North American Journal of Fisheries Management

ISSN: 0275-5947 (Print) 1548-8675 (Online) Journal homepage: http://www.tandfonline.com/loi/ujfm20

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To cite this article: Michael A. Bozek , Thomas M. Burri & Richard V. Frie (1999) Diets of Muskellunge in Northern Wisconsin Lakes, North American Journal of Fisheries Management, 19:1, 258-270, DOI: 10.1577/1548-8675(1999)019<0258:DOMINW>2.0.CO;2

To link to this article: http://dx.doi.org/10.1577/1548-8675(1999)019<0258:DOMINW>2.0.CO;2

Published online: 08 Jan 2011.

North American Journal of Fisheries Management 19:258–270, 1999

Diets of Muskellunge in Northern Wisconsin Lakes

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Abstract.—The muskellunge *Esox masquinongy* is an important sport fish in Wisconsin and elsewhere, but more information about its diet is needed to better understand its role in aquatic systems and its effects on other fish. Stomach contents were examined for 1,092 muskellunge (226–1,180 mm total length, TL) captured in the littoral zone from 34 Wisconsin water bodies from July 1991 to October 1994. Food occurred in 34.3% ($N = 375$) of the stomachs, with most (74%) containing a single item. Overall, the proportion of muskellunge with food differed significantly among seasons, with the greatest proportion occurring in fall (69.0%), followed by summer (53.5%) and then spring (25.4%). Prey items consisted of 547 fish, representing 12 families and 31 species, along with 35 nonfish items; fish composed 98% of the diet. Relative importance values of diet items varied by taxa, season, and water body, but the main food items eaten by muskellunge in each season were yellow perch *Perca flavescens* and white sucker *Catostomous commersoni.* Black basses *Micropterus* spp., northern pike *Esox lucius,* walleye *Stizostedion vitreum,* cyprinids, and other taxa were less common in the diet. Prey fish ranged in size from 6% to 47% of muskellunge total length and prey length increased significantly as muskellunge size increased. Yet the size of prey in proportion to muskellunge size remained the same for all sizes of muskellunge. The results of this study indicate that, if readily available, yellow perch and catostomids will compose a large proportion of the muskellunge diet. Additional studies assessing muskellunge diet among lakes having different prey community types and assessing diet in deeper offshore areas of lakes are needed to better understand the role that muskellunge play in aquatic communities.

Muskellunge *Esox masquinongy* are ecologically important to aquatic systems (Mooradian and Shepherd 1973; Belusz and Witter 1986; Hanson 1986; Smith 1996) and their fisheries are economically important to communities near them. Because of their increasing popularity, the range of the muskellunge is being expanded in North America as many states and provinces introduce muskellunge to new water bodies and initiate more intensive stocking programs (Crossman 1978; Ragan et al. 1986). However, some fisheries personnel and sport anglers are concerned that the introduction of muskellunge to new waters and additional supplemental stocking of lakes where muskellunge fisheries already exist, particularly where oversaturation stocking or ''cramming'' occurs, may negatively affect other sport fish (Crossman 1986; Ragan et al. 1986; Seelbach 1988).

Although the muskellunge is an important sport fish in Wisconsin and elsewhere, more information about its food habits is needed to better understand its role in aquatic systems and its effects on other fish species. Limited diet studies on muskellunge have been conducted (Hourston 1952; Krska and Applegate 1982; Deutsch 1986), but sample sizes have been small, and generally only smaller muskellunge were sampled. These studies have shown muskellunge to be primarily piscivorous, although they are opportunistic feeders that eat a variety of prey, from aquatic insects to fish to small mammals. Moreover, ontogenetic shifts in diet occur as age-0 fish shift from zooplankton and invertebrate prey to cyprinids and later to larger prey (MacKay and Werner 1934; Elson 1940; Muir 1960). Catostomids, cyprinids, and percids have been reported to be important foods of muskellunge (Hourston 1952; Krska and Applegate 1982; Deutsch 1986), yet in waters beyond the native range of the muskellunge, (e.g., southern reservoirs) gizzard shad *Dorosoma cepedianum* and

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common carp *Cyprinus carpio* are also known prey items (Vasey 1972; Axon 1981; Kinman 1989).

Comprehensive studies of muskellunge diet have been hampered by a variety of difficulties that stem from the problem of obtaining adequate numbers of samples. Muskellunge usually occur at low densities, are dispersed over large areas, often have empty stomachs, and are difficult to handle. Muskellunge are usually considered too valuable to kill for removal of stomach contents, and agency personnel often are reluctant to remove stomach contents from live fish for fear of injuring the fish (Deutsch 1986; Ragan et al. 1986; Kinman 1989). Thus, fisheries personnel have indicated that more studies are needed to determine the diet of muskellunge and the effects of the species on other fishes (Ragan et al. 1986). The objective of this study was to determine the diet of muskellunge in a suite of water bodies across northern Wisconsin during spring, summer, and fall and to assess any patterns of prey consumption.

Methods

Muskellunge were collected from 34 water bodies in Wisconsin from July 1991 to October 1994 to determine their diet. The lakes were predominantly in the northern third of the state and included those scheduled for routine assessments by the Wisconsin Department of Natural Resources. Study lakes contained diverse assemblages of prey and a wide range of muskellunge densities (Tonn and Magnuson 1982).

