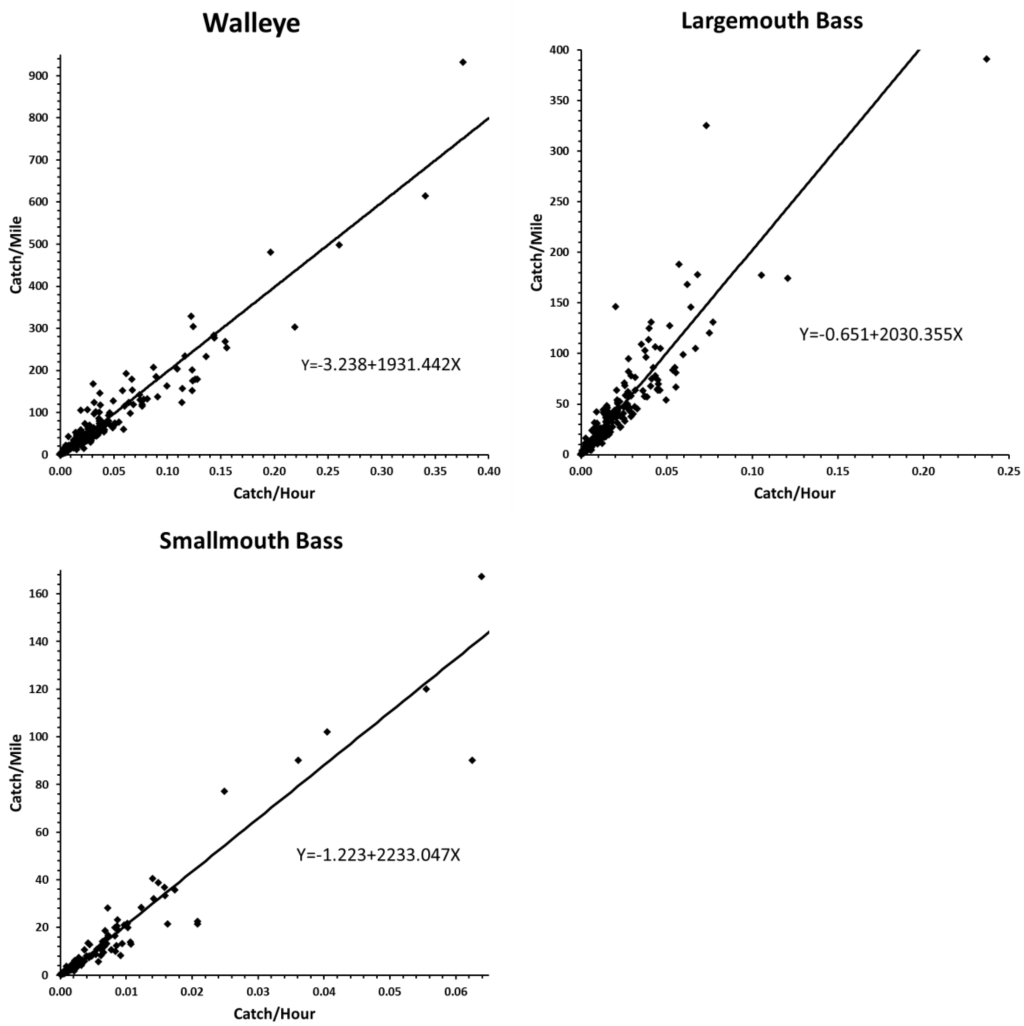


FIGURE 1. Catch per mile of electrofishing plotted against catch per hour electrofishing for walleye, largemouth bass, and smallmouth bass in northern Wisconsin lakes during 1945-2011, fit with a geometric mean regression function (equation in figure).

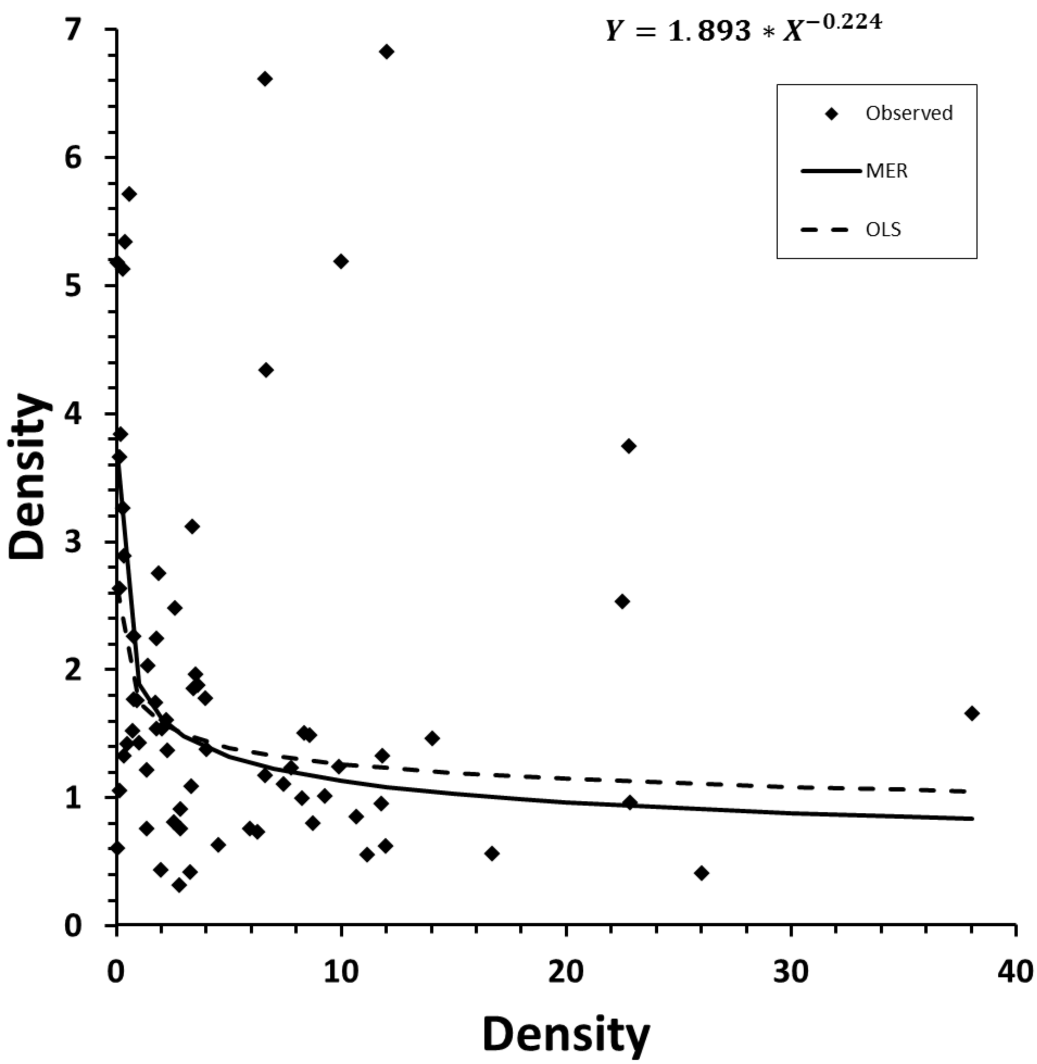


FIGURE 2. Walleye density plotted against largemouth bass density in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

