Interactions between Walleye and Black Bass in Lakes: A Literature Review

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Introduction

Fishery managers are beginning to realize the low probability of maintaining fish community integrity and satisfactory fishing for self-sustaining populations of walleye and largemouth bass in the same lake. Ryder and Kerr (1978) illustrated the instability of mixed assemblages of percids and centrarchids in lakes bordering between mesotrophy and eutrophy (Figure 1). Based on their model and subsequent research throughout the Midwest, the following hypothesis has emerged: In a wide range of meso-eutrophic lakes with environmental conditions and prey assemblages conducive to the reproduction, growth, and survival of walleye and largemouth bass, one or the other becomes dominant until exogenous forces – changes in climate, habitat, or differential exploitation by humans – shift the unstable relationship.

Evans et al. (1987) argued the need for improved understanding of community and ecosystem dynamics in fishery management based on the failure of traditional single-species models and on growing evidence that species interactions govern the production dynamics of aquatic ecosystems. Research in northern Wisconsin lakes has identified inverse relationships between the relative abundance of walleye and largemouth bass in co-occurring populations (Nate et al. 2003; Fayram et al. 2005). Several studies documenting predation and diet overlap between walleye and largemouth bass suggest these species are classic intra-guild predators as defined by Polis et al. (1989). This review summarizes the extent to which these potential competitors have been shown to eat each other and to eat the same food in similar habitat. Mechanisms identified in field and laboratory studies are examined. Adapting the criteria described by MacLean and Magnuson (1977) for estimating the likelihood of competitive interactions between species, the results of experimental manipulations are examined for consistency with the hypothesis that walleye and largemouth bass are intra-guild predators.

Smallmouth bass interactions with walleye and largemouth bass are included in this review in order to initiate discussion of a policy that treats all black bass as ecological equivalents for purposes of regulating angler harvest in Wisconsin. All these interactions have serious implications for fishery managers who must select harvest strategies responsive to the known preferences of sport anglers and native subsistence fishers for walleye over largemouth bass in most meso-eutrophic lakes capable of supporting either as the dominant predator.

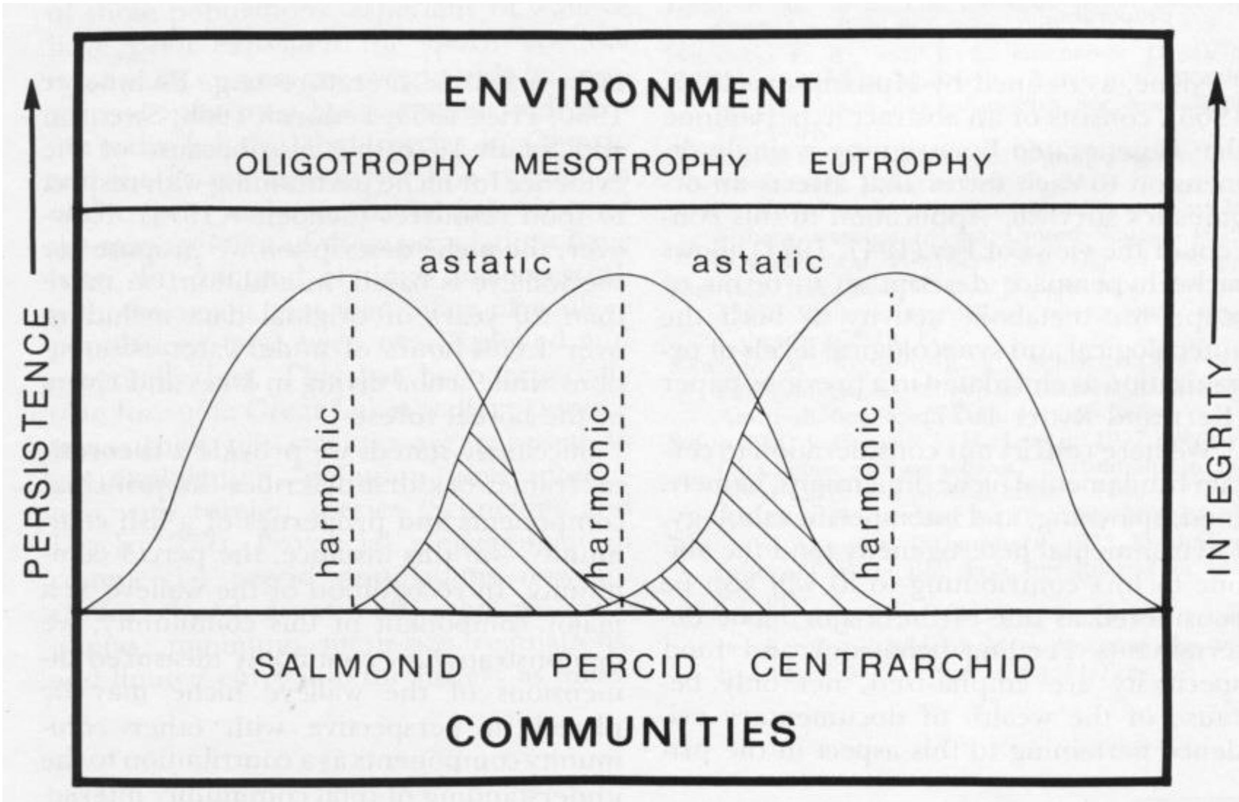

Figure 1. Schematic representations of three fish communities of the boreal forest zone showing the medians of central tendency (----) producing harmonic species associations complementary to prevailing environmental conditions. This, in turn, results in high levels of community persistence and integrity. The crosshatched areas indicate astatic species associations of low persistence and variable levels of community integrity. *Reproduced from Ryder and Kerr (1978).*