Data collection and analyses were stratified into spring (April and May), summer (June, July, and August), and fall (September and October) periods. Fyke netting, electrofishing, and angling were the primary methods used to collect muskellunge. Fyke nets were fished from ice-out until after the peak of spawning in spring and occasionally during summer fish removal projects. The fyke nets (13–38-mm stretched mesh) were fished with leads perpendicular to shore. All fish were removed once daily to minimize postcapture digestion and feeding while captured. After peak spawning until sampling ceased in October, muskellunge were caught using electrofishing boats operating with 175–425 V, 1–4 A of AC and two dippers. Electrofishing was conducted along the 1-m depth contour of water bodies where muskellunge could be effectively dipped. A rate of speed higher than idling speed was used during electrofishing to compensate for avoidance behavior that is common among esocids. Electrofishing usually began at dusk and ended after one trip around the entire shoreline. Additional boats were used on large lakes so that the entire shoreline could be electrofished in one night. Although electrofishing may cause regurgitation in fish (Bowen 1983), this was not observed during this study.

Muskellunge were measured to the nearest 0.5 cm total length (TL), stomach contents were removed by flushing with a pump, and the fish were then released. Muskellunge were restrained in a 1.0-m by 0.4-m cradle with 1.0-cm stretched-mesh netting during stomach flushing. One person restrained the muskellunge and massaged the stomach to maneuver food items anteriorly in the stomach cavity. The pump used for flushing stomachs was a modification of the one described by Crossman and Hamilton (1978; see Burri 1997). A copper probe used for insertion into stomachs was affixed to a bilge pump powered by a 12-V battery. Stomach contents were first flushed into a 25-cm by 18-cm aquarium net of 2-mm stretched mesh, and then the stomach was examined for residual prey items. On four occasions, we also used tubes similar to those described by Van Den Avyle and Roussel (1980) to visually identify and estimate size of food items not removable by flushing.

Food items were identified in the field to the greatest level of taxonomic resolution possible, grouped into taxonomic categories for analyses (Table 1), and measured to the nearest millimeter (TL for fish). Stomach contents that were difficult to identify were labeled, frozen in separate containers filled with water, and brought to the laboratory for identification using taxonomic keys (Hilsenhoff 1981; Becker 1983; Pennak 1989; Oates et al. 1993).

In the laboratory, whole food items were thawed and blotted dry, and volume was determined by water displacement. Fish specimens from the University of Wisconsin–Stevens Point Ichthyological Museum were used to estimate initial volume for diet items that were partially digested. For prey fish where neither weight nor volume was measured, length–weight regression equations from Carlander (1969, 1977) were used to estimate volume. The mean of the five length–weight regression equations (i.e., coefficients were averaged) having the largest sample sizes in Carlander (1969, 1977) was used to develop a single equation for each food type, which was then used to estimate weights from known lengths (Table 2). When there were fewer than five length–weight regression equations for a given species, all available equations were averaged. Weight was converted to volume (mL) on the assumption that 1 g of diet dis-

TABLE 1.—Scientific and common names of muskellunge prey classified into categories that were used in diet analyses.

Prey category	Common name	Scientific name
Catostomidae	White sucker	*Catostomus commersoni*
	Northern hog sucker	*Hypentelium nigricans*
	Shorthead redhorse	*Moxostoma macrolepidotum*
Cyprinidae	Common shiner	*Luxilus cornutus*
	Hornyhead chub	*Nocomis biguttatus*
	Golden shiner	*Notemigonus crysoleucas*
	Bigmouth shiner	*Notropis dorsalis*
	Blacknose shiner	*Notropis heterolepis*
	Blacknose dace	*Rhinichthys atratulus*
	Longnose dace	*Rhinichthys cataractae*
	Creek chub	*Semotilus atromaculatus*
	Unidentifiable	Cyprinidae
Yellow perch	Yellow perch	*Perca flavescens*
Lepomis spp.	Pumpkinseed	*Lepomis gibbosus*
	Bluegill	*Lepomis macrochirus*
	Unidentifiable	*Lepomis* spp.
Pomoxis spp.	Black crappie	*Pomoxis nigromaculatus*
	Unidentifiable	*Pomoxis* spp.
Rock bass	Rock bass	*Ambloplites rupestris*
Micropterus spp.	Smallmouth bass	*Micropterus dolomieu*
	Largemouth bass	*Micropterus salmoides*
	Unidentifiable	*Micropterus* spp.
Walleye	Walleye	*Stizostedion vitreum*
Cisco	Cisco	*Coregonus artedi*
Sculpin	Mottled sculpin	*Cottus bairdi*
Stickleback	Ninespine stickleback	*Pungitius pungitius*
Mudminnow	Central mudminnow	*Umbra limi*
Darter	Iowa darter	*Etheostoma exile*
	Johnny darter	*Etheostoma nigrum*
	Unidentifiable	*Etheostoma* spp.
	Logperch	*Percina caprodes*
Esocidae	Northern pike	*Esox lucius*
	Muskellunge	*Esox masquinongy*
	Unidentifiable	*Esox* spp.
Bullhead	Black bullhead	*Ameiurus melas*
Trout-perch	Trout-perch	*Percopsis omiscomaycus*
Common carp	Common carp	*Cyprinus carpio*
Unidentified fish	Unidentifiable to any taxon	
Crayfish	Rusty crayfish	*Orconectes rusticus*
	Virile crayfish	*Orconectes virilis*
Aquatic insect	Dragonfly	*Epitheca* spp.
	Stonefly	Plecoptera
Frog	Unidentifiable	Ranidae
Mudpuppy	Mudpuppy	*Necturus maculosus*
Tadpole	Unidentifiable	Ranidae
Mouse	Unidentifiable	Rodentia

places 1 cm^3 of water. Although this technique may underestimate volume slightly, we considered the error negligible. Because data for yellow perch were not found in Carlander (1969, 1977), length–volume regression equations were developed from data collected in this study: $\log_e(\text{volume}) = -4.84 + 3.038 \log_e(\text{TL, cm})$. For some unidentifiable food items where length was not measured, we assigned volume as the mean volume calculated from all other unidentifiable fish measured of that size.