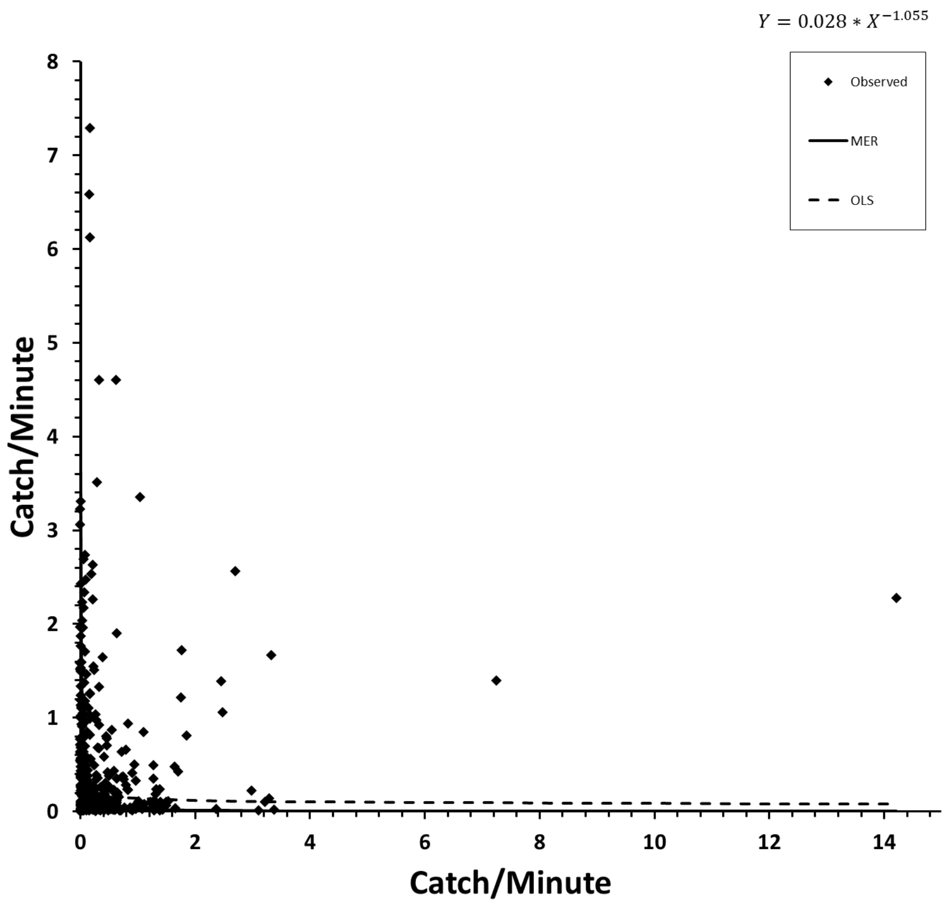


FIGURE 3. Walleye catch per minute of electrofishing plotted against largemouth bass catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

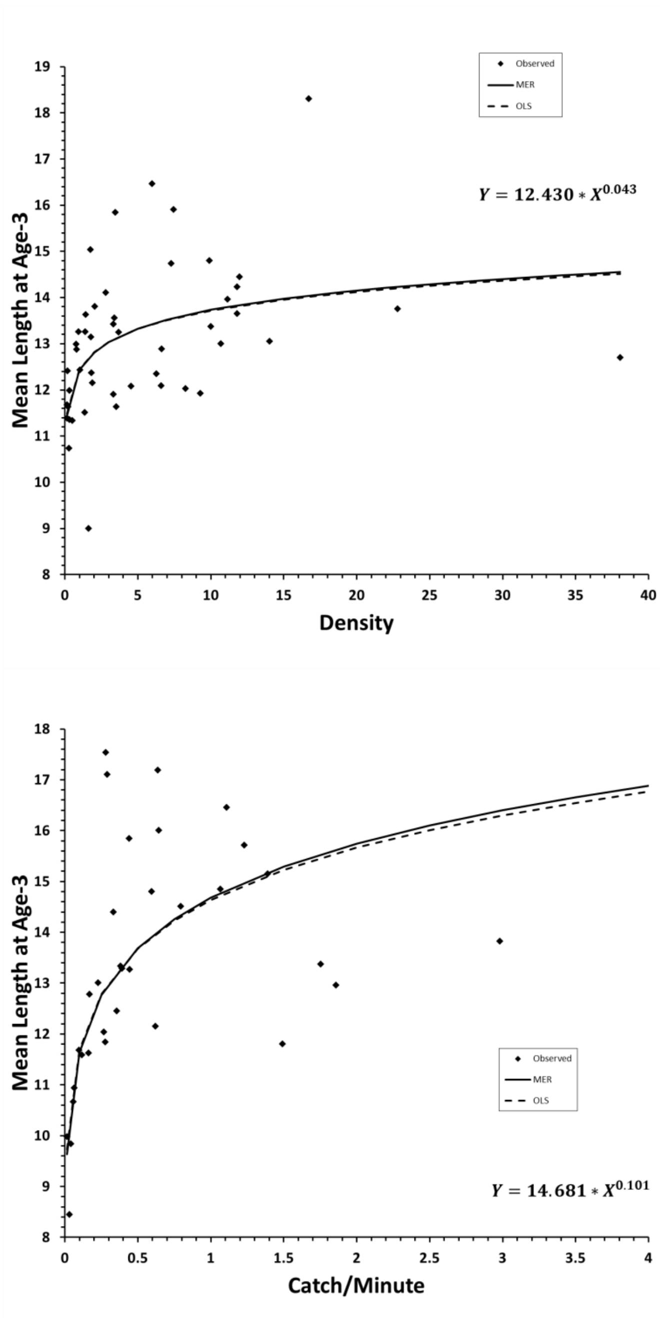


FIGURE 4. Walleye mean length at age-3 plotted against largemouth bass density and catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

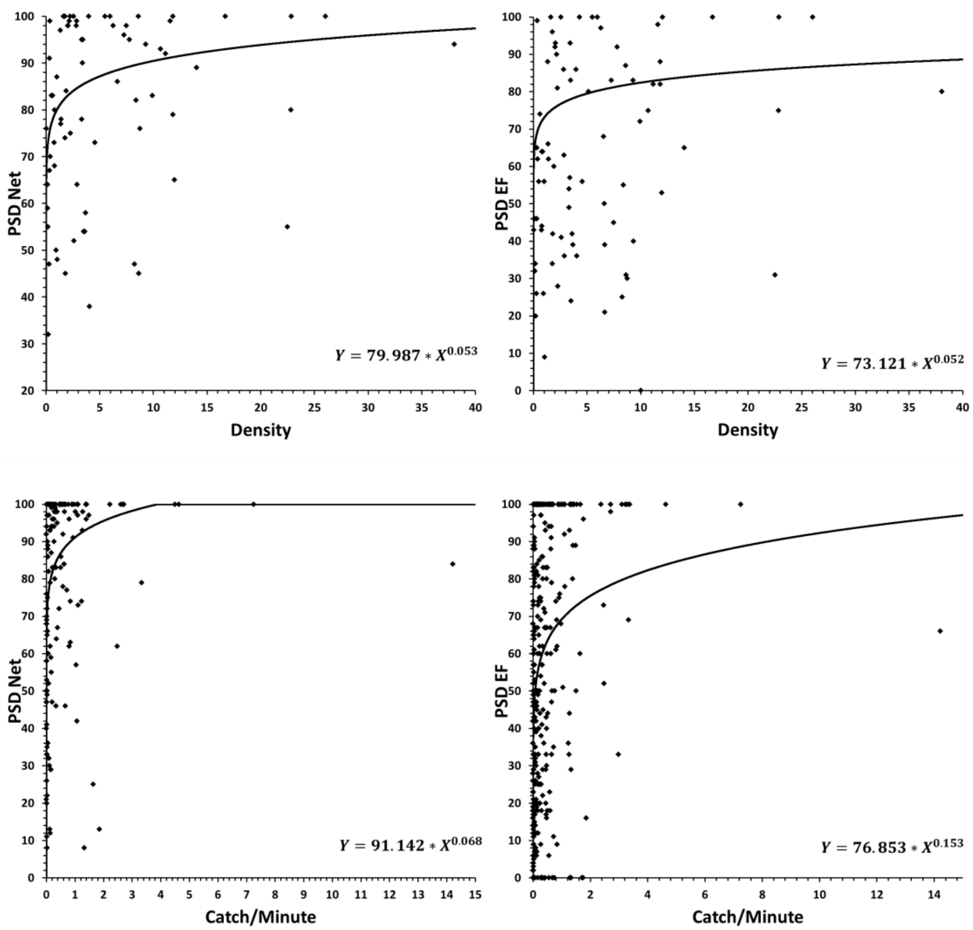


FIGURE 5. Walleye proportional stock density from net-based and electrofishing-based sampling gears plotted against largemouth bass density and catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model.

