

## Interactions between Walleyes and Four Fish Species with Implications for Walleye Stocking

ANDREW H. FAYRAM\*

Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection, 101 South Webster Street, Madison, Wisconsin 53711, USA

MICHAEL J. HANSEN

College of Natural Resources, University of Wisconsin–Stevens Point, 800 Reserve Street, Stevens Point, Wisconsin 54481, USA

TIMOTHY J. EHLINGER

Department of Biological Sciences, University of Wisconsin–Milwaukee, 3209 North Maryland Avenue, Milwaukee, Wisconsin 53211, USA

**Abstract.**—We used a number of different data sets and four criteria to evaluate evidence of competition and predation between walleye *Sander vitreus* and northern pike *Esox lucius*, muskellunge *E. masquinongy*, smallmouth bass *Micropterus dolomieu*, and largemouth bass *M. salmoides* in northern Wisconsin lakes. The four criteria were as follows: (1) indices of population abundance were inversely related, (2) two species had shared resources or one species preyed on the other, (3) competition or predation was strong enough to produce a measurable effect, and (4) experimental manipulations produced results consistent with the hypothesis of competition or predation. Using these criteria, we identified which species interact most strongly with walleyes, determined the most likely mechanism for interaction (predation, competition, or both), and characterized the effects of walleye stocking on these species. Largemouth bass was the only species that strongly interacted with walleyes: (1) indices of largemouth bass and walleye population abundance were inversely related in lakes with self-sustaining walleye populations; (2) the diet of largemouth bass included juvenile walleyes; (3) walleye growth was positively related to indices of largemouth bass abundance; and (4) survival of stocked walleyes was negatively related to indices of largemouth bass abundance, and indices of largemouth bass abundances increased as an index of walleye stocking intensity increased. A bioenergetics analysis of one lake that was stocked with 39,300 juvenile walleyes, but also has some natural reproduction of walleyes, suggested that the largemouth bass population could consume up to 82,500 juvenile walleyes per year. Our findings suggest that largemouth bass interact strongly with walleyes through predation, that they can limit the survival of stocked walleyes, and that walleye stocking can result in increased largemouth bass populations. Therefore, management goals seeking to simultaneously maximize largemouth bass and walleye populations may be unrealistic.

Walleye *Sander vitreus* may interact with populations of other important fish species, such as largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, northern pike *Esox lucius*, and muskellunge *E. masquinongy*, through competition or predation. Walleye populations could potentially affect or be affected by other fish populations depending on the nature and strength of their interaction. Previous investigations have suggested that walleye abundances may be inversely related to abundances of fish species such as northern pike (Anthony and Jorgensen 1977; Nate et al. 2003),

smallmouth bass (Johnson and Hale 1977; Inskip and Magnuson 1983), and largemouth bass (Inskip and Magnuson 1983; Nate et al. 2003). Northern pike and walleyes have similar diets (Cohen et al. 1993), so may compete for food resources. Walleyes also prey on northern pike (Craig and Babaluk 1989); thus, abundances of these two species may be negatively related. Smallmouth bass prey on walleyes (Zimmerman 1999) and have been suggested as a cause of the inverse relationship between abundances of these two species (Johnson and Hale 1977). Similarly, muskellunge consume walleyes (Bozek et al. 1999) and largemouth bass may prey heavily on stocked walleyes (Santucci and Wahl 1993). It is important to determine the strength of species interactions to determine appropriate management goals.

\* Corresponding author: andrew.fayram@dnr.state.wi.us

Received November 29, 2004; accepted May 5, 2005  
Published online October 20, 2005

Walleye stocking is essentially a broad-scale population manipulation that can be used to examine competitive and predatory interactions. Hatchery supplementation of a fish population may intensify competitive or predatory interactions. Increases in the population of a species is likely to decrease the population of competitors, decrease the population of prey species, and increase the population of predators of that species (Gotelli 1998).

Walleyes are stocked in most states and provinces in North America, where about  $1 \times 10^9$  walleyes are stocked each year (Fenton et al. 1996). In Wisconsin alone, nearly 30 million walleyes are stocked annually by the Wisconsin Department of Natural Resources (WDNR, unpublished data) and similar numbers are stocked by other agencies (GLIFWC 2001). Given the widespread and intensive stocking of walleyes and their potential to either positively or negatively affect populations of other fish species, a comprehensive analysis of interactions between walleyes and other fish species and the effects of walleye stocking seems warranted.

Our objectives were to (1) identify whether largemouth bass, smallmouth bass, northern pike, and muskellunge interact with walleyes, (2) determine the most likely mechanism for these interactions, and (3) characterize the effects of walleye stocking on these species' populations. The effect of walleye stocking on population abundances of other fish species should be quantified because other fish species are popular with anglers and because the presence of these other fish species may limit the success of walleye stocking.