<u>Criteria for Review</u>

Polis et al. (1989) defined intra-guild predation as “the killing and eating of species that use similar, often limiting, resources and are thus potential competitors.” Thus, intra-guild predators (IGPs) are potential competitors that eat each other (e.g., muskellunge and northern pike). To evaluate whether walleye and black bass are IGPs in meso-eutrophic lakes, I slightly modified four of the criteria described by MacLean and Magnuson (1977) for use in evaluating inter-specific competition. The criteria for this review are: 1) relative abundance of suspected IGPs should be inversely related; 2) suspected IGPs should eat each other and use common resources (e.g., prey and habitat); 3) suspected IGPs should influence each other’s rate processes (e.g., recruitment and/or growth); and 4) results of experimental manipulations should be consistent with the hypothesis that predation and competition occur between suspected IGPs. Fayram et al. (2005) used a similar format in their analysis, stating, “The use of these criteria to indicate the likelihood of predation or competition provides only circumstantial evidence, and each criterion taken individually may not be overly convincing, but the sum of all criteria strongly suggests that a conclusion of competition or predation is unlikely from chance alone.”

Criterion 1 – Evidence of Inverse Relationships

Walleye vs. Smallmouth Bass

There is no credible evidence that walleye population density is negatively associated with abundance of smallmouth bass. Despite frequent and misleading citations of such a relationship in a four-lake study in northeastern Minnesota (Johnson and Hale 1977), long-term trends in gillnet capture rates of walleye and smallmouth bass failed to demonstrate negative interactions between the two because there were no controls, there were 5- to 10-year gaps in the "trend" data, sample size was very small in one lake, and data from one lake greatly contradicted the hypothesis of intra-guild predation.

In 20 northern Wisconsin lakes with at least 50% natural recruitment of walleye, Fayram et al. (2005) found no significant relationship between estimated adult walleye density and multi-season electrofishing capture rate of smallmouth bass (Spearman r = 0.08; p = 0.72).

Walleye vs. Largemouth Bass

There is strong evidence that walleye population density is negatively associated with abundance of largemouth bass**.** Nate et al. (2003) indexed relative abundance of five gamefish species on the basis of general angler catch rates from creel surveys on 60 lakes in northern Wisconsin during 1990-2001. Principal components analysis revealed higher angler catch rates (presumably greater abundance) of largemouth bass and northern pike on 30 lakes with "stocked" walleye populations (demonstrably lower walleye density), and higher angler catch rates for walleye and muskellunge on 30 lakes with "self-sustaining" walleye populations where angler catch rates (and presumed abundance) of largemouth bass were lowest. According to the authors, "Our results suggest that interactions with northern pike and largemouth bass, rather than differences in the physical characteristics of lakes, may hinder the presence of self-sustaining walleye populations in northern Wisconsin lakes." It seems these interactions may be facilitated in a wide range of meso-eutrophic lakes that are either too shallow to stratify thermally or are deep enough to develop anoxic hypolimnia in mid summer – conditions under which MacLean and Magnuson (1977) stated, "…there is little opportunity to segregate on the basis of temperature because the temperature range available at any one time is narrow."

In 20 northern Wisconsin lakes with at least 50% natural recruitment of walleye, Fayram et al. (2005) found a significant negative relationship between estimated adult walleye density and multi-season electrofishing capture rate of largemouth bass (Spearman r = -0.50; p = 0.02).

Largemouth Bass vs. Smallmouth Bass

Olson and Young (2003) studied populations of co-occurring largemouth bass and smallmouth bass in 16 New York lakes ranging between 102 and 1,998 acres in area. Despite a wide range of relative abundance among lakes, spring electrofishing capture rates of largemouth bass (3-90/hour) and smallmouth bass (1-56/hour) during 1996-1998 were not correlated ($r = +.002$; $p > .90$).

Summary of Criterion 1 (Inverse Relationships)

Among the species combinations tested, only walleye and largemouth bass exhibited inverse relationships in abundance indicative of intra-guild predation. But absence of evidence is not necessarily evidence of absence, so other criteria will be examined before concluding that smallmouth bass are not intra-guild predators of walleye.

Criterion 2a – Evidence of Predation

Largemouth Bass Predation on Walleye

Several major diet studies in Ohio, Illinois, and Iowa revealed that largemouth bass ate walleyes to a significant extent when available. Hurley and Austin (1987) found walleyes in 14% of 115 largemouth bass stomachs two to three days after 1.7-inch walleyes were stocked into 2,828-acre Caesar Creek Lake, Ohio. Bass that had eaten walleyes consumed an average of 10 fingerlings each. In 14-acre Ridge Lake, Illinois, Santucci and Wahl (1993) estimated that largemouth bass ate 8% of 2.2-inch and 17% of 5.5-inch walleyes within the first week after stocking during four years of study, but walleyes stocked at 8.1 inches were not found in the stomachs of largemouth bass big enough to consume them (3/acre ≥ 14.2 inches). Liao et al. (2004) found that walleyes comprised 16% of the diet, by weight, of largemouth bass in 5,506-acre Spirit Lake, Iowa in 1997, when largemouth bass consumed an estimated 0.15 pound/acre of abundant young walleyes. And in 15 Illinois impoundments, Hoxmeier et al. (2006) reported the frequency of occurrence of stocked walleye fingerlings in largemouth bass stomachs (1.6% of 12,226 samples) was four times higher than the frequency of walleye cannibalism (0.4% of 10,040 walleye stomachs examined).