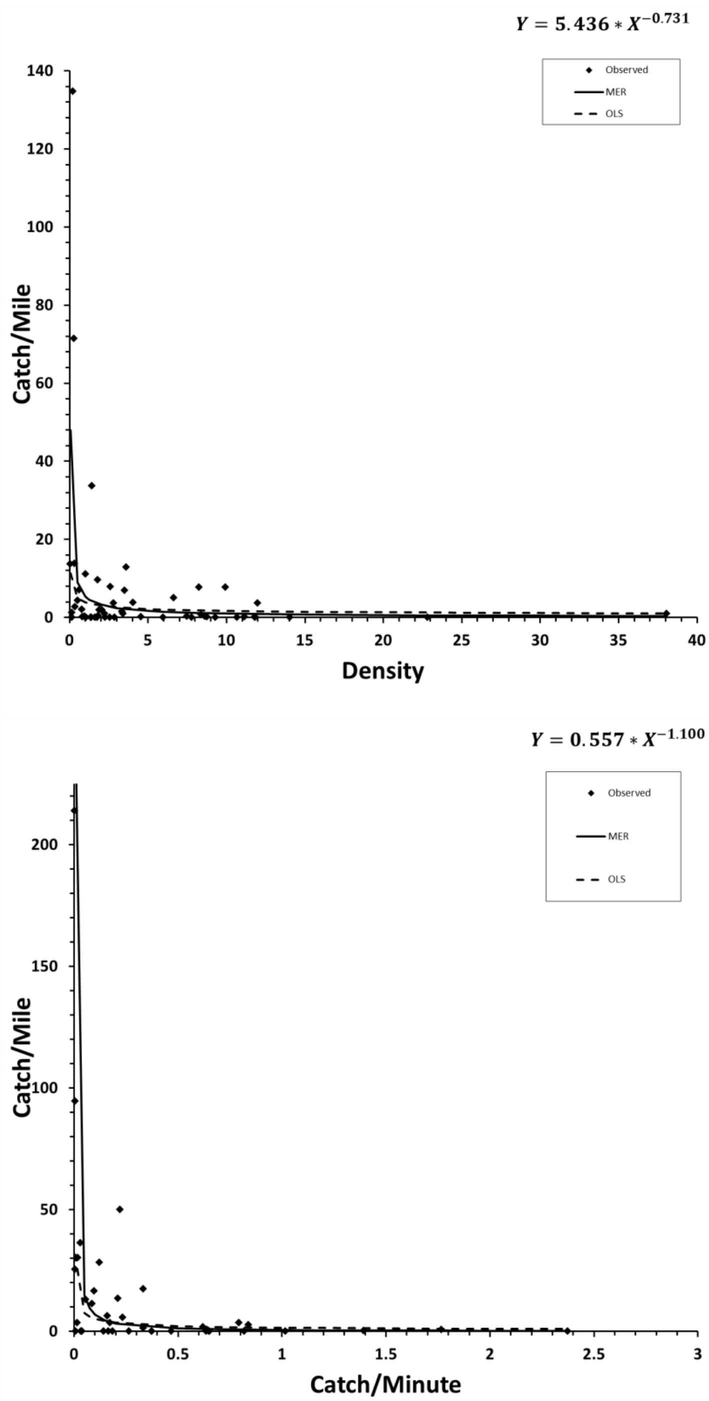


FIGURE 6. Walleye age-0 electrofishing catch per mile of electrofishing plotted against largemouth bass density and largemouth bass catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

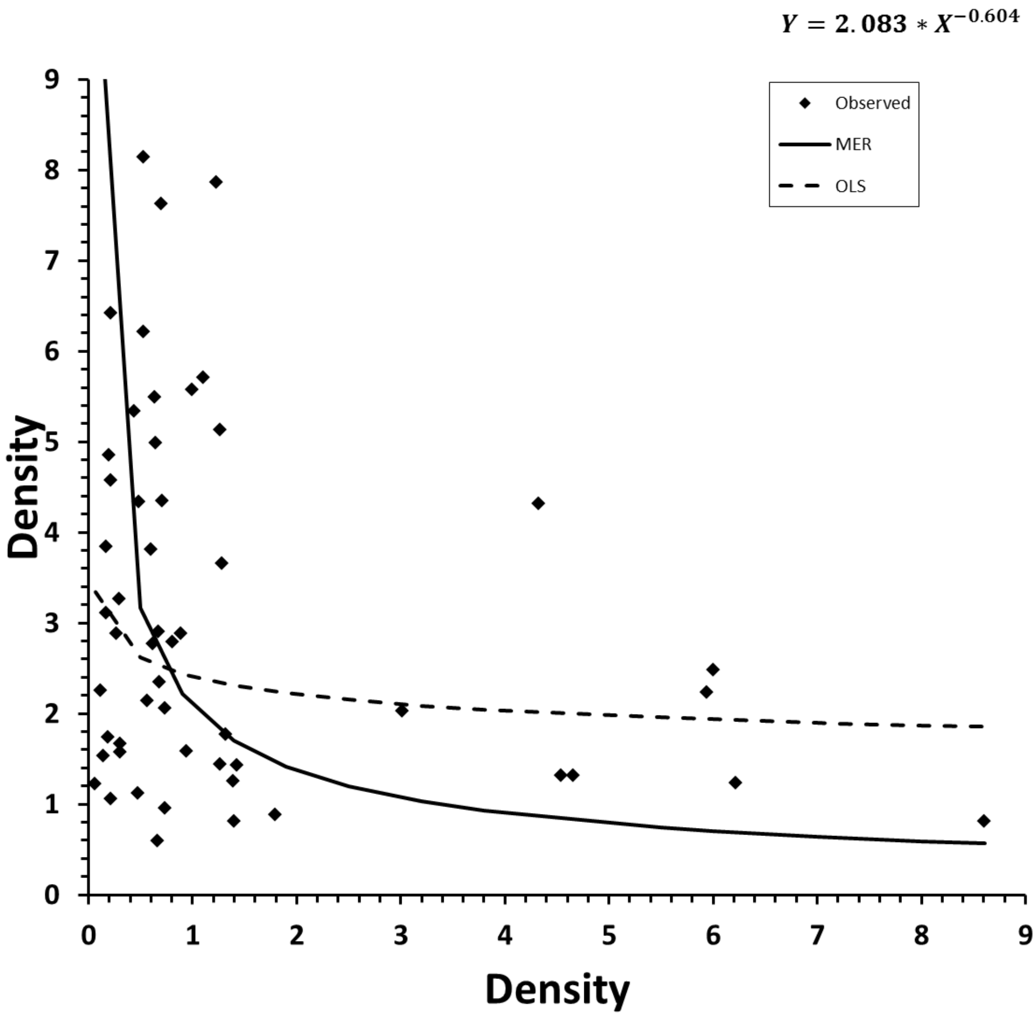


FIGURE 7. Walleye density plotted against smallmouth bass density in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