### Methods

Reynoldson and Bellamy (1972) suggested criteria for demonstrating competition between fish species. MacLean and Magnuson (1977) further refined these criteria and suggested that they are also valid for demonstrating predation. We used these criteria as evidence of competitive and predatory interactions between walleyes and other fish species. We treated each of the criteria as a filter, the first criterion being relatively coarse and each subsequent criterion becoming an increasingly finer filter. The first criterion indicates whether an interaction is possible, whereas subsequent criteria indicate whether the interaction is probable. The first criterion is met when the "relative abundance of potential competitors and predators is consistent with the hypothesis that competition or predation occurs" (MacLean and Magnuson 1977). In other

words, the abundances of two species are inversely related: high abundances of one species are generally associated with low abundances of another and vice versa. The second criterion is met if the two species use a common resource for which competition can occur or prey directly on one another (MacLean and Magnuson 1977). The goal of the second criterion is to determine whether a mechanism exists through which one species can impact another species. The third criterion is met if the "fecundity, survival, growth, or some other appropriate factor indicate that predation or competition occurs" (MacLean and Magnuson 1977). Essentially, the third criterion establishes whether the competition or predation interaction is strong enough to affect a measurable feature of the other species. Finally, the fourth criterion suggests that "results of experimental manipulations are consistent with competition or predation hypotheses" (MacLean and Magnuson 1977). If, in fact, strong competition or predation is the cause of the first three criteria being met, then a manipulation designed to demonstrate the interaction should provide expected results.

We concluded that intense competition or predation was likely only if all four criteria were met for a pair of fish species. 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. We evaluated species interactions with these criteria and data from adult walleye mark-recapture surveys, electrofishing surveys, creel surveys, age-0 walleye abundance surveys, annual stocking information, diet samples, and walleye length-at-age samples from lakes located in northern Wisconsin that were sampled during 1990–2002 (Table 1). We considered that a given criterion was met if it was satisfied with any data set. The level of significance for all tests was  $P \leq 0.05$ . The number of lakes or data points available for a specific comparison was less than the total number of lakes sampled if all species were not present in all lakes (Table 1).

### Data Collection

Using methods described by Beard et al. (1997), walleye abundance was estimated by mark-recapture surveys on 20–25 lakes each year during 1990–2001. Walleye abundance was estimated with the Chapman modification of the Petersen estimator (Ricker 1975) and then transformed into

TABLE 1.—Number of lakes (*n*) and data types available from lakes in northern Wisconsin that were sampled during 1990–2002 and used to judge whether each criterion associated with competition or predation with walleye for northern pike, muskellunge, largemouth bass, and smallmouth bass was satisfied.

Criterion	Data types	Species	<i>n</i>		
(1) Relative abundance	Adult walleye population estimates versus creel catch per effort	Northern pike	204		
		Muskellunge	196		
		Smallmouth bass	208		
		Largemouth bass	197		
	Adult walleye population estimates versus electrofishing catch per effort	Northern pike	20		
		Muskellunge	20		
		Smallmouth bass	20		
		Largemouth bass	20		
(2) Shared resources or predation	Diet	Northern pike	2		
		Muskellunge	2		
		Smallmouth bass	2		
		Largemouth bass	1		
(3) Measurable response	Creel catch per effort versus walleye growth	Northern pike	139		
		Muskellunge	126		
		Smallmouth bass	140		
		Largemouth bass	135		
	Electrofishing catch per effort versus walleye growth	Northern pike	17		
		Muskellunge	17		
		Smallmouth bass	17		
		Largemouth bass	17		
		(4a) Consistent manipulation results (stocking rate)	Walleye stocking density versus creel catch per effort	Northern pike	58
				Muskellunge	50
Smallmouth bass	58				
Largemouth bass	58				
	Walleye stocking density versus electrofishing catch per effort	Northern pike	14		
		Muskellunge	14		
		Smallmouth bass	14		
		Largemouth bass	14		
		(4b) Consistent manipulation results (survival)	Fall electrofishing catch per effort versus stocked walleye survival	Northern pike	23
				Muskellunge	23
Smallmouth bass	23				
Largemouth bass	23				

number per hectare as an index of population abundances. Ages of 5 walleyes from each 1.3-mm length-group were estimated from scales or spines depending on their length; ages of all walleyes shorter than 30.5 cm were estimated from scales and ages of all walleyes longer than 30.5 cm were estimated from dorsal spines (DeVries and Frie 1996).