We used percent frequency of occurrence of each taxon, percent of total number of diet items per taxon, and percent total volume of each taxa to analyze data from muskellunge stomachs. To reduce biases yet produce a single measure of diet (Windell 1971), a relative importance (RI) index was also calculated for each for each food type (George and Hadley 1979). We modified the index by substituting percentage of total volume for percentage of total weight:

$$RI_a = (100 \times AI_a) \Big/ \sum_{a=1}^{n} AI_a,$$

TABLE 2.—Equations used to convert prey total length (TL, mm) to weight (W, g) or volume (V, mL) and the source used to derive equations. The equation for yellow perch was developed using data from this study.

Prey species	Equation	Number of equations used
	Equation from this study	
Yellow perch	$\log_e V = -4.84 + 3.0380 \log_e \text{TL}$	
	Equations from Carlander (1997)	
Largemouth bass	$\log_{10} W = -5.215 + 3.140 \log \text{TL}$	5
Smallmouth bass	$\log_{10} W = -4.758 + 3.007 \log \text{TL}$	5
Bluegill	$\log_{10} W = -5.286 + 3.201 \log \text{TL}$	5
Rock bass	$\log_{10} W = -4.724 + 2.987 \log \text{TL}$	5
Black crappie	$\log_{10} W = -5.271 + 3.200 \log \text{TL}$	5
	Equations from Carlander (1969)	
Cisco	$\log_{10} W = -5.304 + 3.073 \log \text{TL}$	5
White sucker	$\log_{10} W = -5.077 + 3.059 \log \text{TL}$	5
Common shiner	$\log_{10} W = -5.560 + 3.290 \log \text{TL}$	1
Trout-perch	$\log_{10} W = -5.032 + 3.080 \log \text{TL}$	1
Black bullhead	$\log_{10} W = -5.257 + 3.097 \log \text{TL}$	5
Northern hog sucker	$\log_{10} W = -4.828 + 2.941 \log \text{TL}$	2
Esocidae	$\log_{10} W = -5.552 + 3.122 \log \text{TL}$	5

[a] Total length in cm.

where n = number of different food types, RI_a = relative importance of prey taxa a, AI_a = absolute importance of prey taxa a in the diet. In turn, $\text{AI}_a = \%F_a + \%N_a + \%V_a$, where $\%F_a$ = percent frequency of occurrence of taxa a, $\%N_a$ = percent of total number of organisms of taxa a, and $\%V_a$ = percent of total volume of food organisms represented by taxa a.

We used simple linear regression to test relations between (1) prey fish TL and muskellunge TL, (2) prey fish TL/muskellunge TL and muskellunge TL, and (3) number of prey items eaten and muskellunge TL. Chi-square analyses were used to assess differences in the proportion of muskellunge having diet items in their stomachs across seasons for all fish combined and for each of nine 100-mm length categories (200–1,000 mm) and to assess differences across length categories during each of three seasons. Alpha was set at 0.05 for all tests.

Results

Diet of Muskellunge

Muskellunge diets were diverse during this study. Contents of 1,092 stomachs from muskellunge (226–1,180 mm TL) captured in the littoral zone of 34 water bodies were examined (Table 3); 34.3% of them contained prey items. Most muskellunge stomachs with food contained a single item (74%), 16% had two items, and 5% had 3 items; yet up to 25 items per stomach were found (Figure 1). Overall, percent of muskellunge with food (i.e., occurrence) decreased as muskellunge size increased (chi-square = 73.95, df = 9, $P <$ 0.001; Table 4). Large and small muskellunge ate the same number of prey, as there was no relation between the number of prey items eaten and muskellunge length.

For the 375 stomachs (34.3%) containing 582 food items, the combined volume of food was 16,130 mL (Table 5). Fish composed 98% of the volume of food, and the 547 fish items included 12 families and 31 species. Overall the two most important food items for muskellunge were yellow perch (RI = 25) and catostomids (RI = 21; Table 5). Yellow perch represented 30% of the total number of prey but only 17% of the total volume of prey (Table 5). Conversely, catostomids represented only 8% of the total number of prey items but 47% of the total volume of food. Cyprinids (RI = 7), walleye, *Micropterus* spp., and esocids ranked low in the muskellunge diet (RI $<$ 4 for each prey type). Unidentifiable fish made up 17% of all food items and 3% of the total volume. The 35 nonfish items (2% of the total volume of food) included crayfish, aquatic insects, frogs, mudpuppies, tadpoles, and one mouse.

In each of the eight lakes that had a minimum sample size of 15 muskellunge, patterns in RI values varied somewhat, but yellow perch and catostomids were consistently important in muskellunge diets. Yellow perch were the most important (highest RI values) of the identifiable prey in five lakes and second most important in three lakes. Catostomids were the most important of the identifiable prey in three of the eight lakes and second most important in three others. Darters and cyp-

TABLE 3.—Location and size of Wisconsin water bodies sampled, number of muskellunge captured, and percentage of muskellunge stomachs containing prey, 1991–1994.

