Diet Overlap and Predation between Smallmouth Bass and Walleye in a North Temperate Lake

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ABSTRACT

Walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieu*) diets from Big Crooked Lake, Wisconsin were examined to assess the degree of diet overlap and predation occurring between these species in an attempt to determine whether walleye influence smallmouth bass recruitment, which is consistently low compared to proximal lakes that do not have walleye. Of 389 adult walleye stomachs examined from June 1999 through March 2000, a total of 879 prey fish was found, but only one was identified as a smallmouth bass. In 303 smallmouth bass stomachs examined, 55 prey fish were found and no cannibalism was evident, nor were walleye preyed upon. Dietary overlap using the Schoener resource overlap index was 0.416, 0.293 and 0.205 for the months June, July and August 1999, respectively, indicating that there was not a significant dietary overlap during summer months. Because neither diet overlap nor predation appeared substantial in Big Crooked Lake, additional research on interactions among younger age classes of walleye, interactions at other times of the year, and interactions with other species are needed to elucidate limitations to smallmouth bass recruitment in this system.

INTRODUCTION

Walleye (*Stizostedion vitreum vitreum)* and smallmouth bass (*Micropterus dolomieu)* are popular sportfishes in North America, and both species have been widely introduced in attempts to establish or enhance fisheries (Scott and Crossman 1973, Colby et al. 1987). These introductions have resulted in a wide range of consequences that are not well understood. Of particular concern are introductions of walleye or smallmouth bass into waterbodies already containing a sustaining population of the other species, which results in a reduction in growth or abundance of the other species (Kempinger and Carline 1977, Johnson and Hale 1977). For instance, smallmouth bass were nearly extirpated from Escanaba Lake, Wisconsin after the introduction and establishment of walleye in the late 1940's (Kempinger and Carline 1977). This occurred despite the fact that the smallmouth bass was the most abundant top predator in the lake. The bass continues to remain in very low abundance nearly 50 years after the introductions, while the walleye sustains a high population (Gauthier 2001). Johnson and Hale (1977) found mixed effects in systems where smallmouth bass were introduced to waterbodies containing walleye. In three of four northeastern Minnesota lakes, introductions of smallmouth bass corresponded to a decrease in walleye abundance. In the fourth lake, both the smallmouth bass and walleye populations initially increased, but after approximately 11 years, the smallmouth bass population decreased to a very low level as the walleye abundance continued to increase. Other less well-documented cases from many north temperate lakes have added to concerns of fisheries managers about walleye and smallmouth bass interactions.

Precise understanding of causal factors in the decline of either species is unclear as studies on feeding interactions between walleye and smallmouth bass are limited. General smallmouth bass and walleye food habit studies indicate that they utilize similar diet items, which suggests that they may compete with each other for food (Dobie 1966, Scott and Crossman 1973, Colby et al. 1979). Because walleye are thought to prey on a wide array of suitable-sized (i.e., gape sized) fish species (Ryder and Kerr 1978), smallmouth bass might be a substantial prey item. Walleye predation has been documented to affect other important fish species such as: yellow perch (Forney 1977, Hartman and Margraf 1993), juvenile salmonids (Maule and Horton 1984 , Rieman et al. 1991) and paddlefish (*Polyodon spathula*) (Mero et al. 1994, Parken 1996), and numerous studies show that walleye indeed prey on smallmouth bass (Rainey and Lachner 1942, Rosebery 1950, Fedoruk 1966, Paxton and Stevenson 1978, Jones et al. 1994). However, the degree to which walleye affect smallmouth bass populations is not well documented.

Big Crooked Lake, Wisconsin is within the native range of both walleye and smallmouth bass (Becker 1983). Big Crooked Lake contains a high standing stock of walleye (18.5 walleye/ha in 1999) and a low standing stock of smallmouth bass (0.3 smallmouth bass/ha in 1999). In stark contrast, nearby Nebish Lake contains a standing stock of 16.2 smallmouth bass/ha (Kempinger and Christenson 1978) suggesting recruitment of smallmouth bass in Big Crooked Lake is limited. The objectives of this study were to examine interactions between walleye and smallmouth bass. Diet overlap was evaluated during June, July and August 1999, and predation on smallmouth bass by walleye was evaluated from June 1999 to March 2000.