Relative abundance, indexed as catch per effort (CPE), was estimated from creel surveys on 20–25 lakes/year during 1990–2001, multiseason electrofishing surveys on 10 lakes/year during 1995–1997, and fall electrofishing surveys on 23 lakes during 2002. Creel surveys used a stratified random roving access design, stratified by month and day type (weekend and holidays or weekday; Pollock et al. 1994; Rasmussen et al. 1998). Multiseason electrofishing surveys consisted of 3.2 km of randomly selected shoreline during spring, summer, and fall on 10 lakes/year during 1995–1997. Fall electrofishing surveys consisted of electrofishing two randomly selected 0.8-km segments of shoreline (for a total of 1.6 km of shoreline) sam-

pled in 2002. All fish species were collected and enumerated during each electrofishing survey.

Percent survival of stocked walleyes was estimated with oxytetracycline (OTC) marking and subsequent fall age-0 electrofishing sampling. In mid-June 2002, 23 lakes were stocked with fingerling walleyes that had been marked with OTC. In the hatchery, 3-d-old walleye fry were treated with OTC powder (Pfizer, Inc., New York; Terramycin-343) containing 75.5% active ingredient. Fish were immersed in a 500-mg/L OTC bath for 6 h. To ensure that the juvenile walleyes received a visible mark, fish from each pond of marked fish were sacrificed and their otoliths examined to determine the effectiveness of the mark. Fingerlings were approximately 4 cm long at the time of stocking and were stocked at a rate of 124/ha, stocking abundances previously recommended by the WDNR (WDNR 1999). In fall 2002, the entire shoreline of each lake (including islands) was sampled by electrofishing when water temperatures ranged from 7°C to 18°C. The total number of age-0 walleyes per kilometer of shoreline

was used to estimate the total number of age-0 walleyes in each lake (Serns 1982). The first 100 age-0 walleyes from electrofishing sampling in each lake were collected and frozen. If fewer than 100 age-0 walleyes were available at the end of one complete electrofishing survey, all age-0 walleyes were retained. Sagittal otoliths were removed from walleye fingerlings and mounted on a slide. A compound microscope (Nikon, Inc., Melville, New York; Model Optiphot) equipped with a 200-W ultraviolet light source, 450- to 490-nm excitation filter, 515-interface barrier filter, and 510-nm dichroic mirror was used to identify OTC marks. This arrangement allowed the detection of a yellow band on the otolith under 250–400× magnification.

Finally, we calculated the percent survival of stocked walleyes given the estimate of the total abundance of age-0 walleyes from electrofishing CPE (Serns 1982), the proportion of the age-0 walleye population that was of hatchery origin from the examination of otoliths, and the total number of walleyes stocked with the following equation:

$$\% \text{ Survival} = \frac{P \cdot (H/T)}{S},$$

where  $P$  is the total population estimate of age-0 walleyes,  $H$  is the number of age-0 walleyes of hatchery origin determined by otolith analysis,  $T$  is the total number of otoliths of age-0 walleyes collected, and  $S$  is the number of age-0 walleyes stocked.

We quantified the diet composition of walleyes, largemouth bass, northern pike, smallmouth bass, and muskellunge in Crab Lake, Vilas County, Wisconsin, and Whitefish Lake, Sawyer County, Wisconsin, to determine the extent of diet overlap and whether these species preyed on one another. Crab Lake and Whitefish Lake are located in northern Wisconsin and are of similar size (384 and 318 ha, respectively). The walleye population in Crab Lake is primarily self-sustaining, whereas the walleye population in Whitefish Lake is primarily sustained by stocking. Stomach contents were collected by gastric lavage (Seaburg 1957) and preserved in 95% ethyl alcohol. To account for seasonal variation in diet composition, stomach samples were collected from fish during spring and fall electrofishing and fyke-netting surveys. Stomach contents were placed in a number 60 sieve (250- $\mu$ m mesh), examined under a dissecting microscope, and identified to the lowest practical tax-

onomic classification (Pennak 1978; Eddy and Hodson 1982; Becker 1983; Oates et al. 1993). Fish in advanced states of digestion were identified through the use of diagnostic bones, such as the cleithrum, opercle, dentary, or vertebrae (Hansel et al. 1988). Each type of prey item was blotted dry on a paper towel and weighed.

#### Data Analysis

*Criterion 1: Relative abundance.*—To meet this criterion, the abundance of walleyes must generally be low and the abundance of other fish species high, and vice versa. We chose to address the first criterion through the use of mark–recapture estimates of adult walleye abundance and CPEs of other species from separate creel and electrofishing surveys. We assumed that CPE was linearly related to abundances of each species (Serns 1982; Cohen et al. 1993; Beard et al. 1997; Edwards et al. 1997; McNerny and Cross 2000), so we treated CPE from standardized electrofishing surveys as an index of relative abundance of all fish species present in sampled lakes. We also treated targeted angling catch rates from creel surveys (defined as angling catch of each species divided by the hours of effort targeted at that species) as an index of relative abundance (Beard et al. 1997). Because the intensity and history of walleye stocking in lakes may influence the abundance of other fish species, we excluded lakes that supported walleye populations through stocking for this portion of the analysis. Lakes were classified as being supported by stocking if more than 50% of recruitment was attributed to stocking efforts (USBIA 1991).