Johnson et al. (1988) studied habitat use by age-0 walleyes in 850-acre Pleasant Hill Reservoir, Ohio and were the first to document a significant co-occurrence of stocked age-0 walleyes with predatory largemouth bass in littoral zone macrophytes in early to mid summer.

Pratt and Fox (2001) modified a Rapid Visual Technique used by coral reef divers to quantitatively assess habitat use by naturally produced age-0 walleyes during the early demersal period (June 15 to July 11) and late demersal period (July 15 to August 21) of 1999 in 843-acre Big Clear Lake, Ontario. During the early demersal period when age-0 walleyes were 2-4 inches long, they were observed in significantly higher abundances in heavy vegetation (>30%) at medium depths (6-17 feet) at a frequency five times higher than any other habitat type. During the late demersal period when age-0 walleyes were 4-6 inches long, they moved inshore and were significantly more abundant in shallow water (0-6 feet) with almost equal frequency over *Chara* and in medium or dense vegetation. They were not seen over shallow rock or mud at that time. These findings are consistent with the observations of Raney and Lachner (1942), who "reported difficulty in sampling YOY walleye in Oneida Lake [New York], which were found almost exclusively in shallow macrophyte beds in the first week of August." Prey fishes in Big Clear Lake (age-0 yellow perch and bluntnose minnows, and adult mimic shiners) were observed in strong association with age-0 walleyes in mid-depth macrophytes during the early demersal period ($p \leq .002$ for Spearman rank correlations), possibly explaining their strong selection of such habitat during that time period. Largemouth bass 2-10 inches long were observed in strong association with age-0 walleyes in shallow macrophytes during the late demersal period (Spearman $r = 0.23$; $p \leq .001$), placing walleyes at risk of predation by the largest of those bass.

Wahl (1995) demonstrated in pool microcosms that 10- to 14-inch largemouth bass can capture 3- to 7-inch walleyes in simulated vegetation (250 stems/m^2) with high efficiency (67% captures per attempt), despite the fact that walleyes always hid on the bottom among the artificial plants. Walleyes rarely fled from approaching bass (remained stationary 60% of the time) in these confined artificial spaces.

Smallmouth Bass Predation on Walleye

Several major diet studies in Minnesota, Oregon, Wisconsin, and Illinois revealed that smallmouth bass ate few, if any, walleyes when crayfish, benthic fish (sculpins, logperch), minnows, yellow perch, and assorted macroinvertebrates were present in satisfactory numbers.

Johnson and Hale (1977) found that walleyes comprised 0.7 and 1.8%, respectively, of the volume of food items in 489 age-1-and-older smallmouth bass stomachs in 810-acre Pike Lake, Minnesota, where crayfish comprised 50% of food volume. In three lower Columbia River impoundments in northern Oregon, no walleyes were found in 983 smallmouth bass stomachs (Zimmerman 1999). Crayfish comprised 48-50% of spring-summer wet weight of food eaten by smallmouth bass, and sculpins accounted for 64% of the wet weight of all fish consumed. Similarly, Frey et al. (2003) found no walleyes in the stomachs of 303 smallmouth bass in 682-acre Big Crooked Lake, Wisconsin, where crayfish comprised over 90% of smallmouth diet, by weight. When that study was performed in 1999, fall electrofishing capture rate of age-0 walleyes was the highest in seven years (55/mile; Steven Gilbert, personal communication); numerous young walleyes were present, but smallmouth bass chose not to eat them. Of 248 smallmouth bass stomachs examined in 15 Illinois impoundments, only two fish (0.4%) had eaten a stocked walleye fingerling (Hoxmeier et al. 2006).

One notable exception to low predation on walleyes by smallmouth bass was in 5,506-acre Spirit Lake Iowa, where an extraordinarily large year class of young walleyes comprised 24% of smallmouth bass diet, by weight, in 1997 (Liao et al. 2004). Yellow perch and crayfish were the most preferred prey of Spirit Lake smallmouth bass during all three years of that study.

Differences in Bass Predatory Behavior

Largemouth and smallmouth bass differ sufficiently in morphology and behavior to explain their different predatory interactions with walleye. Winemiller and Taylor (1987) demonstrated that largemouth bass generally engulf their prey by undirected burst suction, allowing them to efficiently extract prey from vegetation where age-0 walleyes are congregated in early to mid summer according to Johnson et al. (1988) and Pratt and Fox (2001). Smallmouth bass, on the other hand, generally bite and reposition their prey before swallowing it. They exhibit low capture efficiency in vegetation but are particularly well adapted to finding and capturing crayfish and benthic fishes over firm, rocky substrate.