STUDY AREA

Big Crooked Lake is located in Vilas County, Wisconsin. The lake is 276 hectares in size, has a maximum depth of 11.5 m, and has 8.0 km of shoreline (Serns 1978). Other predatory fishes in Big Crooked Lake, besides walleye and smallmouth bass, include yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), burbot (*Lota lota*), muskellunge (*Esox masquinongy*) and northern pike (*Esox lucius*). Forage species included white sucker (*Catostomus commersoni*), pumpkinseed (*Lepomis gibbosus*), bluntnose minnow (*Pimephales notatus*), mimic shiner (*Notropis volucellus*), common shiner (*Nortopis cornutus*), log perch (*Percina caprodes*), johnny darter (*Etheostoma nigrum*), and Iowa darter (*Etheostoma exile*). Crayfish (*Orconectes* sp.) are very abundant along with several taxa of Ephemeroptera, Diptera and Odonata.

METHODS

Population Estimates

Adult walleye and smallmouth bass populations were estimated using a Schnabel mark-recapture estimate (Ricker 1975). Both walleye and smallmouth bass were captured prespawn using fyke nets consisting of 19mm stretch mesh and 1m hoops. Fish were marked with tags (e.g., aluminum jaw tags for walleye and Floy® tags for smallmouth bass) and dorsal spines were clipped. Recaptures were obtained using night boat AC current electrofishing. Multiple runs, each encompassing the entire shoreline were preformed.

Estimates of smallmouth bass eggs and fry were obtained by locating smallmouth bass nests using snorkeling and SCUBA in the littoral zone. Estimates of eggs and fry were obtained by placing a 30-cm^2 grid divided into 25, 6-cm^2 squares on each nest. Visual estimates of number of eggs and pre swim-up black fry in each square were summed to estimate the total number of eggs deposited or fry produced from each nest. Estimates were highly correlated with actual counts conducted on a subset of nests used to validate this technique (eggs: r^2=0.98, fry: r^2=0.97).

Population estimates of fall young-of-year (YOY) walleye and smallmouth bass were obtained during September using a Schnabel mark-recapture estimate (Ricker 1975). YOY smallmouth bass were captured by seining the littoral zone and initially marked by clipping of the upper caudal fin. Recapture was conducted by subsequent multiple night boat electrofishing runs of the entire shoreline. YOY walleye populations were estimated by multiple night boat electrofishing runs. Fish were marked by fin clips and later recaptured by multiple recapture runs, one to five nights later.

Diet

Walleye and smallmouth bass stomach samples were collected from June through August 1999 to assess diet overlap and predation. Additional walleyes were collected from open water during September and October and through the ice (winter samples) during November through March. Fish were captured primarily by fyke net and night electrofishing and by angling in winter. Fyke nets (19 mm stretch mesh and 1m hoops) were fished daily and emptied during early morning to minimize digestion. Net size of 19 mm allowed prey fish to pass through the net precluding foraging inside the nets. There were no significant differences in the proportion of any diet taxa found in stomachs of walleye caught by fyke net verses electrofishing except bluntnose minnow in July (X^2=4.996, p=0.025) and yellow perch in August (X^2=12.830, p=<0.001) suggesting bias in diet items obtained between gear types was minimal.

Stomach contents were flushed from live fish by gastric lavage using a pump similar to those described by Crossman and Hamilton (1978) and Gilbert and Johnson (1997). Stomach contents were preserved in 10% formalin. Validation was performed on 10 walleye to determine the effectiveness of this technique; 100% of diet items were removed by this technique. For stomach samples, each prey item present was counted and wet mass was measured to the nearest 0.001 gram. Partially digested prey items were identified using diagnostic body parts (Scott and Crossman 1973, Becker 1983, Oates et al. 1993, Merritt and Cummins 1996), and whole prey fish and invertebrates were collected as voucher specimens for evaluating partially digested prey.