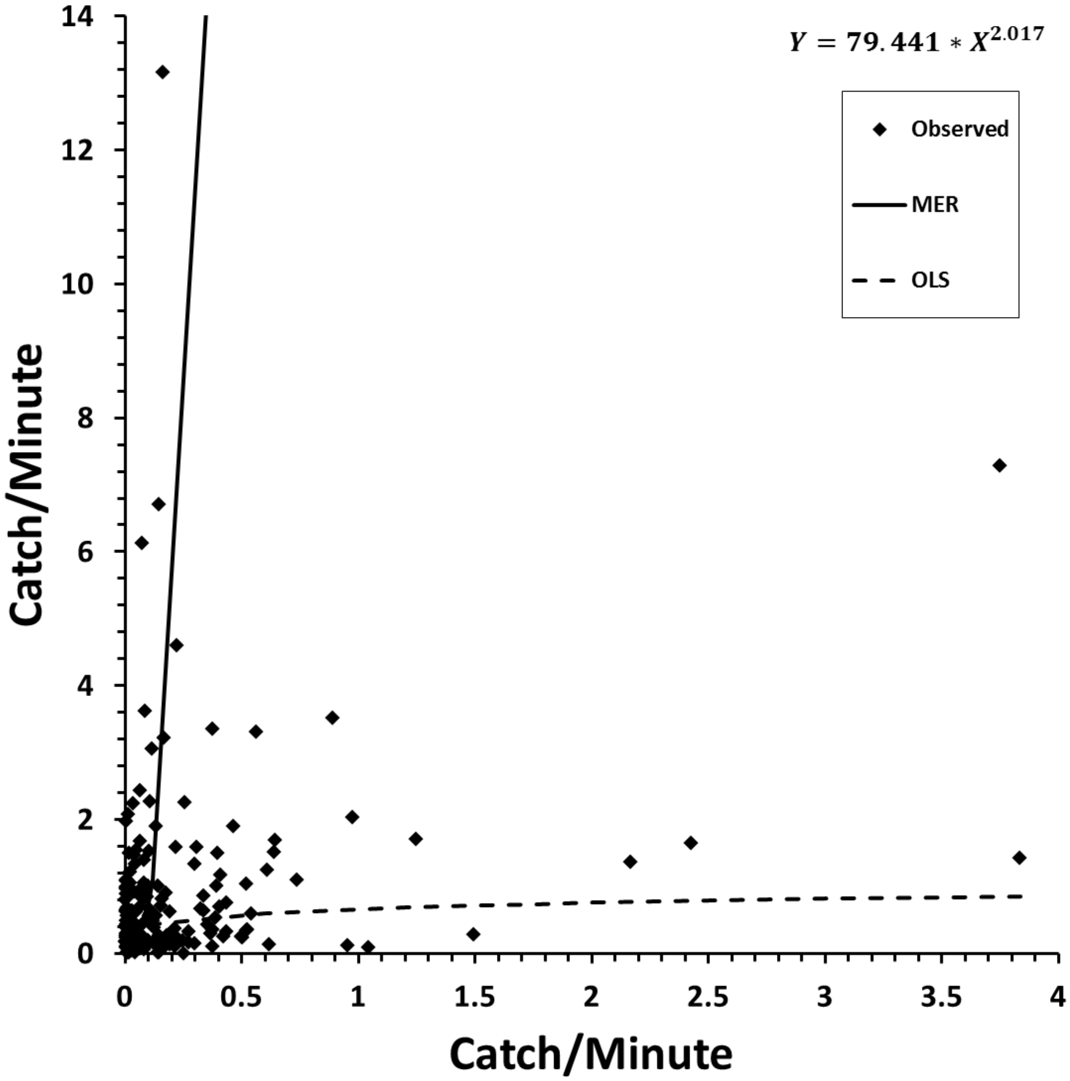
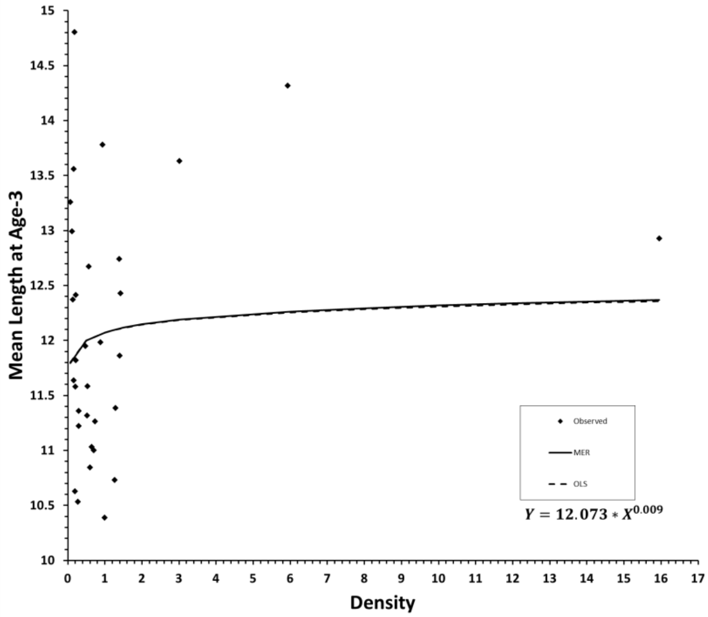


FIGURE 8. Walleye catch per minute of electrofishing plotted against smallmouth bass catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.



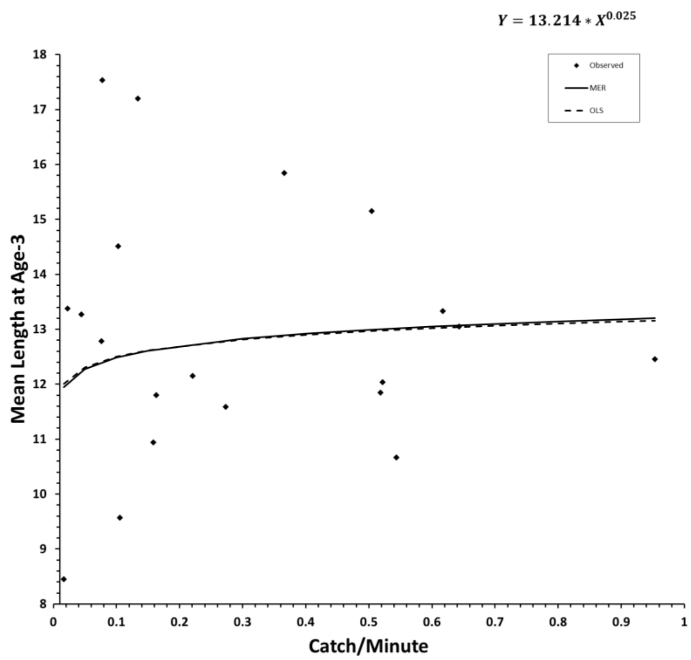


FIGURE 9. Walleye mean length at age-3 plotted against smallmouth bass density and catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS and measurement error ratio (MER; equation in figure) methods.

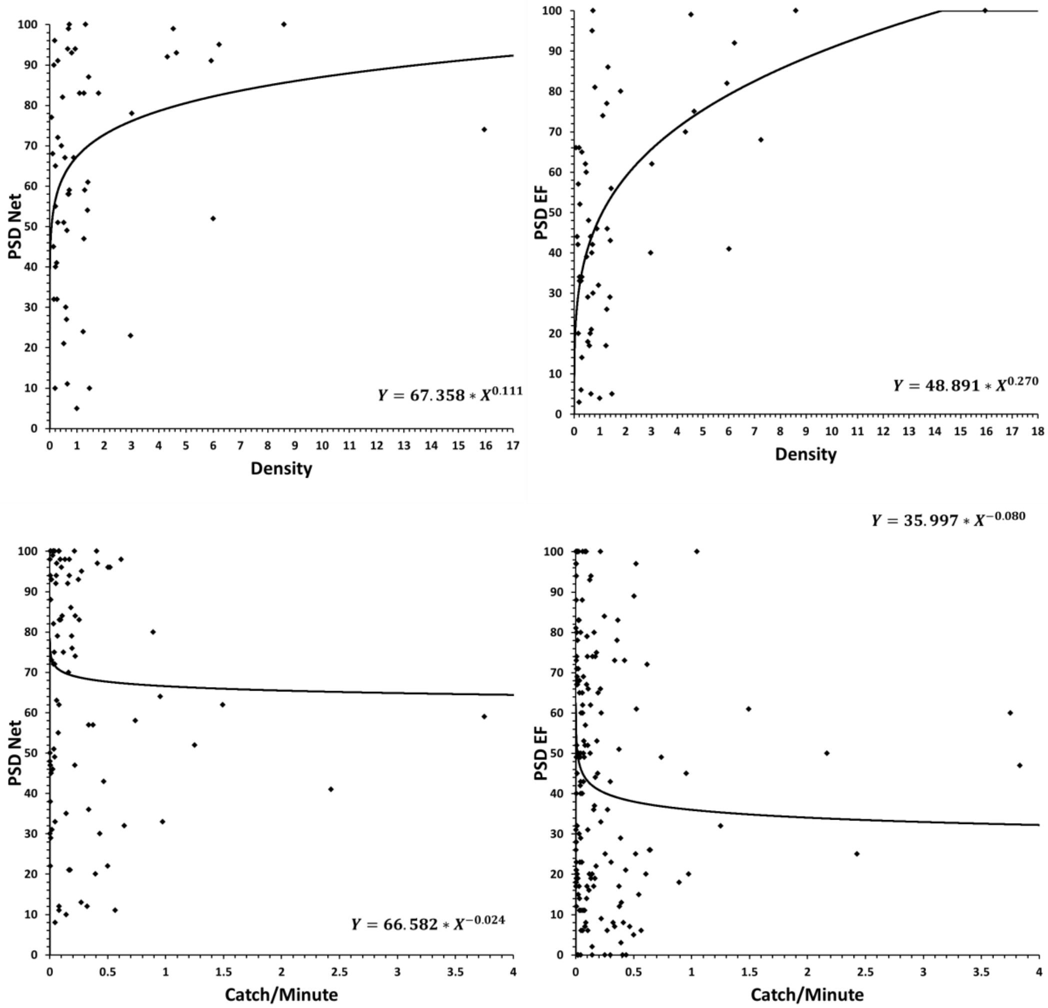


FIGURE 10. Walleye proportional stock density from net-based and electrofishing-based sampling gears plotted against smallmouth bass density and catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model.