Walleye Predation on Black Bass

In the four major diet studies cited previously, there was no evidence of predation by walleye on smallmouth bass (Johnson and Hale 1977; Zimmerman 1999; Frey et al. 2003; Liao et al. 2004). Predation by walleye on largemouth bass was documented only by Liao et al. (2004) in Spirit Lake, Iowa, where largemouth bass (estimated density ≥ 6 inches = 1.3/acre) comprised approximately 48%, by weight, of the summertime (July through August) diet of walleye (estimated density ≥ 6 inches = 126/acre) in 1997. Largemouth bass must have had an unusually large hatch that year, resulting in estimated consumption by abundant walleyes of 6.8 pounds of largemouth bass per acre in a 5,506-acre lake. This rare documentation reveals how walleyes in sufficient number can maintain dominance over largemouth bass.

Summary of Criterion 2a (Predation)

Largemouth bass frequently ate substantial numbers of walleyes in study lakes. Predation on walleyes was probably facilitated by cohabitation of age-0 walleyes and largemouth bass in littoral zone macrophytes during much of the summer season. In pool mesocosm trials, largemouth bass captured walleyes in simulated vegetation with high efficiency.

Smallmouth bass rarely ate walleyes in study lakes. Their diet was comprised of 50-90% crayfish wherever crayfish were common. Benthic fishes like mottled sculpin and logperch were significant supplements to crayfish in the diets of smallmouth bass in lakes where rock cobble habitat was available. In a rare instance of relatively low crayfish abundance and extraordinarily high density of young walleyes, smallmouth bass were opportunistic and ate some walleyes.

Differences in morphology-related feeding behavior explain why largemouth bass are effective predators of young walleye in the littoral zone vegetation they cohabit, while smallmouth bass are ineffective at foraging in plants but superbly adapted for feeding on benthic prey over firm, rocky substrates.

Predation by walleye on smallmouth bass in lakes has not been documented in the primary literature. But the estimate by Liao et al. (2004) of high consumption by walleyes of largemouth bass in Spirit Lake, Iowa reveals how walleyes in sufficient number can maintain their status as the dominant intra-guild predator in a 5,506-acre meso-eutrophic lake.

Criterion 2b – Evidence of Shared Resources

Largemouth Bass with Walleye

Both species preyed heavily on yellow perch in study lakes. In 2,000-acre Lake Canadarago, New York, Green (1986) reported that over-abundant yellow perch comprised more than 90% of identifiable fish in the stomachs of 113 walleyes and approximately 70% of the diet, by volume, of largemouth bass. Liao et al. (2004) estimated that yellow perch comprised 47% of the total weight of food consumed by walleyes and 32% of the diet of largemouth bass in 5,506-acre Spirit Lake, Iowa during 1995-1997. Fayram et al. (2005) reported high dietary overlap (modified Pianka's index = 0.61) between largemouth bass and juvenile walleye in 786-acre Whitefish Lake, Wisconsin, though sample sizes were small (27 largemouth bass stomachs and 29 stomach samples from walleye < 8 inches).

Smallmouth Bass with Walleye

Dietary overlap between smallmouth bass and walleye was relatively low in most studies, but both species ate yellow perch when particularly abundant.

Johnson and Hale (1977) examined stomach contents of 429 smallmouth bass and 470 walleyes in 810-acre Pike Lake, Minnesota, where 70% of the littoral zone shoreward of the five-foot depth contour was comprised of boulders and rubble. Smallmouth bass ate mostly crayfish (50% of food volume), odonate nymphs (11%), leeches (9%), and sculpins (8%); walleyes ate mostly yellow perch (23%), burrowing mayfly nymphs (22%), and crayfish (18%). Smallmouth bass and walleyes shared no food items in three Columbia River impoundments studied by Zimmerman (1999), except for sculpins, which comprised 34% and 27% of the wet weight of smallmouth bass stomach contents (N = 983) in spring and summer, and 12% and 27% of walleye stomach contents (N = 117) in spring and summer, respectively. Frey et al. (2003) examined stomachs of 389 adult walleye and 303 smallmouth bass in 682-acre Big Crooked Lake, Wisconsin and reported the Schoener dietary overlap index was only 0.42, 0.29, and 0.21 in June, July, and August of 1999, respectively, indicating no significant (0.60) summer dietary overlap. Greatest overlap was in June when both species ate crayfish, before walleye switched to perch in July. In 5,506-acre Spirit Lake, Iowa, Liao et al. (2004) estimated that abundant yellow perch comprised 47% of the total weight of food consumed by walleyes and 34% of the diet of smallmouth bass during 1995-1997. Crayfish were somewhat important in the diet of Spirit Lake smallmouth bass (22%) but were not reported in walleyes.

The extent to which smallmouth bass share prey with other piscivores in lakes may depend on littoral zone substrate and prey species composition. Danehy and Ringler (1991) found that 45 smallmouth bass captured by gillnet over cobble/rubble substrate in the near-shore zone of southeastern Lake Ontario were benthic feeders (mottled sculpin, johnny darter, and crayfish), while 55 smallmouths captured over sand substrate were pelagic feeders (> 90% fish, primarily alewife).

Largemouth Bass with Smallmouth Bass

Black bass ate many of the same foods in study lakes, but they exploited various prey species to significantly different degrees. Hodgson et al. (1997) studied dietary overlap among unexploited populations of largemouth bass (22/acre) and smallmouth bass (10/acre) ≥ 6 inches in 20-acre Long Lake in the Upper Peninsula of Michigan. The littoral zone had entirely sand substrate, and crayfish were unimportant in bass diets. Fish (mostly yellow perch and age-0 largemouth bass) comprised 26% and 43% of total dietary biomass of largemouth bass (N = 376 stomach samples) and smallmouth bass (N = 257), respectively. Insects (mostly odonates) were important to both, but terrestrial vertebrates (mostly frogs) comprised a much greater proportion of the diet of largemouth bass (31%) than smallmouth bass (13%).