We used rank correlation to quantify the relationships between abundances of walleyes (number per hectare from mark–recapture surveys) and relative abundances of largemouth bass, smallmouth bass, northern pike, and muskellunge (CPEs from creel and electrofishing surveys). We used rank correlation to avoid making a priori assumptions about the linearity of the relationships between the variables necessary with linear correlation and regression; this procedure does not require that the data be normally distributed.

*Criterion 2: Evidence of shared resources or predation.*—To meet this criterion, the diets of two species must overlap or one species must be eaten by another species. To further support the hypotheses of competition or predation between walleyes and species satisfying the first criterion, we used a modified version of Pianka's niche overlap index to quantify the degree of resource overlap by potential competitors (Christensen et al. 2000). Per-

cent wet weights were used in the following formula to estimate diet overlap between fish species:

$$O_{jk} = \frac{\sum_{i=1}^n (p_{ij} \cdot p_{ki})}{\sum_{i=1}^n (p_{ij}^2 + p_{ki}^2)/2},$$

where  $P_{ij}$  and  $P_{ki}$  are the proportions of the resource  $i$  used by species  $j$  and  $k$ , respectively (Christensen et al. 2000). The modified Pianka's niche overlap index ranges from zero to one, a value of one suggesting that the two species have exactly the same diet composition and any value other than zero indicating potential competition. We assumed that the presence of a walleye in the stomach of a largemouth bass, smallmouth bass, northern pike, or muskellunge was evidence of predation by those species on walleyes. We split walleye diet composition into juvenile (<200 mm) and adult categories because of potential ontogenetic diet shifts (Becker 1983) and because a reasonable number of juvenile walleyes were sampled ( $n = 29$ ). Few juveniles of other fish species were sampled; therefore, diets were not split into juvenile and adult categories.

*Criterion 3: Measurable effect of competition or predation.*—We chose walleye growth as a response variable. To meet this criterion, walleye growth must be significantly correlated to abundances of another species. Walleye growth depends partly on prey availability, which in turn can vary with intraspecific or interspecific competition. Therefore, growth should respond accordingly in the presence of strong competition or predation (Knight et al. 1984). A significant relationship between walleye growth and abundances of another species would suggest that the interaction between the other species and walleyes was strong enough to affect walleye growth.

We used rank correlation to quantify the relationships between walleye growth and relative abundances of other fish species. First, we used nonlinear regression to estimate parameters of the von Bertalanffy growth model for walleye length-at-age data. Second, we indexed growth with the parameter  $\omega = K \times L_{\infty}$  from the modified von Bertalanffy growth model (Gallucci and Quinn 1979). Third, we indexed relative abundances of largemouth bass, smallmouth bass, northern pike, and muskellunge as CPEs from separate creel and electrofishing surveys. Last, we examined the relationship between walleye growth rate ( $\omega$ ) and relative abundance (CPE) of each species through

the use of rank correlation. Again, because the intensity and history of walleye stocking in a given lake may have influenced the abundance of other fish species, we excluded lakes that supported walleye populations through stocking for this portion of the analysis. We were only able to examine effects of the abundance of other species on walleye growth and not the effects of walleye abundance on the growth of other species because we did not have sufficient data to estimate  $\omega$  values for species other than walleyes.

*Criterion 4: Manipulation results consistent with competition or predation.*—To meet this criterion, experimental results must conform to those expected in the presence of competition or predation for species interactions supported by the first three criteria. As an experimental manipulation, we stocked 23 lakes with OTC-marked juvenile walleyes at a constant rate of 124 walleyes/ha and estimated the survival of stocked fish in relation to the relative abundances of predators or competitors. We used rank correlation to determine whether relative abundances of largemouth bass, smallmouth bass, northern pike, or muskellunge, indexed by electrofishing CPE, were associated with stocked walleye survival.

We also used creel and electrofishing survey data from lakes that supported walleye populations through stocking to determine whether increased stocking of walleyes produced results broadly consistent with the hypotheses of competitive or predatory interactions between walleyes and other fish species, as supported by the three previous criteria. As a measure of stocking intensity, we calculated the mean number of fingerling walleyes stocked per hectare in the 10 years before the year in which the creel or electrofishing survey was completed. We then used rank correlation to relate the mean stocking intensity of small fingerling walleyes to relative abundances of each fish species. We assumed that a significant positive or negative relationship between walleye stocking intensity and relative abundances of other fish species would support the presence of a strong competitive or predatory interaction between walleyes and the other fish species.