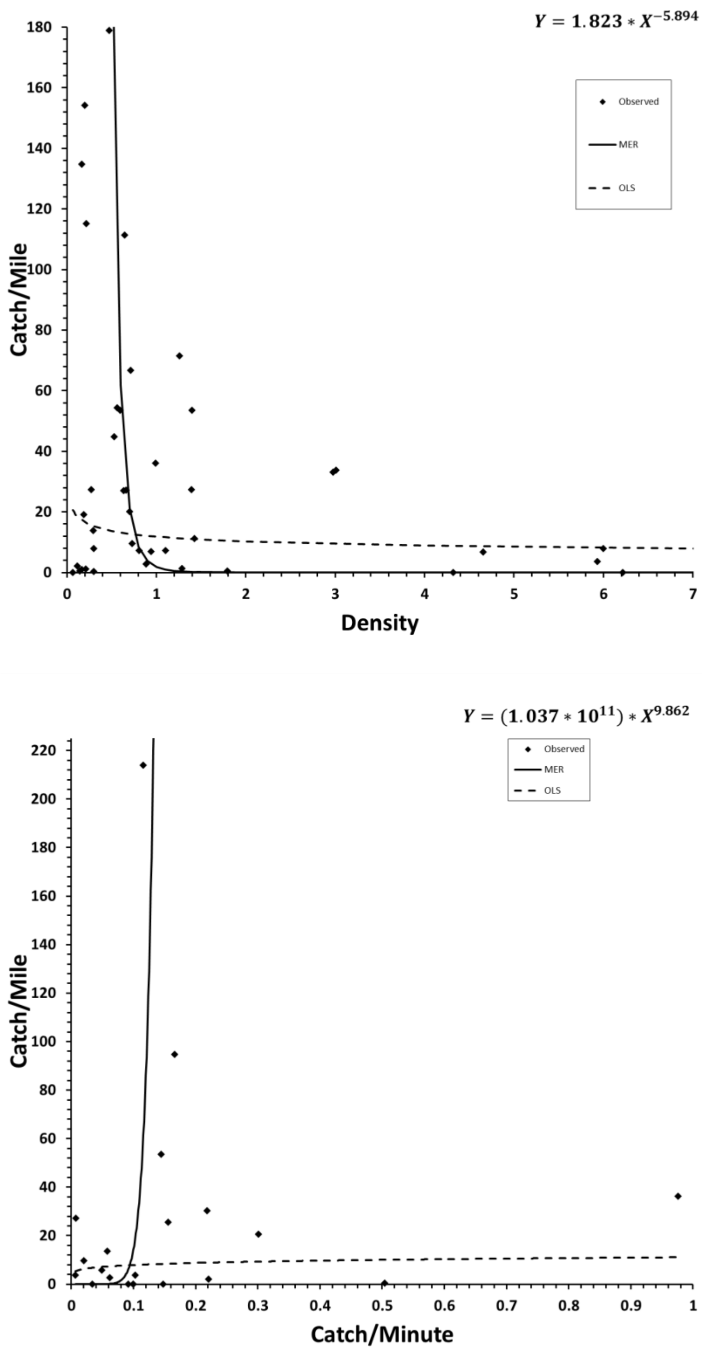


FIGURE 11. Walleye age-0 electrofishing catch per mile of electrofishing plotted against smallmouth bass density and smallmouth bass catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

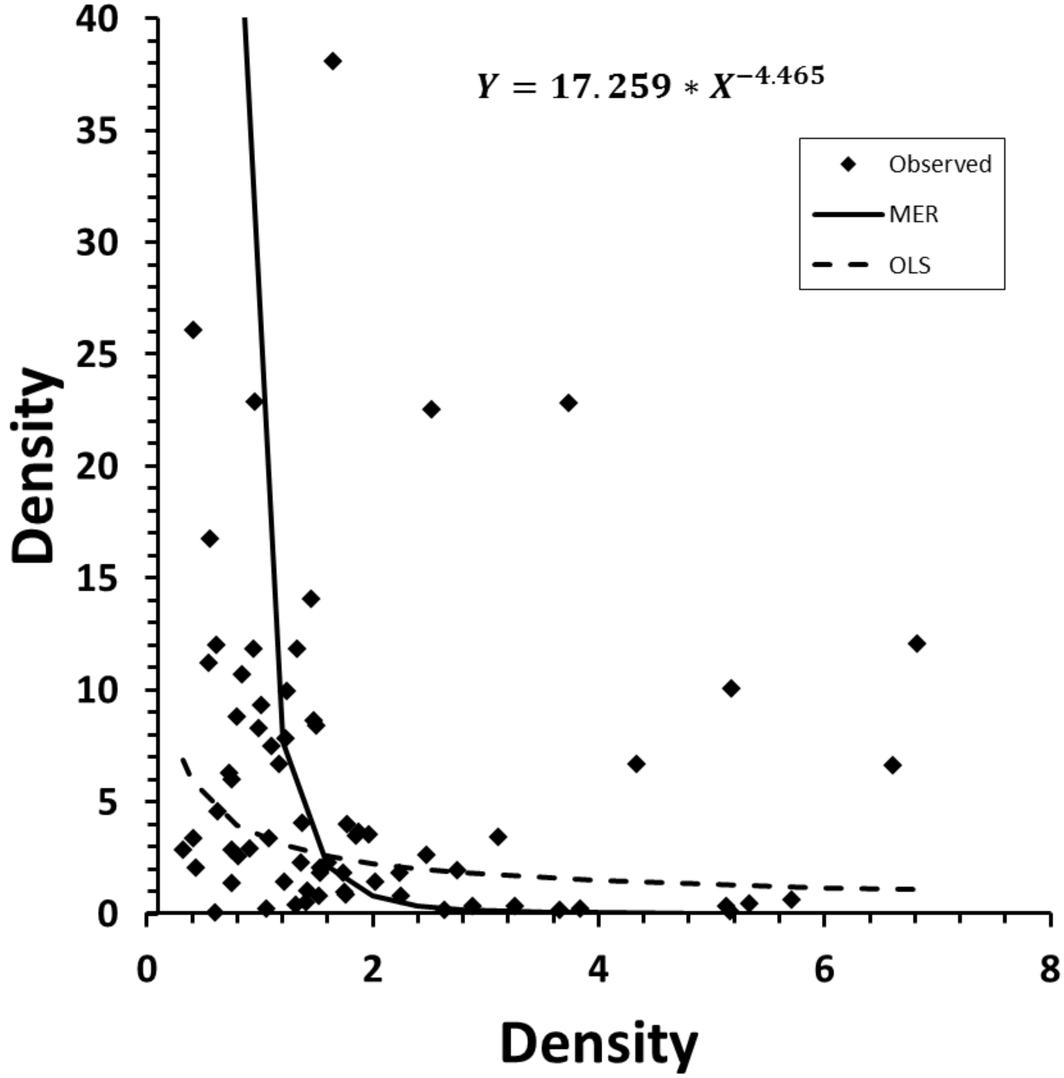


FIGURE 12. Largemouth bass density plotted against walleye density in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