Olson and Young (2003) examined summertime monthly food habits of co-occurring largemouth and smallmouth bass by two-inch size classes in four New York lakes during 1996-1998. Investigators collected ~30 stomach samples monthly at each lake over three years, for an estimated total of 1,440 stomach samples. Odonate nymphs were important in the diets of small bass of both species, but by 3 inches largemouth bass had switched to eating larval sunfish, while smallmouth bass continued eating insects. Schoener's index of diet similarity for black bass 4-6 inches long was zero. Largemouth bass 4-6 inches long ate small fish almost exclusively, whereas 4- to 6-inch smallmouth bass transitioned from insects to crayfish. Fish remained important in largemouth bass diets into adulthood (50-75% by dry mass), though crayfish assumed importance as largemouths grew from 8-10 inches (35%) to 12-14 inches (46%). Smallmouth bass predation on fish peaked at 6-8 inches (25% by dry mass) and declined steadily as smallmouths got larger and crayfish became their predominant food (from 68% at 8-10 inches to 93% at 12-14 inches).

<u>Summary of Criterion 2b (Shared Resources)</u>

Where yellow perch and other fish were available, largemouth bass and walleye preyed upon them heavily, resulting in significant dietary overlap. Smallmouth bass ate yellow perch if abundant, but only if their highly preferred prey – crayfish and benthic fishes – were scarce or unavailable. Smallmouth bass and walleye diets did not overlap significantly in study lakes, but they may share pelagic fish as prey in lakes where coarse substrates are unavailable to serve as habitat for the preferred prey of smallmouths.

In the absence of crayfish, largemouth bass and smallmouth bass shared fish and insects in one study, but largemouth bass ate significantly more terrestrial vertebrates (frogs) than smallmouths, probably due to differences in predatory behavior identified by Winemiller and Taylor (1987). This may contribute to the ability of largemouth bass to achieve numerical dominance over other piscivores in many lakes (Hodgson et al. 1997). Where crayfish were available, smallmouth bass preyed upon them heavily starting at a very early age, whereas largemouth bass ate primarily fish at an early age and gradually incorporated some crayfish into their diets as they reached adult size.

Criterion 3 – Evidence of Rate Alterations

Evidence of altered rates of growth or survival was rare in studies conducted outside the scope of experimental manipulations. Most documented impacts on rate functions, primarily survival to recruitment, are discussed in the experimental manipulation section of this review.

Walleye vs. Largemouth Bass

Fayram et al. (2005) reported walleye growth rate (ω) was positively correlated with angler catch rates of largemouth bass in 135 northern Wisconsin lakes (Spearman $r = 0.23$; $p = 0.02$) during 1990-2002, suggesting lakes with high relative abundance of largemouth bass had faster-growing walleyes because predatory largemouth bass reduced walleye density and intra-specific competition. However, Sass and Kitchell (2005) demonstrated that walleye growth rate did not predict walleye density when analyzing 1990-1999 data from a similar subset of lakes, so the underlying assumption of Fayram et al. (2005) may need to be examined and validated.

Walleye vs. Smallmouth Bass

There was no evidence of rate function alteration between walleye and smallmouth bass in the studies reviewed. According to Ryder and Kerr (1978), "… several years after the introduction of smallmouth bass into a boreal percid community favoring survival of both taxa, a new steady state may be achieved as the principal predators – walleyes, northern pike, and smallmouth bass – occupy substantially different niches with respect to feeding, reproduction, and habitat over time."

Largemouth Bass vs. Smallmouth Bass

Olson and Young (2003) compared size-specific similarity in summer diet and growth between co-occurring largemouth and smallmouth bass in 16 New York lakes based upon diet analyses at a subset of four lakes. Combining three years of results for both species ($N \approx 1,440$ stomach samples), the degree of similarity in size-based growth rate between largemouth and smallmouth bass in all 16 lakes closely followed the same trend as the degree of similarity in size-based diet in the subset of four lakes. Growth rates of co-occurring black bass were significantly similar at sizes for which diet overlap was high. Growth rate was density-dependent regardless of black bass species composition; and the negative effect of density on growth was greatest at 9 to 11 inches for both species, which is the size range at which diet overlap was highest.

Summary of Criterion 3 (Rate Alterations)

Evidence of specific rate alterations between walleye and either species of black bass in un-manipulated populations is rare. But Olson and Young (2003) proved that degree of diet overlap influenced growth rate of co-occurring largemouth and smallmouth bass on a size-specific basis. They suggested efforts to reduce density of black bass 6 to 11 inches long could improve growth and size structure of both species, regardless of which species is removed.

Criterion 4 – Experimental Manipulations

The results of experimental manipulations, including rate alterations, must be consistent with the hypothesis that two species are intra-guild predators.