Analysis of stomach contents included frequency of occurrence, percentage of total number of each food type, and percentage of total mass for each food type. The relative importance (RI) index (George and Hadley 1979) was used to evaluate the importance of each diet item. Comparisons of food items consumed between walleye and smallmouth bass were made using the Schoener (T) resource overlap index (Schoener 1970). Values range from 0 to 1, with 0 indicating no overlap and 1 indicating complete overlap. In addition to diet overlap, we also evaluated the occurrence of predation on smallmouth bass by both walleye and smallmouth bass.

RESULTS

The standing stock of smallmouth bass in Big Crooked Lake was low, ranging from 0.3 to 0.9/ha from 1998 to 2000 (Table 1). For the stock size present, egg deposition was substantial, ranging from 131,000 to 202,000 smallmouth bass eggs on nests. However, smallmouth bass mortality during the first summer of life was high; survival of eggs to fall YOY ranged from 1.7 to 4.8%, resulting in estimates of only 3,083 to 9,700 YOY smallmouth bass by September.

Table 1. Abundance and survival of smallmouth bass young-of-year (YOY) in Big Crooked Lake 1998-2000. Fry counted were black fry just prior to swim-up. Fall YOY estimates were collected in September using seining for marking fish and electrofishing for recaptures.

Year	Adult smallmouth bass population estimate (number/ha)	Number of smallmouth bass nests	Estimated number of eggs	Estimated number of fry	Estimated number of fall YOY	Survival from egg to fall YOY	Survival from fry to fall YOY
1998	0.6	38	202,000	146,000	9,700	4.8%	6.6%
1999	0.3	49	172,000	101,000	3,000	1.7%	3.0%
2000	0.8	48	131,000	105,000	4,146	3.2%	3.9%

Length of walleye and smallmouth bass examined for stomach contents from June 1999 to March 2000 ranged from 100-545 mm TL (Table 2). Percentage of empty stomachs in walleye was highest during the winter months (89%) and lowest during June (14%). For smallmouth bass, the lowest percentage of empty stomachs occurred in June (23%); the highest was in July (46%). The Schoener resource overlap index showed that diet overlap between walleye and smallmouth bass was highest in June (0.416) followed by July (0.293) and August (0.205).

Crayfish was the most important diet item for walleye during June (RI = 25) with Ephemeroptera (RI = 24) and yellow perch (RI = 23) almost as important (Table 3, Figure 1). Yellow perch was the most important diet item during the remainder of the sampling period. Walleye continued to consume crayfish in July, but its importance in their diet continued to decline. Ephemeroptera were utilized frequently during June, when peak emergence occurred; otherwise few were encountered. YOY burbot were also utilized during June and July but not after that time. Only one smallmouth bass was eaten during this period.

Relative importance of diet taxa for smallmouth bass showed that crayfish was the most important diet item during all three summer months having a RI value ranging from 68 to 79, nearly 2.4 to 7.2 times that of walleye (Table 3, Figure 1). Smallmouth bass also utilized invertebrates such as Ephemeroptera and Odonata, with peak use of Ephemeroptera occurring during their emergence in June (RI = 22). Unlike walleye, prey fish were not heavily utilized by smallmouth bass and no young smallmouth bass were found in any stomachs.

After August, smallmouth bass were difficult to sample but diet analyses for walleye continued. There were 51 walleye stomachs examined in September, 13 in October, and 62 collected during winter sampling (Table 2). Diet of walleye from September through March was comprised mainly of yellow perch (Table 3, Figure 2). Crayfish were utilized during both September and October, while Ephemeroptera and Diptera were utilized during September. Evidence of predation by walleye on smallmouth bass was not detected. A total of 23 prey fish was found in walleye stomachs during this time period and none was smallmouth bass.

Table 2. Size and mass of walleye examined for stomach contents during June, July, August, September, October and winter (November through March) 1999 - 2000 and smallmouth bass examined during June, July and August 1999. Values indicate the mean ± one standard error; ranges are values in parentheses.