			Muskellunge	
Water body	County	Lake area (ha)	Number captured	Percentage with prey
Mineral	Ashland	91	171	39.2
Lake of the Pines	Sawyer	110	167	36.5
Lower Clam	Sawyer	93	120	40.0
Spillerberg	Ashland	30	81	30.9
Ghost	Sawyer	151	45	42.2
Lyman	Douglas	163	41	43.9
Lac Courte Oreilles	Sawyer	2,039	51	29.4
Pine	Iron	126	51	29.4
Potter	Ashland	12	22	59.1
English	Ashland	99	66	16.7
Amik	Price	91	17	64.7
Namekagon	Bayfield	1,306	32	28.1
Lower Park Falls Flowage	Price	29	14	64.3
Round	Price	294	22	36.4
Upper Park Falls Flowage	Price	174	14	57.1
East Twin	Ashland	45	11	54.5
Solberg	Price	348	27	18.5
Holcombe flowage	Chippewa	1,574	12	41.7
Papoose	Vilas	173	60	6.7
Eagle River Chain of Lakes	Vilas	1,457	12	25.0
Pixley Flowage	Price	135	6	50.0
Pike	Price	326	7	28.6
Turner	Price	60	7	28.6
Galilee	Ashland	86	6	33.3
Black	Sawyer	52	5	20.0
Moquah	Ashland	20	5	20.0
Musser Flowage	Price	228	4	25.0
South Fork Flambeau River	Price		4	25.0
Crowley Flowage	Price	171	2	50.0
Petenwell Flowage	Juneau	9,324	1	100.0
Spider	Ashland	42	5	0.0
Buffalo	Bayfield	72	2	0.0
Swan	Columbia	164	1	0.0
Thompson	Price	45	1	0.0
All			1,092	34.3

rinids were the second most important of the identifiable prey in the other two lakes and catostomids were third.

Seasonal Diet of Muskellunge

The occurrence of food in muskellunge increased significantly from spring (25.4%) to summer (53.5%) to fall (69.0%; chi-square = 36.31, df = 2, $P < 0.001$; Table 4). The greatest number of prey categories also occurred in fall, in part at least, because the greatest number ($N = 608$) of muskellunge were caught in fall.

Patterns in RI values among prey types varied among seasons, but yellow perch and catostomids were consistently important foods in each season sampled (Figure 2). Yellow perch RI values ranked second in spring and first in summer and fall. Yellow perch also made up the largest percentage of the total number of prey in summer and fall and the second largest percentage in spring (Table 6). Catostomid RI values ranked first in spring and second in summer and fall. (Figure 2) Catostomids composed the greatest percentage of total volume of prey in all seasons sampled (Table 6). Relative importance values across all seasons indicated that the next most important food items were generally cyprinids (mean RI = 7), *Lepomis* spp. (mean RI = 6), and *Pomoxis* spp. (mean RI = 6). Walleyes were eaten in each season sampled, but RI values were always less than 3, and *Micropterus* spp. were found eaten in summer (RI = 5) and fall (RI = 4).

Other foods varied in their importance seasonally. Darters were important (RI = 14) in spring but not in summer (RI = 1) or fall (RI = 2). Although darters represented 31% of the number of prey items in spring, they occurred in only 14% of the stomachs, and composed less than 1% of

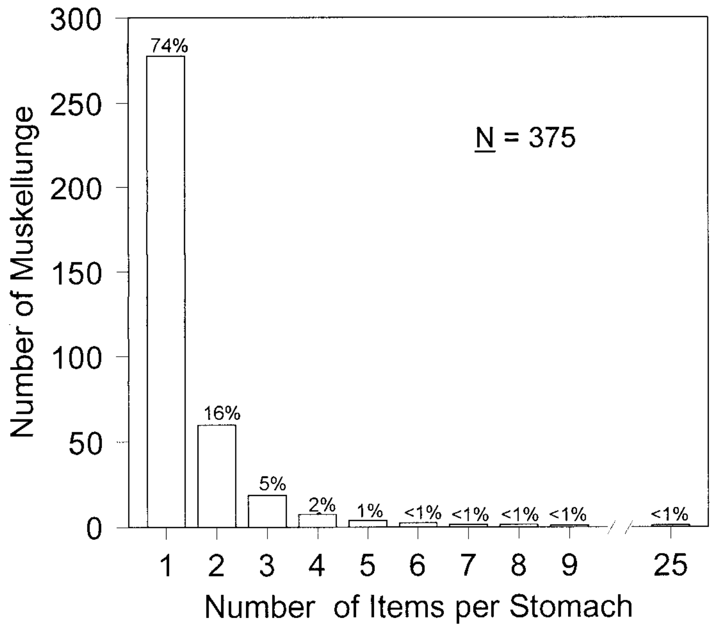

FIGURE 1.—Number of prey items per stomach for muskellunge that had food in their stomachs. Muskellunge were collected from Wisconsin lakes during spring through fall, 1991–1994.

the total volume in spring (Table 6). Esocids, ciscoes, and bullheads were eaten in spring and fall but were not of major importance in the diet (Figure 2; Table 6). Crayfish were eaten by muskellunge in summer (RI = 6) and fall (RI = 1). Although crayfish represented 12% of the prey items in summer, they occurred in only 4% of the muskellunge stomachs, and represented less than 2% of the total volume in summer.