Walleye vs. Smallmouth Bass

Green (1986) evaluated survival of walleye fingerlings stocked at 3-4 inches in September in eutrophic 2,000-acre Lake Canadarago, New York between 1977 and 1982. Prior to the experiment, there were virtually no walleyes in the lake despite a long history of fry stocking. Yellow perch were extremely abundant and slow-growing; and perch population size structure was poor. In summer of 1983, over 90% of identifiable fish in the stomachs of 113 walleyes were yellow perch, which also comprised ~70% of the diet of smallmouth bass. By 1983, walleye CPE had increased from zero to 16.8 per 300 feet of gillnet, while smallmouth bass CPE had increased from 2.9 to 5.6. The increase in walleye density must have been significant, because yellow perch PSD increased steadily from a stabile 35% five years prior to walleye stockings to 70% by 1983. The results of this experiment were not consistent with the hypothesis that walleye and smallmouth bass are intra-guild predators. The walleye population increased dramatically, despite a doubling of smallmouth bass gillnet CPE and almost complete dietary overlap for abundant yellow perch.

Walleye vs. Largemouth Bass

Santucci and Wahl (1993) stocked 14-acre Ridge Lake, Illinois with walleye fry (.35” in April), small fingerlings (2.2” finished on artificial feed before stocking in June), medium fingerlings (5.5” in fall) and large fingerlings (8.1” in fall) annually from 1987 through 1990. (Medium and large fingerlings were reared in ponds with natural forage and were stocked at about the same time.) This research lake (controlled outlet with tower weir and emergency spillway weir to catch emigrating fish) had been drained in fall 1985 and restocked in 1986 with juvenile and adult largemouth bass, and black crappies. Predatory mortality was assessed by examining stomachs of largemouth bass, black crappies, and walleyes (from previous stockings) on days 1 and 2 after walleyes were stocked and on two additional days during the week after each stocking. Angler effort (by permit only), catch, and harvest were documented by creel census. There was a 14-inch minimum length limit for both largemouth bass and walleye. Based on weekly ichthyoplankton samples to estimate abundance of larval bluegills as potential prey, there was no walleye natural reproduction during the study.

Practically no walleyes stocked as fry or small fingerlings were ever recovered in four years of post-stocking evaluation. Escapement was minor; only 21 walleyes stocked as medium or large fingerlings were captured in the outlet weirs. Immediate post-stocking mortality of medium and large fingerlings was negligible (1%). Mean survival one year after the 1987-1989 stockings averaged 7% for medium fingerlings and 31% for large fingerlings. Mean survival of the 1987 and 1988 stockings of medium fingerlings declined from 6% after one year to 4.5% after two years. Large fingerling survival declined from 20% after one year to 10% after two years at large. Throughout the study, anglers caught a higher proportion of walleyes stocked as large fingerlings (91%) than as medium (9%) or small (0%) fingerlings.

Predation by largemouth bass (estimated mean density 34/acre ≥ 9.7”) was an important source of mortality for small and medium-size stocked walleye fingerlings during the week-long periods of evaluation following each stocking event (Table 1). Based on examination of 801 bass stomachs during the four-year study, largemouth bass consumed an estimated 8% of small (2.2”) walleye fingerlings and 17% of medium-size (5.5”) walleye fingerlings within approximately one week of stocking. Of all the walleyes recovered from largemouth bass stomachs during that first week, 76% were eaten within 48 hours of stocking. Largemouth bass theoretically capable of consuming large (8.1”) walleye fingerlings were present in the lake (3/acre ≥ 14.2”), but no large walleye fingerlings were observed in the 22 large bass stomachs examined during the study. Investigators concluded, “For all sources and all estimates of survival, large fingerlings (7.3-8.5”) were the most economical walleye to stock.”

Neither walleye nor black crappie appeared to prey heavily on stocked walleye fingerlings in the Ridge Lake study. Only five walleyes from the small size groups were found in 72 walleye stomachs examined, and none were found in the 121 black crappie stomachs examined. Ichthyoplankton tows indicated that larval bluegill were available as prey to stocked walleye from May through mid August of each year at densities of 12 to 64 larvae per cubic meter. For age-1-and-older walleyes of all sizes, juvenile bluegills (mostly 1.0 to 1.5 inches long) comprised a higher proportion of the diet (87% by volume) and occurred in more stomachs containing food (84%) than all other prey. Walleyes ate only young bluegills in the fall. In spring and summer, largemouth bass, black crappie, unidentifiable fish remains and invertebrates combined to make up 13% of the volume of walleye diets.

Table 1. Estimated consumption of stocked walleyes by largemouth bass during the first week following each stocking event in 14-acre Ridge Lake, Illinois during 1987-1990 (modified from Santucci and Wahl 1993). Consumption estimates are for the immediate post-stocking period only, and therefore reflect the minimum impact of bass predation upon stocked walleyes. Researchers examined an average of 200 stomachs annually of bass deemed large enough to consume recently stocked walleyes (effective size of bass = 1.75X walleye length). In order to maximize relevance and interpretability of this information to fish managers and anglers, I have combined data from Table 1 (walleye stocking) and Table 3 (bass density and diet) of Santucci and Wahl (1993), converted their reported units of measure from metric to English, converted select numbers to densities based upon a 14-acre lake area, added four-year averages, and clarified that consumption estimates are for the week-long post-stocking periods only.