Species	Month	*n*	Mean Length (mm)	Mean mass (kg)
Walleye	June	70	313 ± 12.9 (142 – 545)	0.33 ± 0.04 (0.03 – 1.28)
	July	106	300 ± 8.2 (194 – 537)	0.31 ± 0.03 (0.05 – 1.30)
	August	87	324 ± 10.7 (209 – 502)	0.37 ± 0.04 (0.05 – 1.20)
	September	51	350 ± 14.4 (100 – 503)	0.37 ± 0.04 (0.01 – 1.06)
	October	13	363 ± 6.6 (363 – 445)	0.68 ± 0.03 (0.42 – 0.87)
	Winter	62	413 ± 7.7 (224 – 533)	0.67 ± 0.05 (0.17 – 1.52)
Smallmouth Bass	June	64	349 ± 13.0 (204 – 514)	0.86 ± 0.08 (0.13 – 2.35)
	July	166	365 ± 10.9 (132 – 508)	1.04 ± 0.06 (0.04 – 2.25)
	August	73	380 ± 12.2 (155 – 225)	1.16 ± 0.09 (0.01 – 2.40)

DISCUSSION

Low standing stocks of adult smallmouth bass (x = 0.6/ha 1998-2000) in Big Crooked Lake verses 16.2/ha in nearby Nebish Lake (Kempinger and Christenson 1978) suggest that recruitment is low in this system. Smallmouth bass mortality during the first summer of life is high in Big Crooked Lake suggesting that a recruitment bottleneck may occur at this time. On average 95.5% of YOY smallmouth bass did not survive through August during the period 1998-2000. With abundant cobble, gravel, and sand/gravel shorelines, it was suspected that walleye may limit survival of smallmouth bass through diet overlap, or that walleye were preying upon young smallmouth bass. These results suggest that neither of these interactions appears to be substantial during the time periods and for size classes of smallmouth bass and walleye sampled.

In studies of diet overlap, despite similarity in diets, competition appears less likely between the two species (Fedoruk 1966, Johnson and Hale 1977, Lott 1996). Fedoruk (1966) found that smallmouth bass introduced into Falcon Lake, Manitoba did not substantially compete with walleye for food. Johnson and Hale (1977) reported similar results from diet analyses in four northeastern Minnesota lakes. Both species utilized a number of common food items but the pattern of feeding intensity showed that each species had different preferences with walleye utilizing a broader range of food items. In riverine systems both Zimmerman (1999) and Stephenson and Momot (1991) again found some utilization of similar prey, but significant overlap appeared minimal. It appears that

Table 3. Diet items consumed by walleye and smallmouth bass with percent occurrence, number of individual items and percent mass for each diet taxa. Fish that did not contain any stomach items were omitted from diet analysis. * indicates values < 1%

	% Occurrence						Number						% by Mass					
Walleye	June	July	Aug.	Sept.	Oct.	Winter	June	July	Aug.	Sept.	Oct.	Winter	June	July	Aug.	Sept.	Oct.	Winter
Fish																		
Yellow Perch	36	75	73	49	67	86	240	251	53	45	11	6	17	36	72	91	65	94
Burbot	28	19					98	28					8	4				
Rock Bass	2						1						1					
Log Perch	2						1						1					
Smallmouth Bass			2						1						2			
Bluntnose Minnow		3						2						1				
Pumpkinseed			2						1						7			
Unidentified fish	33	18	39	32	56	14	91	20	18	6	5	1	33	18	39	4	33	6
Invertebrates																		
Crayfish	34	30	16	21	11		69	57	9	4	1		51	58	12	2	2	
Ephemeroptera	38	11	5	16			291	11	4	7			13	1	*	2		
Odonata	2	1					6	1					1	1				
Hirudinea		4						3						*				
Diptera				58						102						1		
Smallmouth Bass																		
Fish																		
Yellow perch	2	4	7				2	4	5				*	1	6			
Burbot	7	7					3	8					1	2				
Log perch		1						4						1				
Darter sp.			2						1						*			
Bluntnose Minnow		2						2						1				
Unidentified fish	7	11	20				6	13	9				1	2	2			
Invertebrates																		
Crayfish	93	83	91				156	183	111				91	93	90			
Terrestrial	2						3						*					
Hemiptera	2	1					1	1					*	*				
Ephemeroptera	48	13					67	16					6	*				
Odonata	5	18	11				2	26	15				*	2	3			
Hirudinea	2	2					1	2					*	*				
Trichoptera		1						1						*				