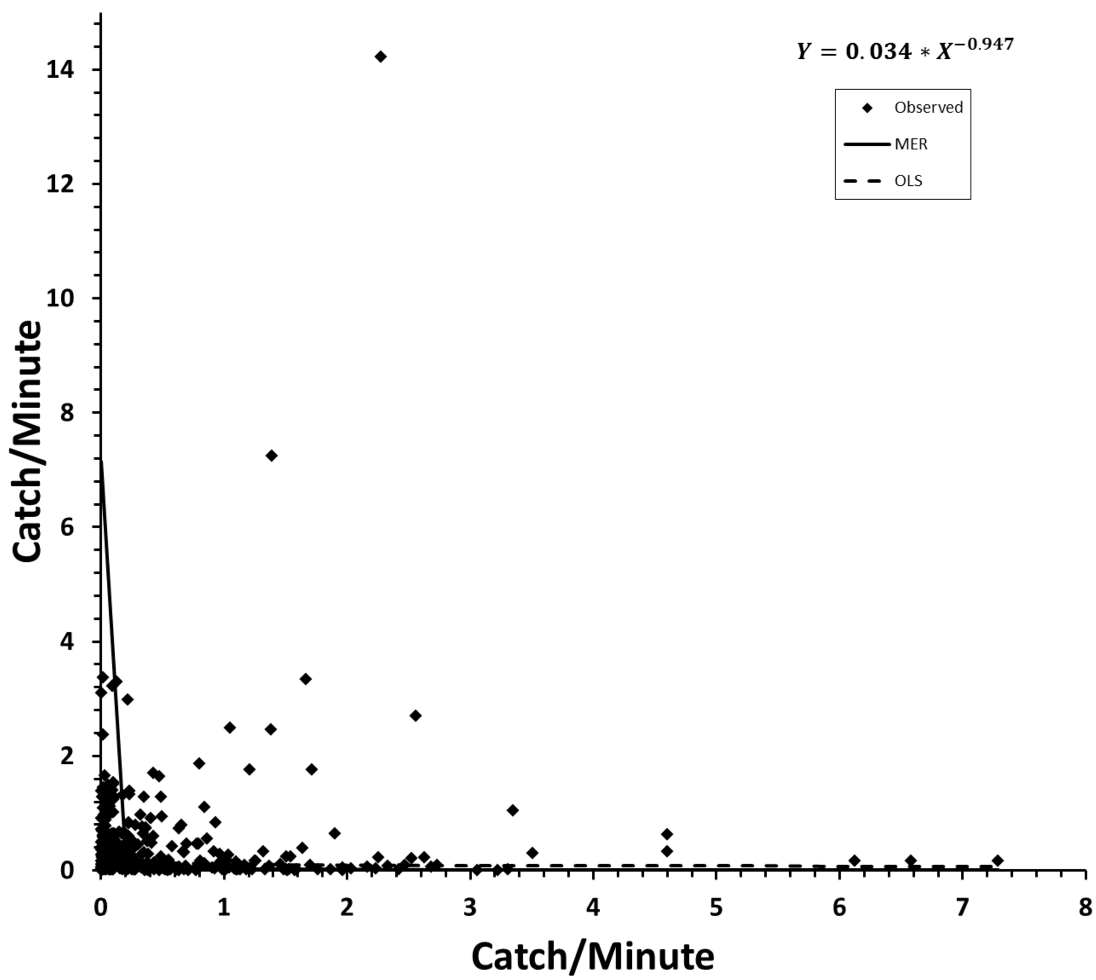


FIGURE 13. Largemouth bass catch per minute of electrofishing plotted against walleye catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

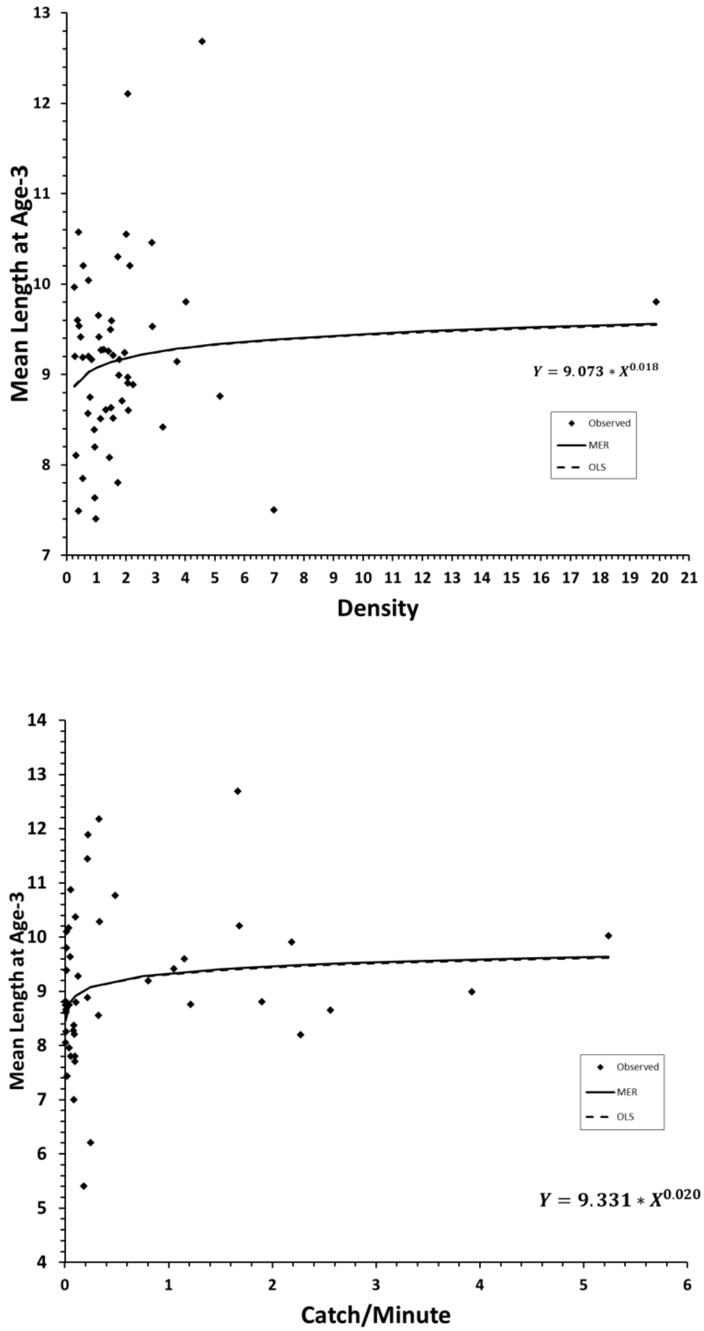


FIGURE 14. Largemouth bass mean length at age-3 plotted against walleye density and catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