Prey Size Selection

Muskellunge ate prey fish that ranged from 6% to 47% of their own total length. Prey total length was positively related to muskellunge total length (r^2 = 0.34, df = 426, $P \leq 0.001$), and while relations varied among prey type, the slope of these relations for individual taxa ranged from 0.087 to 0.276 (Table 7; Figure 3). Residuals of the linear relation between muskellunge total length and prey

TABLE 4.—Number of muskellunge, by length-class, with food in their stomachs and with empty stomachs. Fish were collected from Wisconsin water bodies during spring through fall, 1991–1994.

Length-class (mm) or statistic	Spring		Summer		Fall		Across season chi-square (*P*)	All seasons	
	Food	Empty	Food	Empty	Food	Empty		Number with food	Percent with food
200–299	1	1	2	0	1	3	3.00 (0.223)	4	50
300–399	7	22	15	15	59	66	5.60 (0.061)	81	44
400–499	4	10	10	20	62	59	4.99 (0.083)	76	46
500–599	6	14	9	13	35	49	0.94 (0.626)	50	40
600–699	8	15	11	20	31	58	0.01 (0.998)	50	35
700–799	72	44	13	28	40	70	0.06 (0.809)	60	30
800–899	1	69	7	23	14	44	0.01 (0.993)	42	24
900–999	3	32	2	7	5	10	4.78 (0.091)	10	17
1,000–1,099	1	16	0	3	1	1	4.56 (0.102)	2	9
1,100–1,199	0	5						0	0
All lengths	58	228	69	129	248	360	36.31 (<0.01)	375	
Among size-class χ^2 (P)	14.41 (0.108)		11.33 (0.184)		17.31 (0.027)			73.95 (<0.001)	

TABLE 5.—Diet analysis of the 582 food items found in stomachs of 375 muskellunge containing food when 1,092 muskellunge from 34 Wisconsin water bodies were examined in 1991–1994. Values for each kind of prey are the percentage of total number, percentage of individual stomachs, percentage of volume, and absolute and relative importance index values.

Prey category	Percent composition by number	Percent frequency of occurrence	Percent of total volume	Absolute importance index value	Relative importance index value
Catostomidae	8.4	12.0	46.6	67.0	21.1
Cyprinidae	6.9	9.3	4.6	20.8	6.6
Yellow perch	30.1	32.8	16.9	79.7	25.1
Lepomis spp.	7.0	9.1	4.5	20.6	6.5
Pomoxis spp.	5.7	7.7	7.0	20.4	6.4
Rock bass	0.5	0.8	0.2	1.5	0.5
Micropterus spp.	2.9	4.5	3.1	10.6	3.3
Walleye	0.9	1.3	3.4	5.6	1.8
Cisco	0.5	0.8	0.9	2.2	0.7
Sculpin	0.3	0.5	0.0	0.9	0.3
Stickleback	0.5	0.8	0.0	1.3	0.4
Mudminnow	0.5	0.8	0.1	1.4	0.4
Darter	9.5	4.3	0.2	14.0	4.4
Esocidae	1.4	2.1	4.7	8.2	2.6
Bullhead	0.9	1.3	2.4	4.6	1.5
Trout-perch	0.2	0.3	0.0	0.5	0.1
Common carp	0.7	0.3	0.1	1.1	0.3
Unidentified fish	17.2	22.4	3.0	42.6	13.4
Crayfish	2.9	1.6	0.4	4.9	1.6
Aquatic insect	0.3	0.5	0.0	0.9	0.3
Frog	1.5	1.9	0.9	4.3	1.4
Mudpuppy	0.7	1.1	0.6	2.3	0.7
Tadpole	0.3	0.5	0.1	1.0	0.3
Mouse	0.2	0.3	0.2	0.6	0.2
Total	100		100	317.1	100

total length indicated that the range of prey lengths increased as muskellunge length increased. Prey size remained a constant proportion of muskellunge size ($r^2 = 0.01$, df = 426, $P = 0.314$; Figure 3); small (<60-cm) and large (≥60-cm) muskellunge both ate fish averaging 20% of their total length.

Discussion

Our finding that muskellunge captured in the littoral zone of northern Wisconsin lakes fed primarily on yellow perch and white suckers across seasons is consistent with other studies (Hourston 1952; Lawler 1965; Diana 1979; Krska and Applegate 1982; Deutsch 1986). Yellow perch are ubiquitous throughout the natural range of muskellunge and clearly are vulnerable to muskellunge predation. In three regions in Canada, yellow perch were also the most frequently eaten food by muskellunge (Hourston 1952). Yellow perch may be a common diet item due to both their availability (i.e., abundance and location) and suitability (i.e., prey choice) to muskellunge. Schools of yellow perch may increase their vulnerability to muskellunge predation by swimming in vegetated areas of littoral zones, which are the same areas occupied by muskellunge during the day (Becker 1983). Thus, yellow perch size and abundance in similar habitats as muskellunge would make them attractive prey.