*Bioenergetics.*—If competitive or predatory interactions were supported by the four criteria outlined above, we used a bioenergetics model (Hanson et al. 1997) to quantify the effects of the interactions. Abundances of walleyes, largemouth bass, and smallmouth bass were estimated by mark-recapture for the two lakes that were sampled for diet composition. The resulting population

TABLE 2.—Rank correlation results for adult walleye abundances versus electrofishing catch per effort and creel survey catch per effort for four other sport fish species in northern Wisconsin sampled during 1990–2002. Only lakes with walleye populations supported primarily through natural reproduction were included in this analysis. Positive relationships are designated with a plus sign and negative relationships are designated with a minus sign. Correlations were measured by Spearman's rank correlation coefficient ( $r$ ), and significant correlations are in bold italics.

Species	Electrofishing survey				Creel survey			
	Number of lakes	$r$	Relationship	$P$	Number of lakes	$r$	Relationship	$P$
Northern pike	20	0.31	–	0.18	204	0.12	–	0.10
Muskellunge	20	0.48	+	<b>0.03</b>	196	<0.01	–	0.91
Smallmouth bass	20	0.08	–	0.72	208	<0.01	–	0.84
Largemouth bass	20	0.50	–	<b>0.02</b>	197	0.03	–	0.72

estimates were used with diet information to estimate total consumption of each fish species by walleyes or total consumption of walleyes by other fish species. Temperatures for the bioenergetics models were measured five times in spring, summer, and fall in each lake and varied between 4.0°C and 18.5°C. Caloric abundances for predators and prey were taken from Hanson et al. (1997) and Cummins and Wuycheck (1971). Simulations lasted 1 year and population sizes were held constant (i.e., no mortalities). The entire population consisted of fish of the average length of all fish sampled of that species in the two lakes. Growth was estimated from the mean change in length for all lakes in Wisconsin (WDNR, unpublished data) and a weight–length relationship for largemouth bass (Carlander 1977). Although data used to construct this model were not precise, our objective was only to provide an order of magnitude estimate of consumption.

## Results

### Criterion 1: Relative Abundance

Muskellunge and largemouth bass abundances were related to walleye abundances, while northern pike and smallmouth bass were not (Table 2). Muskellunge electrofishing CPE was positively correlated to walleye abundances and largemouth bass electrofishing CPE was negatively correlated

to walleye abundances (Table 2). Because muskellunge abundances were positively correlated to walleye abundances, direct competition or predation is unlikely to be occurring between these two species. As a result, muskellunge were not considered further. Neither northern pike nor smallmouth bass CPE values were significantly correlated to walleye abundances, so smallmouth bass and northern pike were not considered further (Table 2).

### Criterion 2: Evidence of Shared Resources or Predation

Diet analysis confirmed the potential for predatory or competitive interactions between walleyes and the species of fish that satisfied criterion 1 (largemouth bass). Largemouth bass ate walleyes, whereas walleyes ate few largemouth bass (Table 3). In addition, diets of juvenile and adult walleyes overlapped with diets of largemouth bass (Table 4).

### Criterion 3: Measurable Effect of Competition or Predation

Walleye growth rate ( $\omega$ ) was positively correlated to angling CPE of largemouth bass ( $r = 0.23$ ;  $N = 135$ ;  $P = 0.01$ ), but walleye growth was not correlated to electrofishing CPE of largemouth bass ( $r = -0.01$ ;  $N = 17$ ;  $P = 0.98$ ).

TABLE 3.—Percentages, by weight, of (1) walleyes in the diets of northern pike and largemouth bass and (2) these same two species in the diet of walleyes in Whitefish and Crab lakes, northern Wisconsin, sampled during 1990–2002. Percentages by individual lake and mean values are presented. The number of fish with identifiable stomach contents that were sampled is shown in parentheses. No largemouth bass were captured in Crab Lake.

Species	Percent of walleye diet			Walleye as percent of diet		
	Crab lake	Whitefish lake	Mean	Crab lake	Whitefish lake	Mean
Northern pike	0.0 (37)	0.0 (31)	0.0 (68)	49.9 (14)	0.2 (20)	25.1 (34)
Largemouth bass		1.0 (27)	1.0 (27)		4.8 (27)	4.8 (27)

TABLE 4.—Modified Pianka's diet overlap index values for northern pike and largemouth bass with adult juvenile walleyes in Whitefish and Crab lakes, northern Wisconsin, sampled during 1999–2002. Individual lake and mean values are presented. No largemouth bass were captured in Crab Lake.