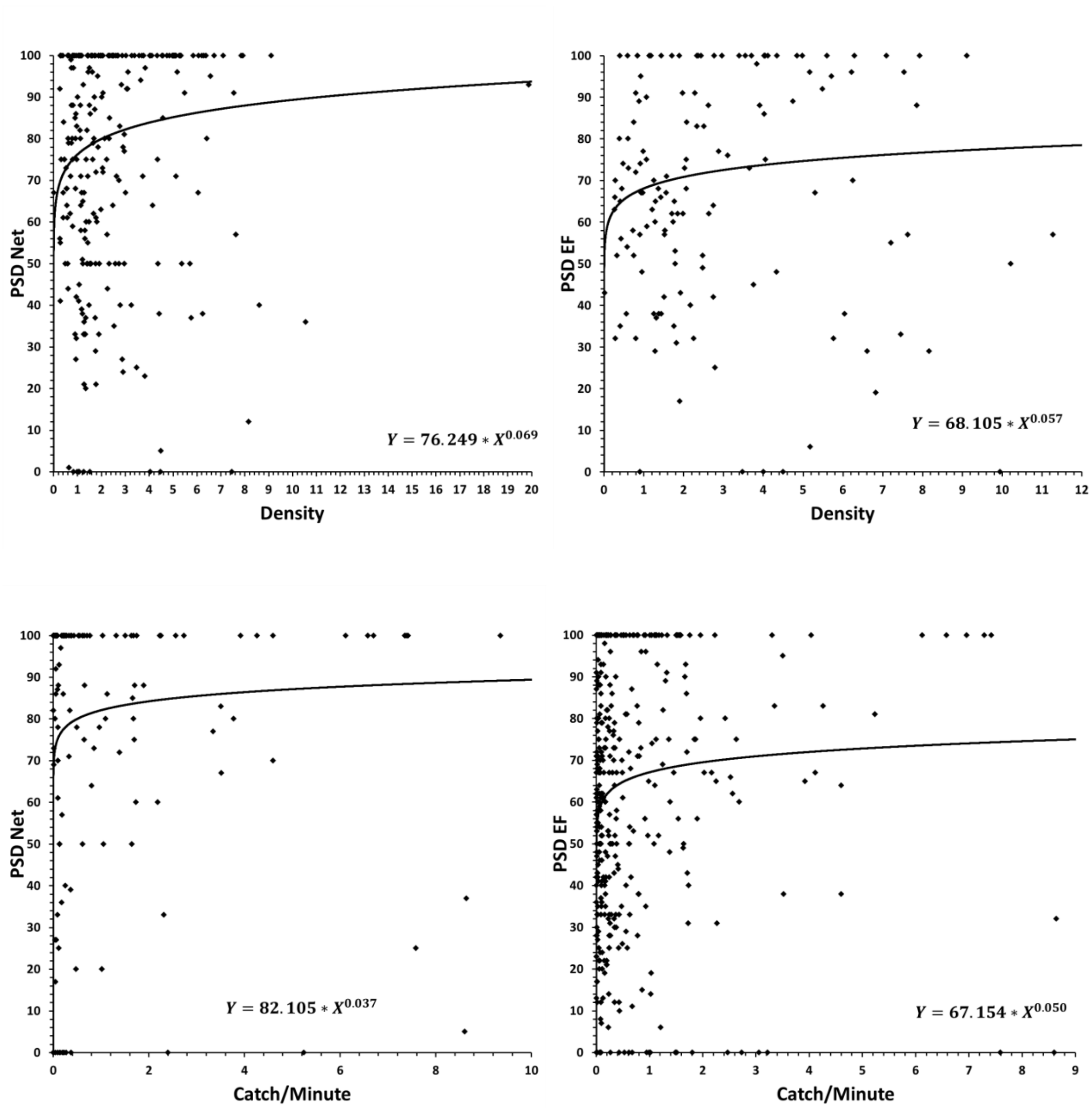


FIGURE 15. Largemouth bass proportional stock density from net-based and electrofishing-based sampling gears plotted against walleye density and catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model.

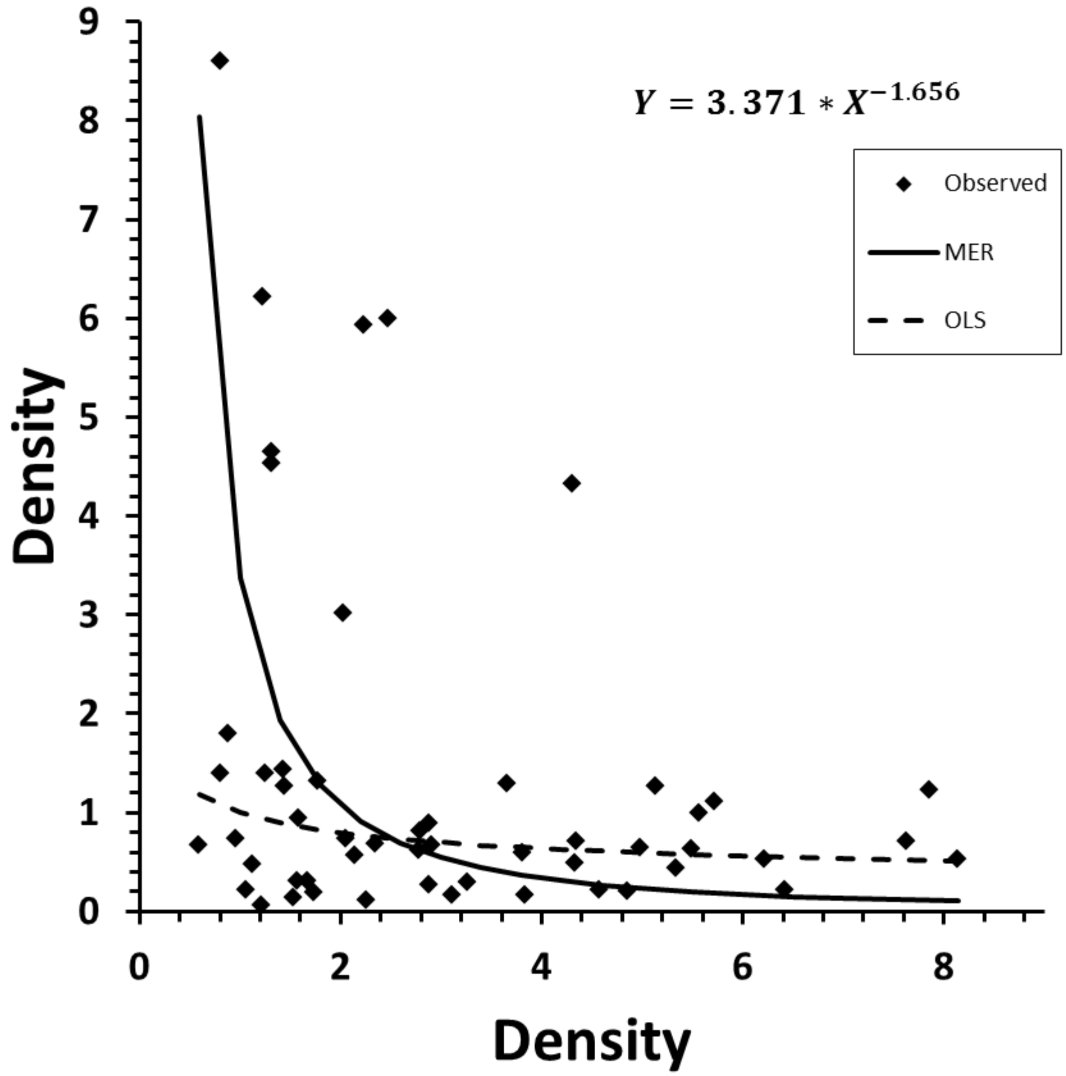


FIGURE 16. Smallmouth bass density plotted against walleye density in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

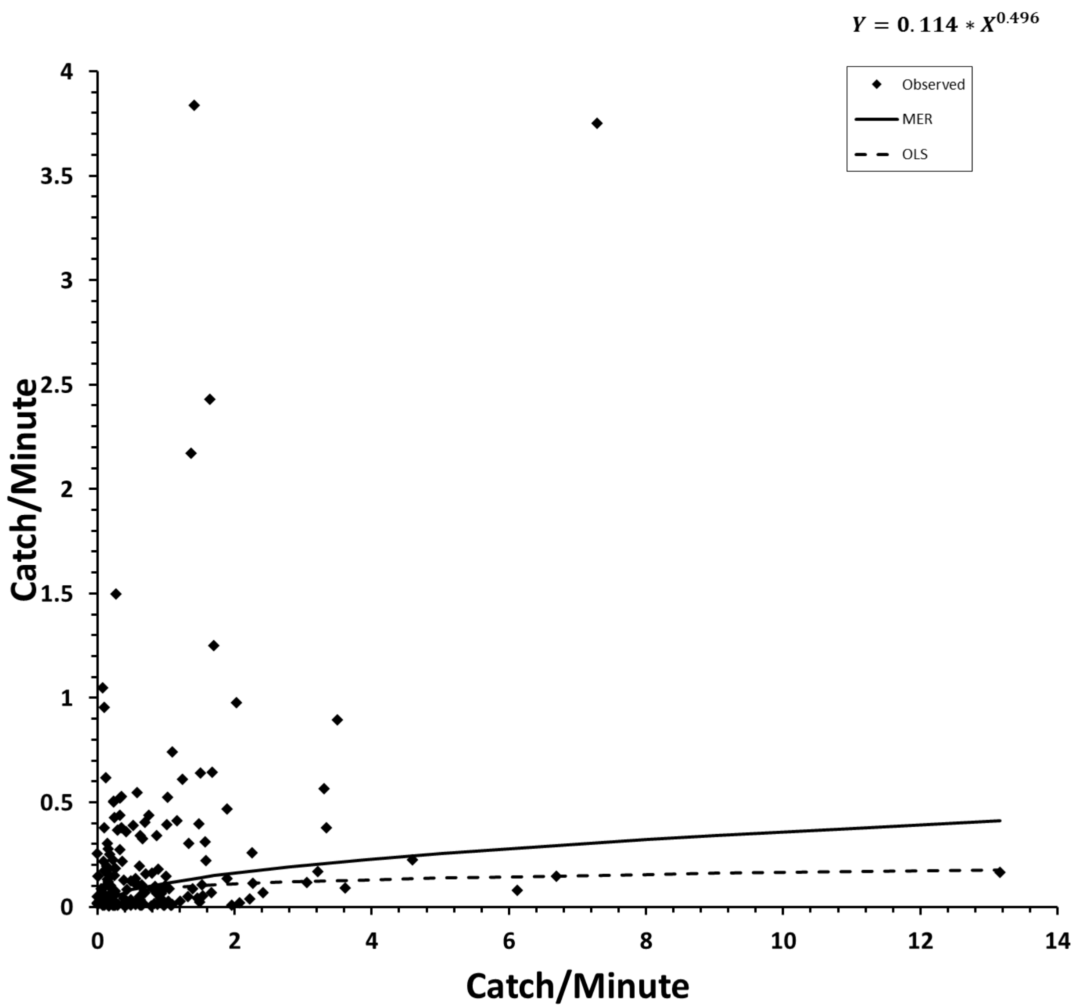


FIGURE 17. Smallmouth bass catch per minute of electrofishing plotted against walleye catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