in many of these studies, smallmouth bass and walleye both use invertebrates and fish as prey, but that smallmouth bass rely heavily on crayfish when present, thereby, reducing diet overlap with walleye (Fedoruk 1966).

The results from the Schoener (1970) index indicate that there was not a significant overlap in the diets of walleye and smallmouth bass. The value of 0.60 is the level at which it is suspected that there is biologically significant dietary overlap (Wallace 1981). The highest value occurred in June (0.416) when both species utilized crayfish and Ephemeroptera. In June, walleye generally remain near shore after spawning (Colby 1979) and if that occurs in Big Crooked Lake, they are spatially proximinal to smallmouth bass, thus creating conditions for higher overlap. Walleye later move offshore where

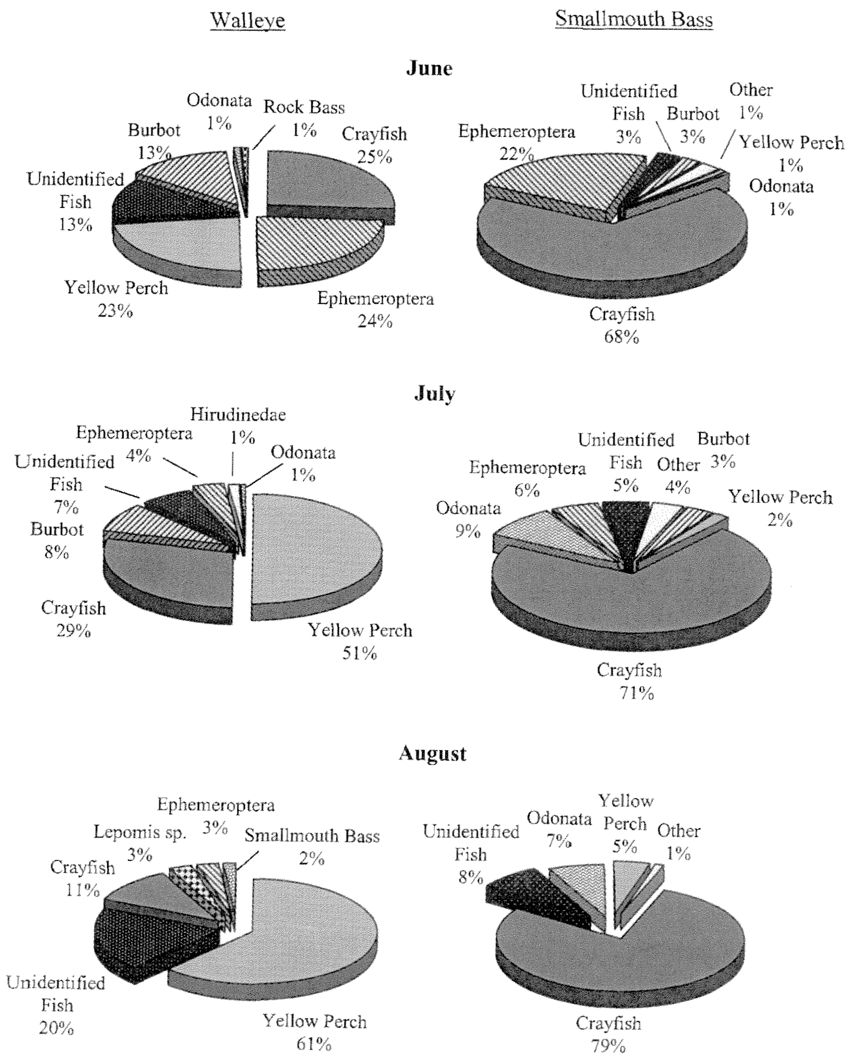

Figure 1. Relative Importance Index for the diets of smallmouth bass and walleye collected during June, July, and August 1999. Other indicates fish species which were very low in relative importance and were subsequently combined.