Date	**Stocked Walleye Mean Length**	**Stocked Walleye Density (No/Ac)**	**Estimated Density of Bass (Number/Acre ≥ Effective Size)**	**Number of Bass Stomachs Examined***	**Walleyes Consumed in 1st Week (No/Acre)**	**Proportion of All Stocked Walleyes Consumed by Bass in 1st Week (%)**
1987						
6/18	2.4”	48	97/A ≥ 4.2”	117	5.5	11
11/3	5.6”	26	39/A ≥ 9.8”	21	3.0	12
11/3	8.2”	9	4/A ≥ 14.4”	6	0	0
1988						
6/20	2.4”	55	81/A ≥ 4.2”	256	5.2	10
11/7	5.7”	24	27/A ≥ 10.0”	104	1.6	7
11/7	8.5”	10	1/A ≥ 14.8”	5	0	0
1989						
5/31	1.9”	48	66/A ≥ 3.3”	303	0	0
11/20	5.2”	28	51/A ≥ 9.1”	46	6.4	23
11/21	7.3”	6	5/A ≥ 12.8”	9	0	0
1990						
6/25	2.2”	50	39/A ≥ 3.9”	125	5.6	11
10/20	5.5”	17	20/A ≥ 9.7”	38	4.8	28
10/20	8.3”	19	<1/A ≥ 14.6”	2	0	0
4 Yr.						
Ave.	**2.2”**	50	71/A ≥ 3.9”	200	4.1	**8% small**
Ave.	**5.5”**	24	34/A ≥ 9.7”	52	4.0	**17% medium**
Ave.	**8.1”**	11	3/A ≥ 14.2”	6	0	**0 % large**

* These numbers are not additive. The highest numbers each year are the total numbers of bass stomachs examined that year; smaller numbers are subsets of the total numbers of stomachs that were from size classes of largemouth bass capable of consuming the larger size classes of stocked walleyes.

Wahl (1995) continued the extended-growth walleye stocking experiments in 14-acre Ridge Lake, Illinois. Contrary to 1987-1990 results reported by Santucci and Wahl (1993), largemouth bass consumption of walleyes stocked in 1991 (7.5-8.7" only) and 1992 (5.1-6.3" only) was insignificant during the week after stocking each year. In 1991, a bass population estimate revealed there were no largemouth bass in Ridge Lake deemed big enough to consume the large (7.5-8.7") walleye fingerlings stocked that fall. In 1992, a reduced-density population of largemouth bass (16/acre vs. 34/acre in previous years) deemed big enough (≥ 9.4") to eat medium-size (5.1-6.3") fall walleye fingerlings was estimated to consume only 2% of those fingerlings in the week after stocking (30 bass stomachs examined, or 12.5% of the estimated population of effective-size fish). These findings begin to identify the threshold density of effective-size largemouth bass below which 5.1-6.3" walleye fingerlings might be expected to survive during the immediate post-stocking period in the fall. Wahl (1995) recommended that walleye be introduced in the fall at large (> 8") sizes in order to reduce losses to largemouth bass predation.

Seip (1995) reported the survival of stocked walleye fingerlings in ten small lakes (57-1,282 acres) in southeastern Ontario characterized as "marginal or sub-marginal" walleye lakes. Nine lakes were stocked with pond-reared 1.6-2.4" walleyes at a density of 50/acre, and one lake was stocked with 3-4" fingerlings in late summer at a density of 10/acre. There were strong negative relationships between stocked walleye fingerling survival and electrofishing capture rate of largemouth bass ($r = -0.80$) and the extent of broad leafy aquatic macrophytes ($r = -0.83$). The author concluded that predation may have played an important role in limiting walleye fingerling survival; however, dietary analysis was insufficient to confirm the role of predation in this study.

Jackson et al. (2003) studied the survival of stocked walleye fingerlings in relation to predator abundance and water clarity in 16 New York lakes between 109 and 808 acres where there was little natural recruitment of walleye. Researchers stocked pond-reared walleyes at 1.5-2.0" in June and trough-reared, pellet-fed walleyes at 3.4-5.5" in mid September during 1991-2001 (usually 20/acre all sizes). Abundance of age-0 walleyes and predators was indexed by night electrofishing in September or October each stocking year. Stocked walleye survival was low. Even though mean fall electrofishing capture rate (CPE) of largemouth bass > 15 inches was only 3.3/hour, fall CPE of age-0 walleyes two to four weeks after stocking at 3.4-5.5" in mid September in 13 of the study lakes averaged only 2.6/hour. Within that narrow range of survival, mean CPE of age-0 walleyes was significantly and negatively correlated to mean CPE of largemouth bass > 15 inches ($r^2 = 0.36$; $p = 0.03$ for log-transformed data).

Age-0 walleye CPE in New York lakes was consistently low when the combined capture rate of large predators (including largemouth bass, chain pickerel and northern pike > 15 inches) exceeded 5/hour, which is consistent with the conclusion of Nate et al. (2003) that interactions with largemouth bass and northern pike may hinder walleye recruitment in northern Wisconsin lakes. Jackson et al. (2003) also found that fall CPE of age-0 walleyes stocked as small fingerlings in June in 15 of the study lakes was significantly and negatively correlated to Secchi disk visibility ($r^2 = 0.30$; $p = 0.03$); survival was extremely low when water clarity exceeded 6 feet.

Fayram et al. (2005) reported that fall electrofishing capture rate of OTC-marked walleye fingerlings stocked into 23 northern Wisconsin lakes in June at a size of 1.6 inches and a density of 50/acre was negatively correlated to electrofishing capture rate of largemouth bass ($r = -0.53$; $p = 0.01$) in those waters.