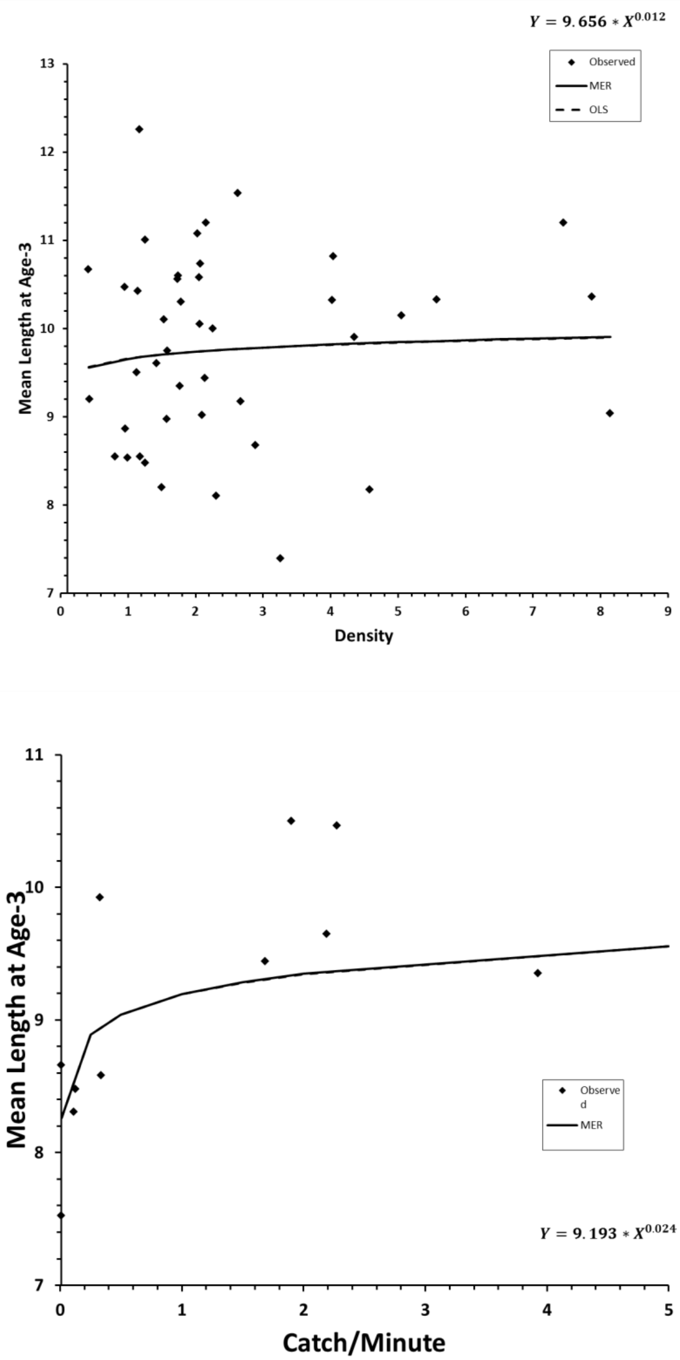


FIGURE 18. Smallmouth bass mean length at age-3 plotted against walleye density and catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model using both ordinary least squares (OLS) and measurement error ratio (MER; equation in figure) methods.

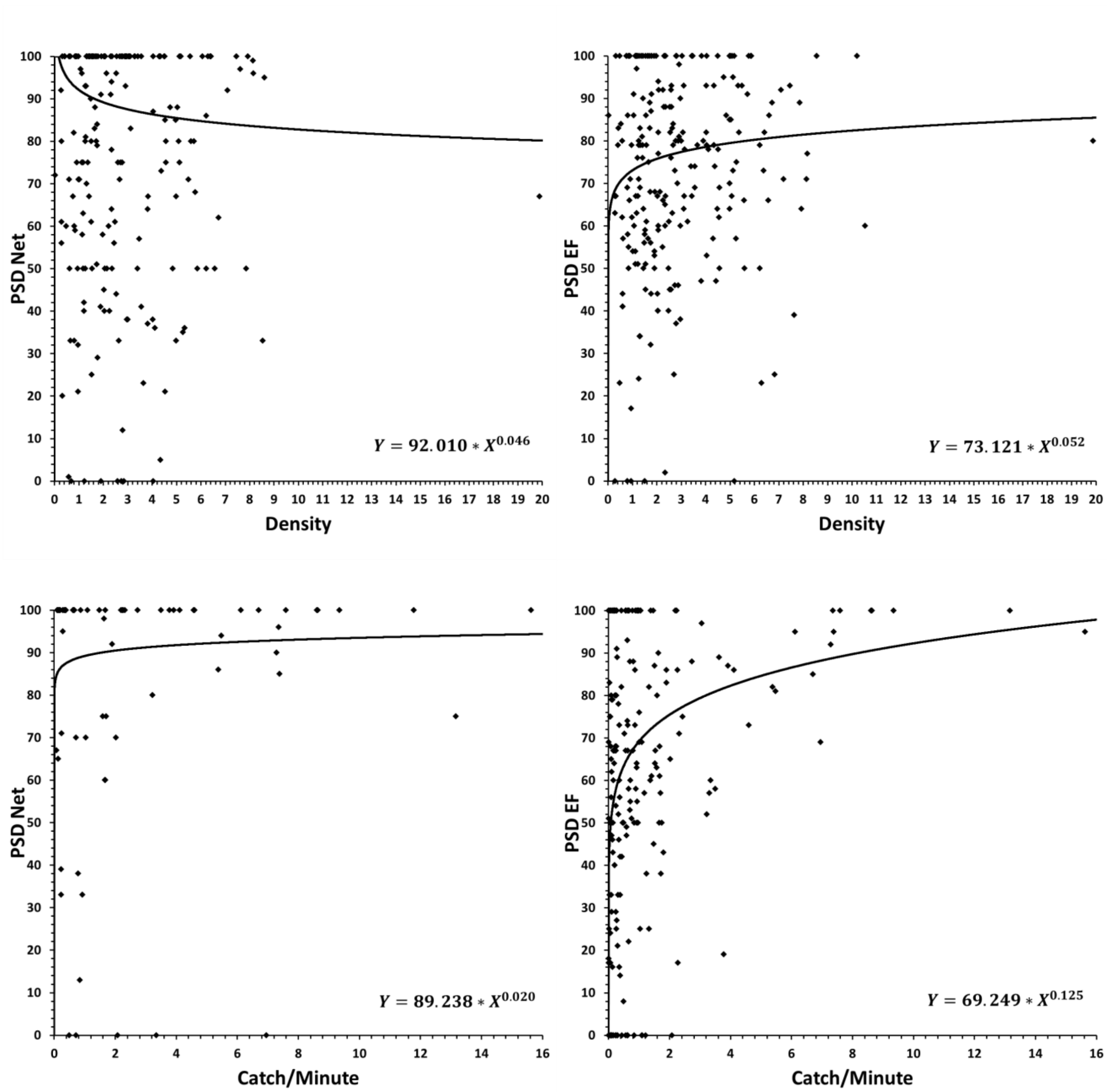


FIGURE 19. Smallmouth bass proportional stock density from net-based and electrofishing-based sampling gears plotted against walleye density and catch per minute of electrofishing in northern Wisconsin lakes during 1945-2011, fit with a power model.

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