Species	Index of diet overlap with adult walleyes			Index of diet overlap with juvenile walleyes		
	Crab Lake	Whitefish Lake		Crab Lake	Whitefish Lake	
		Mean	Crab Lake		Mean	
Largemouth bass		0.38	0.38		0.61	0.61
Northern pike	0.14	0.27	0.21	0.05	0.61	0.33

#### *Criterion 4: Manipulation Results Consistent with Competition or Predation*

The survival of stocked walleyes was lower when electrofishing CPE of largemouth bass was high ( $r = 0.53$ ;  $N = 23$ ;  $P = 0.01$ ), which would be expected if largemouth bass preyed heavily on stocked juvenile walleyes.

The mean stocking rate of small fingerling walleyes was positively related to creel survey CPE of largemouth bass ( $r = 0.29$ ;  $n = 58$ ;  $P = 0.03$ ) but not to CPE from electrofishing surveys ( $r = 0.32$ ;  $n = 14$ ;  $P = 0.26$ ).

#### *Bioenergetics*

The estimated abundance of 946 adult largemouth bass in Whitefish Lake, each of which weighed 0.7 kg and experienced annual growth of 0.3 kg in our model, consumed approximately 49.5 kg of juvenile walleyes during the year. We made the assumption that all consumed walleyes were the weight at which they were stocked in June (0.6 g/fingerling walleye). This level of consumption corresponds to 82,500 fingerling walleyes consumed during the year, which greatly exceeds the 39,300 walleyes that were actually stocked in June 2002.

### **Discussion**

Largemouth bass was the only species we examined that satisfied all four criteria suggested by MacLean and Magnuson (1977), but this does not preclude the possibility that other species may interact with walleyes through competition or predation or that they may be affected directly or indirectly by walleye stocking. The data we used were relatively coarse, and interactions with other species may have been too subtle or indirect to be detected by our data or analysis. We only examined the interactions between walleyes and four other fish species. Undoubtedly, there are potentially strong interactions between walleyes and fish species not examined here (Lyons and Magnuson 1987). Nonetheless, our results suggest that large-

mouth bass affect walleye populations and that walleye stocking affects largemouth bass populations.

Our findings agree with those of Santucci and Wahl (1993), Nate et al. (2003), and Inskip and Magnuson (1983), who found an inverse relationship between largemouth bass and walleye abundances. Santucci and Wahl (1993) also found that largemouth bass predation limited survival of stocked walleyes in Ridge Lake, Illinois. Similarly, our results suggest that largemouth bass may limit success of stocked walleyes in general.

The number of juvenile walleyes that we estimated were consumed by largemouth bass (82,500) was based on the assumptions that all walleyes consumed by largemouth bass weighed 0.6 g and that our estimate that walleyes comprised 4.8% of the largemouth bass diet in Whitefish Lake was accurate. The total number of walleyes consumed by largemouth bass may be higher or lower depending on the actual weight of walleyes when they are consumed. For example, the impact of largemouth bass predation would be less if we assumed that all walleyes were consumed in September, when individual walleyes were substantially larger than 0.6 g. However, results from Santucci and Wahl (1993) suggest that our assumption is reasonable; they found that largemouth bass predation was related to the length of stocked walleyes and that vulnerability to predation was greatest immediately after stocking. Similarly, the total number of walleyes consumed may be higher or lower depending on the actual percentage of walleyes in the diet of largemouth bass. Although we only have largemouth bass diet information from one lake, our estimate that walleyes comprised 4.8% of the largemouth bass diet was similar to findings by Liao et al. (2004), and our goal was only to provide an order of magnitude estimate of consumption. In addition, some juvenile walleyes that were consumed by largemouth bass were probably produced naturally in the lake. Although some juvenile walleyes that were consumed by

largemouth bass were probably produced naturally in the lake, the fact that the number of walleyes stocked was substantially smaller than the estimated number consumed by largemouth bass suggests that survival of stocked walleyes is significantly reduced by largemouth bass predation.

We found that largemouth bass abundances were positively related to walleye stocking rates, so largemouth bass may benefit from walleye stocking. Prey availability can influence reproductive potential (Kershner et al. 1999), growth (Yako et al. 2000), and survival (Miranda and Pugh 1997). If largemouth bass are limited by prey availability, additional prey may increase their survival and abundance (Miranda and Pugh 1997). Walleye stocking may provide the additional prey resources necessary for largemouth bass populations to increase. Alternatively, fisheries managers may stock walleyes at a higher rate in lakes with high largemouth bass abundances in hopes of some degree of walleye survival. With our data, we cannot determine whether high stocking rates caused high largemouth bass abundances or if high largemouth bass abundances caused high stocking rates. However, given the large number of walleyes that largemouth bass may consume, largemouth bass populations would probably benefit from stocking of juvenile walleyes.