Catostomids, also ubiquitous in the natural range of muskellunge, have been considered important prey for esocids and were also important in the diet of muskellunge during all seasons sampled. The importance of catostomids to muskellunge has been corroborated circumstantially as growth in muskellunge is positively correlated with catostomid density in northern Wisconsin lakes (Hanson 1986). Again, availability and suitability of catostomids in the study lakes probably made them a common prey item. Catostomid RI values ranked highest in spring, presumably because catostomid spawning behavior increased their vulnerability to muskellunge that are found in nearshore areas of lakes. Many muskellunge were observed near catostomid spawning areas during spring sampling, and many muskellunge that were collected close to spawning catostomids contained large catostomids in their stomachs. Although the number of catostomids eaten declined

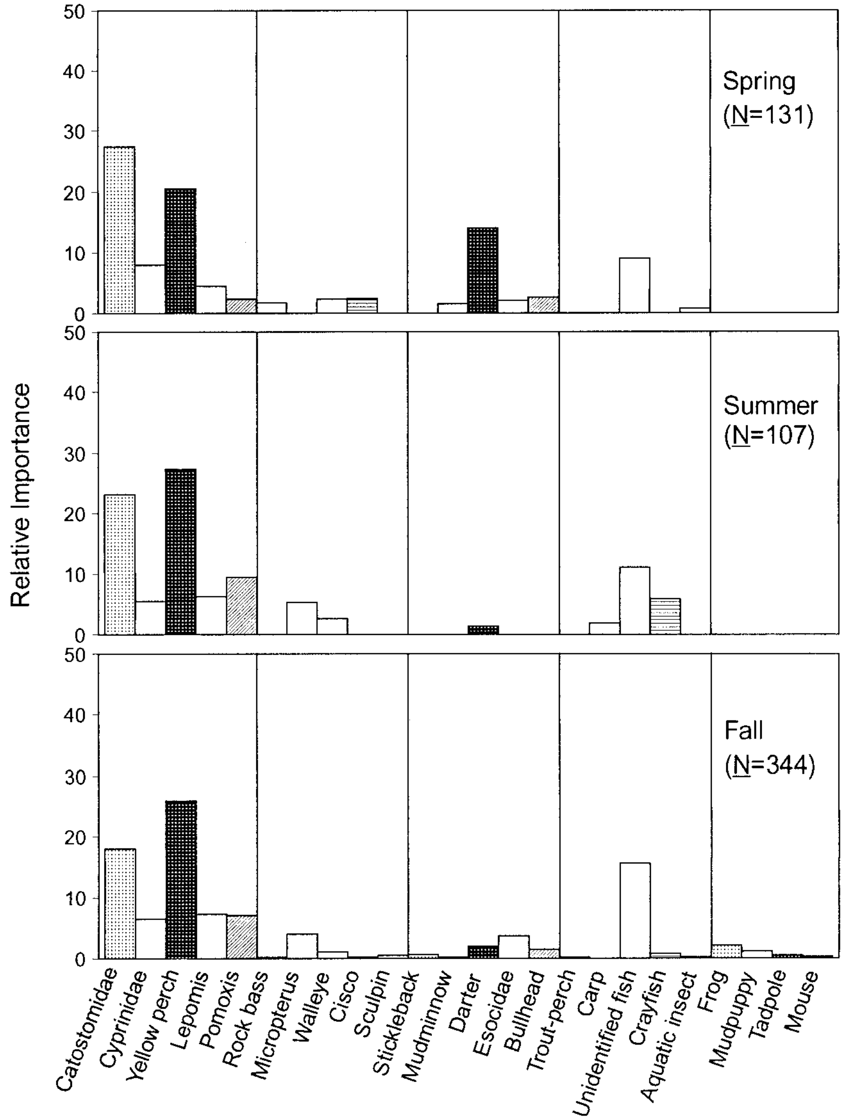

FIGURE 2.—Relative importance of prey consumed by muskellunge collected from 34 Wisconsin water bodies during spring through fall, 1991–1994. Of the 1,092 muskellunge examined, 375 contained food items; N is the number of items identified (total $N = 582$).

after spring, RI values remained high partly because many of the catostomids eaten later in the year were large in size compared with other forage.

Overall, other fish taxa were more variable and less important in the muskellunge diet. The low dietary importance of black bass, sunfish, crappies, and rock bass in this study was consistent with results of other laboratory and field studies that have shown that esocids do not prefer centrarchids (e.g., Hourston 1952; Beyerle 1971; Mauck and Coble 1971; Weithman and Anderson 1977; Deutsch 1986; Wahl and Stein 1988). However, Krska and Applegate (1982) found that young muskellunge ate *Lepomis* spp. when those species formed a prominent part of the available prey base and were of appropriate size. Despite large walleye populations in several of the study lakes (e.g., >50 fish/ha), walleyes did not appear to be an important food for muskellunge. While muskellunge and walleyes can be spatially segregated at times, we frequently found walleyes and muskellunge in close proximity at night; yet when fresh prey in

TABLE 6.—Diets in spring (Sp, 58 stomachs with 131 food items), summer (Su, 69 stomachs with 107 food items), and fall (Fa, 248 stomachs with 344 food items) of muskellunge collected from 34 Wisconsin water bodies, 1991–1994. Values for each kind of prey taxa are the percentage of total number of items, percentage of occurrence in individual stomachs, percentage of volume, and absolute importance index values.