Hoxmeier et al. (2006) studied survival of stocked walleye fry (41 stockings in 10 lakes), 2" fingerlings (55 stockings averaging 36/acre in 14 lakes), and 4" fingerlings (26 stockings averaging 26/acre in 7 lakes) in 15 largemouth bass-dominated lakes (no natural reproduction of walleye) in Illinois during 1991-1997. Fall electrofishing capture rate (CPE) of age-0 walleye stocked as fry was negatively correlated to shoreline seining capture rate of juvenile centrarchids ($r = -.79$; $p = .01$); and fry stockings never resulted in age-0 walleye CPE > 3/hour. In stocked years, fall age-0 walleye CPE averaged ≥ 5/hour (~3/mile) in only 4 of 14 lakes (29%) stocked with 2" fingerlings and in 3 of 7 lakes (43%) stocked with 4" fingerlings (highest when August water temperature was coolest and where benthic invertebrate density was highest). Mean age-0 walleye CPE exceeded 11/hour (~6/mile) at only one lake. The authors recommended, "In northern lakes in which centrarchid predation is high, large sizes of walleye should be considered for stocking."

Summary of Criterion 4 (Experimental Manipulations)

The single experiment that might have indicated intra-guild predation between walleye and smallmouth bass failed to do so (Green 1986). This was predictable considering the general lack of evidence among all other criteria for evaluating intra-guild predation between walleye and smallmouth bass.

In contrast, the results of several experiments were consistent with the hypothesis of intra-guild predation between walleye and largemouth bass. Several studies documented low, size-dependent survival of stocked walleye fingerlings as a result of high post-stocking predation by largemouth bass (Santucci and Wahl, 1993; Wahl 1995; Hoxmeier et al. 2006). Seip (1995), Jackson et al. (2003), and Fayram (2005) did not identify mechanisms but documented negative correlations between stocked walleye fingerling survival and largemouth bass density. Fayram et al. (2005) concluded, "Given the seemingly strong predatory interaction between walleyes and largemouth bass, management of both species in the same water body may be difficult. In addition, walleye stocking may be ill advised in lakes with even moderate abundances of largemouth bass, given their potentially large impact on survival of juvenile walleyes."

Conclusions

There is virtually no published evidence of intra-guild predation between walleye and smallmouth bass. They often co-occur in high numbers. They rarely eat each other during the open-water season when diet studies have been conducted. They rarely eat the same food, especially if coarse substrates are available as habitat for the preferred prey of smallmouth bass – crayfish and benthic fishes. Age-0 walleyes spend most of their time in littoral zone macrophytes during early to mid summer, but smallmouth bass are inefficient predators in vegetation. And there have been no experiments showing that smallmouth bass adversely affect the reproduction, growth, or survival of walleyes. These two species seem to be complementary in most north temperate lakes.

Walleye and largemouth bass meet all the criteria for classification as intra-guild predators. Estimates or indexes of their relative abundance are inversely related. Largemouth bass eat age-0 walleyes significantly because they co-occur during much of the growing season in littoral zone macrophytes, where largemouth bass are very efficient predators. Walleye and largemouth bass often eat the same food, especially yellow perch when available. And finally, the results of experimental manipulations consistently indicate that largemouth bass predation reduces the survival and recruitment of stocked walleyes. Likewise, research at Spirit Lake, IA demonstrated how abundant walleyes maintain dominance over largemouth bass via predation.

Management Implications and Recommendations

Confirmation of intra-guild predation between walleye and largemouth bass requires us to acknowledge the low probability of managing self-sustaining populations and satisfactory fishing for these species in the same lake. Fortunately, in Wisconsin we have so many lakes of diverse type and character that it should be possible to provide well-distributed opportunities for quality fishing for both species. The challenge will be to decide which lakes are to be managed as "walleye lakes" and which are to be managed as "largemouth bass" lakes. These species are highly adaptable to a wide range of conditions between mesotrophy and eutrophy, so the choice will not always be obvious based on trophic state alone. Assessing and responding to statewide and local angler preferences should be part of the process for developing management priorities.

The good news is that we can, in a unique way, have our cake and eat it too. We can still provide good black bass fishing in lakes managed for walleye as the featured species, but the species of black bass in such waters must be smallmouth. Liberalizing harvest for largemouth bass while further restricting harvest of smallmouth bass would be consistent with the goal of creating and maintaining quality fishing for both walleye and bass in such waters. This would require that we recognize the morphological and behavioral differences between the two black bass species, and that we manage them as separate regulatory entities.

We must also acknowledge the low expectation of survival of small walleye fingerlings stocked into lakes with even moderate populations of effective-size largemouth bass. Exceptions may exist for lakes where basin morphometry and thermal regime facilitate niche segregation, or for lakes where significantly reduced visibility (due to phytoplankton production or other sources of turbidity) may favor walleyes over largemouth bass. But generally speaking, 1.5- to 2.5-inch walleye fingerlings stocked into "largemouth bass lakes" have very low probability of survival.

Also, we must be aware that stocking large, "extended-growth" walleye fingerlings (6 to 8 inches long) may establish moderate-density walleye populations capable of interfering (via predation and competition) with largemouth bass as the featured species. It may be possible to stock (or permit stocking) of limited numbers of large walleye fingerlings in order to create and maintain "bonus" fisheries that provide an element of diversity in lakes managed primarily for largemouth bass. But stocking of extended-growth walleye fingerlings should not be allowed to threaten the integrity of bass fisheries in waters where largemouth bass have priority status.

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