spatial and diet partitioning become more likely, thus decreasing the level of dietary overlap that we found. Diet overlap in Big Crooked Lake was similar to that observed in Pine Lake, Minnesota (Johnson and Hale 1977). Both walleye and smallmouth bass consumed fish and invertebrates. Ephemeroptera nymphs were consumed by both species, while walleye consumed more fish and smallmouth bass consumed crayfish. Likewise, diet overlap in the Kaministiquia River, Ontario was minimal with walleye consuming fish and smallmouth bass utilizing crayfish (Stephenson and Momot 1991).

Crayfish constituted the major diet item for adult smallmouth bass during the summer of 1999. This predominance of crayfish in the diet is consistent with previous studies (Hubbs and Bailey 1938, Doan 1940, Fedoruk 1966, Clady 1974, Kilambi et al. 1977). The only other major diet taxon used by smallmouth bass during the study was Ephemeroptera in June. The decrease in relative importance of Ephemeroptera occurring after June likely corresponded to the end of the emergence period occurring during June and July. During June, Ephemeroptera were high in abundance and easily susceptible to predators. Other less important diet taxa included burbot that were utilized in June and July but non-existent in the smallmouth bass diet in August, possibly due to a decrease in the abundance of burbot or an increase in their size or perhaps a shift in habitat. The relative importance of both yellow perch and Odonata increased as the summer progressed but these remained minor components of the diet.

Yellow perch made up a major proportion of the diet of walleye. The importance of yellow perch in the diet of walleye is common in percid-dominated lakes (Parsons 1971, Forney 1974, Forney 1977, Swenson 1977). In Oneida Lake, New York, Forney (1974) found that young yellow perch was the most important diet item of all size classes and that walleye predation caused substantial decreases in yellow perch abundance. Similar to smallmouth bass, the relative importance of Ephemeroptera in June was high

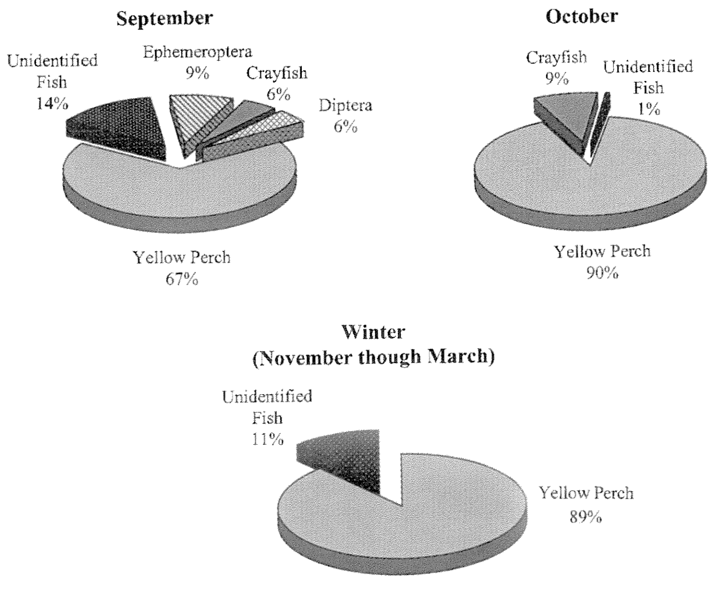

Figure 2. Relative Importance Index for the diet of walleye during September and October 1999 and the winter sampling period of November 1999 through March 2000.

and declined afterwards as walleye are also known to change their diet as prey abundance and accessibility change (Parsons 1971, Swenson 1977, Knight et al. 1984, Lyons and Magnuson 1987, Vigg et al. 1991). Dobie (1966) saw a shift of diet in Lake Vermilion, Minnesota where in May and early June burrowing mayflies were the major diet items in adult walleye stomachs. In our study, once emergence of the mayflies ended in early July, YOY yellow perch became the main food item and continued into autumn. The largest overlap was with crayfish, primarily occurring in June and declining thereafter.