	Percent composition by number			Percent frequency of occurrence			Percent of total volume			Absolute importance index value		
Prey category[a]	Sp	Su	Fa	Sp	Su	Fa	Sp	Su	Fa	Sp	Su	Fa
Catostomidae	13.0	7.5	7.0	22.4	11.6	9.7	53.6	53.1	40.5	88.9	72.2	57.1
Cyprinidae	6.1	5.6	7.6	13.8	8.7	8.5	5.9	2.9	4.5	25.8	17.2	20.5
Yellow perch	22.9	36.4	30.8	25.9	37.7	33.1	18.0	11.1	18.3	66.7	85.3	82.2
Lepomis spp.	4.6	5.6	8.4	6.9	7.2	10.1	3.1	6.8	4.5	14.6	19.7	23.0
Pomoxis spp.	1.5	7.5	6.7	3.4	11.6	7.7	2.7	10.7	8.1	7.7	29.7	22.4
Rock bass	1.5	0.0	0.3	3.4	0.0	0.4	0.7	0.0	0.0	5.7	0.0	0.7
Micropterus spp.	0.0	3.7	3.8	0.0	5.8	5.2	0.0	6.8	3.5	0.0	16.4	12.5
Walleye	0.8	1.9	0.6	1.7	2.9	0.8	5.4	3.3	2.3	7.9	8.1	3.6
Cisco	1.5	0.0	0.3	3.4	0.0	0.4	3.1	0.0	0.1	8.1	0.0	0.7
Sculpin	0.0	0.0	0.6	0.0	0.0	0.8	0.0	0.0	0.1	0.0	0.0	1.5
Stickleback	0.0	0.0	0.9	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	2.1
Mudminnow	1.5	0.0	0.3	3.4	0.0	0.4	0.2	0.0	0.0	5.2	0.0	0.7
Darter	31.3	2.8	3.2	13.8	1.4	2.8	0.5	0.0	0.2	45.6	4.3	6.2
Esocidae	1.5	0.0	1.7	3.4	0.0	2.4	2.1	0.0	7.7	7.1	0.0	11.9
Bullhead	1.5	0.0	0.9	3.4	0.0	1.2	3.7	0.0	2.6	8.7	0.0	4.7
Trout-perch	0.0	0.0	0.3	0.0	0.0	0.4	0.0	0.0	0.1	0.0	0.0	0.8
Common carp	0.0	3.7	0.0	0.0	1.4	0.0	0.0	0.8	0.0	0.0	6.0	0.0
Unidentified fish	11.5	13.1	20.6	17.2	18.8	24.6	0.9	2.8	4.2	29.6	34.7	49.4
Crayfish	0.0	12.1	1.2	0.0	4.3	1.2	0.0	1.6	0.2	0.0	18.1	2.6
Aquatic insect	0.8	0.0	0.3	1.7	0.0	0.4	0.0	0.0	0.0	2.5	0.0	0.7
Frog	0.0	0.0	2.6	0.0	0.0	2.8	0.0	0.0	1.6	0.0	0.0	7.1
Mudpuppy	0.0	0.0	1.2	0.0	0.0	1.6	0.0	0.0	1.1	0.0	0.0	3.9
Tadpole	0.0	0.0	0.6	0.0	0.0	0.8	0.0	0.0	0.1	0.0	0.0	1.5
Mouse	0.0	0.0	0.3	0.0	0.0	0.4	0.0	0.0	0.3	0.0	0.0	1.0
All	100	100	100				100	100	100	324.1	311.6	316.9

[a] See Table 1.

muskellunge stomachs was examined in these cases, walleyes were rare. It appears that walleyes are either not preferred by muskellunge or are capable of avoiding muskellunge. Walleyes become more active at night, and the presence of a subretinal tapetum lucidium (Ali et al. 1977) may help walleyes avoid muskellunge. Esocids were rare in the diet of muskellunge, but our study did provide solid evidence of cannibalism. Cannibalism has been used as an indicator of food shortages in esocids (Beyerle 1971; Casselman 1978). Nonfish items were not ranked as important food items for muskellunge in this study. However, these prey items, along with small or uncommon fish may be important during specific periods when their abundance increases (e.g., fall migration of frogs, mayfly hatch, etc.) or in water bodies where prey fish are limited, are not vulnerable, or are undesirable to muskellunge (Beyerle 1971).

Muskellunge diet has been shown to change as their size increases. Newly hatched muskellunge initially feed on zooplankton, but they eat mostly fish after 4–5 weeks (MacKay and Werner 1934; Elson 1940). Muir (1960) and Deutsch (1986) suggested that muskellunge change from eating primarily minnows to larger prey (e.g., catostomids,

TABLE 7.—Significant relations between prey fish total length (TL, cm) and muskellunge TL (cm) for muskellunge collected in Wisconsin during spring through fall, 1991–1994.

Prey	*N*	r^2	Equation	*F*	*P*
Total	427	0.340	Prey TL = 0.220 (muskellunge TL) − 1.1985	219.223	0.001
Catostomidae	45	0.393	Prey TL = 0.276 (muskellunge TL) + 2.9647	27.847	0.001
Cyprinidae	37	0.189	Prey TL = 0.105 (muskellunge TL) + 5.9866	8.147	0.007
Yellow perch	166	0.101	Prey TL = 0.087 (muskellunge TL) + 5.4286	18.415	0.001
Lepomis spp.	39	0.670	Prey TL = 0.190 (muskellunge TL) − 1.5726	75.054	0.001
Pomoxis spp.	30	0.606	Prey TL = 0.209 (muskellunge TL) − 1.6321	43.139	0.001
Micropterus spp.	17	0.404	Prey TL = 0.206 (muskellunge TL) − 0.0064	10.171	0.006