Another possible explanation for the negative relationship between largemouth bass abundances and juvenile walleye survival is that lakes with high abundances of largemouth bass may have physical and chemical conditions that are not conducive to walleye survival. Nate et al. (2003) showed that habitat parameters could be used to predict the presence or absence of walleyes, but could not differentiate between lakes with self-sustaining and stocked walleye populations in northern Wisconsin. This suggests that lakes with walleyes, regardless of their origin, are roughly similar in their habitats. In addition, we found that the hypothesis of largemouth bass preying heavily on stocked walleyes was supported by all four criteria. Our results were obtained from lakes experimentally stocked with marked walleyes, lakes whose walleye populations were supported by stocking, and lakes whose walleye populations were self-sustaining, so an alternative explanation is difficult to support.

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 abun-

dances of largemouth bass, given their potentially large impact on survival of juvenile walleyes. Stocking walleyes may initially be successful in lakes with low abundances of largemouth bass, but may have the unintended effect of providing additional prey for largemouth bass. If a largemouth bass population is limited by prey availability, walleye stocking may lead to increased largemouth bass abundances that reduce poststocking survival of walleyes through time.

### Acknowledgments

We thank all WDNR fisheries biologists, technicians, and creel clerks past and present for collecting data associated with this investigation. In particular, we thank Mike Coshun, Jamison Wendel, Steve Kramer, Cal Glessing, and Todd Brecka. We also thank the Great Lakes Indian Fish and Wildlife Commission for providing some of the data used here. Pat Schmalz, Sarah Fayram, and Jeff Jorgensen provided helpful comments on an earlier draft of this manuscript. Comments from Carolyn Griswold, the Associate Editor, and three anonymous reviewers also greatly improved this manuscript. Betsy Ott completed the majority of the stomach content identification. The preparation and examination of otoliths for OTC marks completed by Mike Vogelsang and Matt Andre was greatly appreciated. Steve Hewett, Mike Staggs, and Dennis Schenborn helped facilitate the completion of this project. The Federal Aid in Sport Fish Restoration Program provided partial funding for this project.

### References

- Anthony, D. D., and C. R. Jorgensen. 1977. Factors in the declining contributions of walleye (*Stizostedion vitreum vitreum*) to the fishery of Lake Nipissing, Ontario, 1960–76. *Canadian Journal of Fisheries and Aquatic Sciences* 34:1703–1709.
- Beard, T. D., Jr., S. W. Hewett, Q. Yang, R. M. King, and S. J. Gilbert. 1997. Prediction of angler catch rates based on population abundances. *North American Journal of Fisheries Management* 17:621–627.
- Becker, G. C. 1983. *Fishes of Wisconsin*. University of Wisconsin Press, Madison.
- Bozek, M. A., T. M. Burri, and R. V. Frie. 1999. Diets of muskellunge in northern Wisconsin lakes. *North American Journal of Fisheries Management* 19: 258–270.
- Carlander, K. D. 1977. *Handbook of freshwater fishery biology*, volume 2. Iowa State University Press, Ames.
- Christensen, V., C. J. Walters, and D. Pauly. 2000. *Eco-path with Ecosim: a user's guide*. Fisheries Centre, University of British Columbia, Vancouver, and In-