Although adult walleye were highly piscivorous during most of the sampling period, there was very little evidence of direct predation on smallmouth bass during that time. This level of predation on smallmouth bass is consistent with other studies where occurrence of smallmouth bass in walleye stomachs was low (Raney and Lachner 1942, Rosebery 1950, Fedoruk 1966, Paxton and Stevenson 1978, Jones et al. 1994). This could have resulted because walleye might not prefer smallmouth bass as forage or because the relative abundances of other preferred prey items (i.e., yellow perch, crayfish, Ephemeroptera) were higher than that of juvenile smallmouth bass. However, young smallmouth bass were abundant at swim up, but still not found in adult walleye stomachs. Because young smallmouth bass were not seen in walleye stomachs, even earlier in the summer when the abundance of YOY smallmouth bass was high, it is clear that predation by adult walleye on smallmouth bass is low.

Effects of predation can often be difficult to predict and evaluate in natural systems, especially when trying to evaluate predation on a prey species which is already in low abundance. However, while adult smallmouth bass were low in abundance in Big Crooked Lake, initial numbers of smallmouth bass fry emerging from nests were substantial. It is clear that mortality rates of YOY smallmouth bass were high, but it is unknown how quickly young smallmouth bass numbers decline, which could provide insight into their availability as forage and causes for low recruitment. The likelihood of detecting walleye predation on smallmouth bass might be low simply due to the relatively small numbers of YOY smallmouth bass available as food later in summer. Mortality of YOY smallmouth bass may be rapid following hatching and emergence from the nest. However, we believe our data indeed represent low predation rates on YOY smallmouth bass. It is unlikely that substantially more predation of smallmouth bass by walleye occurred than what was observed. We saw only one YOY smallmouth bass in 389 walleye stomachs from June 1999 to March 2000. When extrapolated to the whole population of 5104 adult walleye in 1999, approximately 13 smallmouth bass would have been eaten. This clearly fails to account for the high mortality in YOYsmallmouth bass.

Our results indicate limited predation on smallmouth bass by adult walleye and low dietary overlap. There clearly must be other reasons for limited smallmouth bass recruitment in Big Crooked Lake. It is possible that other species beside walleye or other size classes of walleye are interacting (i.e., diet overlap or predation) with smallmouth bass. Muskellunge, northern pike, burbot, yellow perch and rock bass are all picivorous (Scott and Crossman 1973) and thus may prey upon smallmouth bass. Perhaps in other lakes with more complex communities, walleye and other species actually suppress smallmouth bass. For instance, smallmouth bass populations increased from an annual harvest of 1.1 smallmouth bass/ha to 6.2/ha, in Nebish Lake following reclamation where walleye, northern pike, yellow perch, rock bass, largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), and other species were entirely eliminated (Kempinger and Christenson 1978). Following reclamation, only smallmouth bass and yellow perch remained. Perhaps another species, or combination of species, is responsible for predation or dietary overlap. In Big Crooked Lake, the rock bass population is abundant and known to inhabit similar habitats of smallmouth bass (George and Hadley 1979) possibly leading to interactions with smallmouth bass. Moreover, there could also be environmental factors, such as starvation, temperature and/or overwinter survival, affecting the smallmouth bass population (Shuter et al. 1989). Further studies need to be conducted on Big Crooked Lake to evaluate how other species and other size classes of fish interact with young smallmouth bass, and what occurs during other time periods.

ACKNOWLEDGEMENTS

We would like to thank Kirby Kohler, Pat Short, Rory Saunders and Gary Kubenik for all their technical assistance. We also thank the US Forest Service, Dairyman's Incorporated, and WICFRU for financial assistance.

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Received: 25 March 2002 Accepted: 7 July 2002