- ternational Center for Living Aquatic Resources Management, Penang, Malaysia.
- Cohen, Y., P. Randomski, and R. Moen. 1993. Assessing the interdependence of assemblages from Rainy Lake fisheries data. *Canadian Journal of Fisheries and Aquatic Sciences* 50:402–409.
- Craig, J. F., and J. A. Babaluk. 1989. Relationship of condition of walleye and northern pike to water clarity, with special reference to Dauphin Lake, Manitoba. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1581–1586.
- Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *International Association of Theoretical and Applied Limnology Proceedings* 18:1–158.
- DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–508 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Eddy, S., and A. C. Hodson. 1982. Taxonomic keys to the common animals of the north central states, 4th edition. Burgess Publishing, Minneapolis, Minnesota.
- Edwards, C. M., R. W. Drenner, K. L. Gallo, and K. E. Reiger. 1997. Estimation of population abundances of largemouth bass in ponds by using mark–recapture and electrofishing catch per effort. *North American Journal of Fisheries Management* 17:719–725.
- Fenton, R., J. A. Mathias, and G. E. Moddie. 1996. Recent and future demand for walleye in North America. *Fisheries* 21(1):6–12.
- Gallucci, V. F., and T. J. Quinn II. 1979. Reparameterizing, fitting, and testing a simple growth model. *Transactions of the American Fisheries Society* 108:14–25.
- GLIFWC (Great Lakes Indian Fish and Wildlife Commission). 2001. Midwest region tribal fish hatcheries 2001 fish production report. GLIFWC, Odanah, Wisconsin.
- Gotelli, N. J. 1998. *A primer of ecology*. Sinauer Associates, Sunderland, Massachusetts.
- Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. *Transactions of the American Fisheries Society* 117:1405–1420.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. *Fish bioenergetics 3.0*. University of Wisconsin, Sea Grant Institute, WISC-T-97-001. Madison.
- Inskip, P. D., and J. J. Magnuson. 1983. Changes in fish populations over an 80-year period: Big Pine Lake, Wisconsin. *Transactions of the American Fisheries Society* 112:378–389.
- Johnson, F. H., and J. G. Hale. 1977. Interrelations between walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieu*) in four northeastern Minnesota Lakes, 1948–69. *Journal of the Fisheries Research Board of Canada* 34:1626–1632.
- Kershner, M. W., D. M. Schael, R. L. Knight, R. A. Stein, and E. A. Marschall. 1999. Modeling sources of variation for growth and predatory demand of Lake Erie walleye (*Stizostedion vitreum*), 1986–1995. *Canadian Journal of Fisheries and Aquatic Sciences* 56:527–538.
- Knight, R. L., F. L. Margraf, and R. F. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society* 113:677–693.
- Liao, H., C. L. Pierce, and J. G. Larscheid. 2004. Consumption dynamics of the adult piscivorous fish community in Spirit Lake, Iowa. *North American Journal of Fisheries Management* 24:890–902.
- Lyons, J., and J. J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. *Transactions of the American Fisheries Society* 116:29–39.
- MacLean, J., and J. J. Magnuson. 1977. Species interactions in percid communities. *Journal of the Fisheries Research Board of Canada* 34:1941–1951.
- McInerney, M. C., and T. K. Cross. 2000. Effects of sampling time, intraspecific abundances, and environmental variables on electrofishing catch per effort of largemouth bass in Minnesota Lakes. *North American Journal of Fisheries Management* 20:328–336.
- Miranda, L. E., and L. L. Pugh. 1997. Relationship between vegetation coverage and abundance, size, and diet of juvenile largemouth bass during winter. *North American Journal of Fisheries Management* 17:601–610.
- Nate, N. A., M. A. Bozek, M. J. Hansen, C. W. Ramm, M. T. Bremigan, and S. W. Hewett. 2003. Predicting the occurrence and success of walleye populations from physical and biological features of northern Wisconsin lakes. *North American Journal of Fisheries Management* 23:1207–1214.
- Oates, D. W., L. M. Krings, and K. L. Ditz. 1993. *Field manual for the identification of selected North American freshwater fish by fillets and scales*. Nebraska Game and Parks Commission, Nebraska Technical Series 19, Lincoln.
- Pennak, R. W. 1978. *Freshwater invertebrates of the United States*, 2nd edition. Wiley, New York.
- Pollock, K. H., C. M. Jones, and T. L. Brown. 1994. *Angler survey methods and their applications in fisheries management*. American Fisheries Society, Special Publication 25, Bethesda, Maryland.
- Rasmussen, P. W., M. D. Staggs, T. D. Beard, Jr., and S. P. Newman. 1998. Bias and confidence interval coverage of creel survey estimators evaluated by simulation. *Transactions of the American Fisheries Society* 127:469–480.
- Reynoldson, T. B., and L. S. Bellamy. 1972. The establishment of interspecific competition in field populations with an example of competition in action between *Polycelis nigra* and *P. tenuis* (Turbellaria, Tricladia). *Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations* (Oosterbeek 1970):282–287.
- Ricker, W. E. 1975. Computations and interpretation of

- biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.
- Santucci, V. J., Jr., and D. H. Wahl. 1993. Factors influencing survival and growth of stocked walleye in a centrarchid-dominated impoundment. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1548–1558.
- Seaburg, K. G. 1957. A stomach sampler for live fish. *Progressive Fish-Culturist* 19:137–139.
- Serns, S. L. 1982. Relationship of walleye fingerling abundances and electrofishing catch per unit effort in northern Wisconsin lakes. *North American Journal of Fisheries Management* 2:38–44.
- USBIA (U.S. Bureau of Indian Affairs). 1991. Casting light upon the waters: a joint fishery assessment of the Wisconsin ceded territory. USBIA, Minneapolis, Minnesota.
- WDNR (Wisconsin Department of Natural Resources). 1999. An evaluation of stocking strategies in Wisconsin with an analysis of projected stocking needs. Wisconsin Department of Natural Resources, Bureau of Fisheries Management and Habitat Protection, Madison.
- Yako, L. A., M. E. Mather, and F. Juanes. 2000. Assessing the contribution of anadromous herring to largemouth bass growth. *Transactions of the American Fisheries Society* 129:77–88.
- Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during out-migration of juvenile anadromous salmonids. *Transactions of the American Fisheries Society* 128:1036–1054.