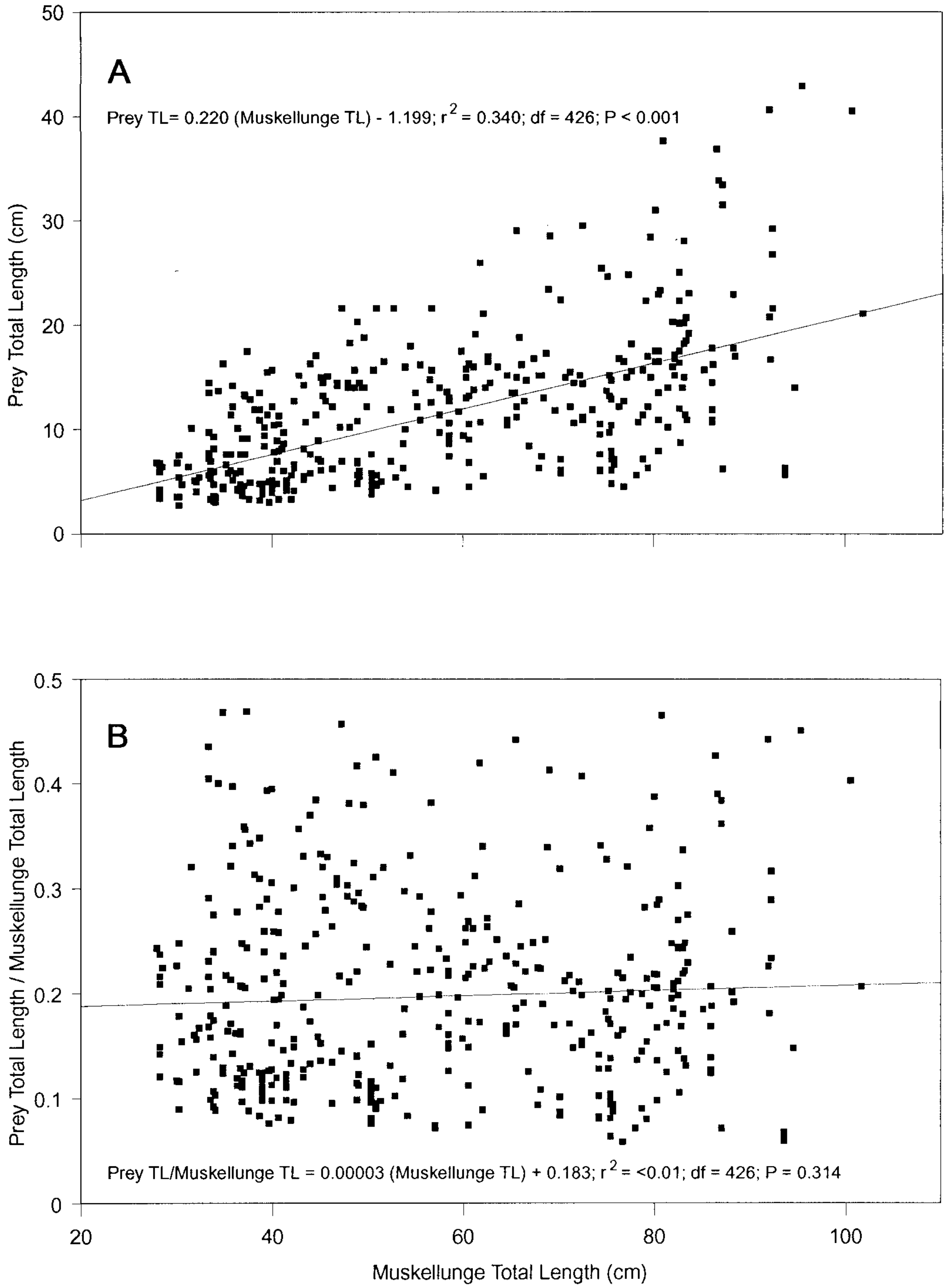

FIGURE 3.—Relations between **(A)** total length of 427 prey fish and total length of muskellunge and **(B)** total length of 427 prey fish/muskellunge total length as a function of muskellunge total length. Muskellunge were collected from 34 Wisconsin water bodies from spring through fall, 1991–1994. Unidentifiable fish and nonfish prey items were not included.

yellow perch) as they grow. In general, small esocids are believed to have a tendency to eat many small items, whereas large esocids commonly eat a single large item (Lawler 1965). In our study, cyprinids were clearly important prey for smaller muskellunge, as was also found by Deutsch (1986), but their small size reduced their overall relative importance in the diet. Cyprinids, however, may also be important for larger muskellunge when large cyprinids are available or when other prey are rare.

The proportion of muskellunge stomachs containing food in our study (34%) was similar to that found in some previous studies (Hourston 1952; Krska and Applegate 1982) but differed from the proportion (54%) found by Deutsch (1986). The difference between the two studies may be attributed to the season the fish were captured or to the size of fish examined. In our study, a larger proportion of fish were caught in fall, and fall-caught fish had higher occurrence of food items. The greatest number of empty muskellunge stomachs coincided with spawning in spring, and may suggest fasting where cooler water temperatures reduce metabolic demands (Frost 1954; Mann 1976; Diana 1979; Bregazzi and Kennedy 1980). Yet despite spawning activities, muskellunge did continue to feed as some ripe males and females contained food items. As spawning progressed, the percentage of muskellunge with food increased.

In our study, most (74%) muskellunge with food contained a single item. However, we found no relation between the size of muskellunge and the number of items eaten. Large and small muskellunge ate the same number of prey. However, we did find that the percentage of muskellunge with food decreased as muskellunge size increased, which is consistent with the results of studies of northern pike. Percent empty stomachs in northern pike has been found to increase with size (Frost 1954; Diana 1979; Sammons 1993) and is generally attributed to the belief that larger northern pike feed on larger food items and, therefore, feed less often. However, this theory does not fully explain the results in our study; although larger muskellunge ate larger food items, those items were proportionately the same size as the food items eaten by smaller muskellunge. The larger prey preferred by large muskellunge was probably less abundant than prey for small muskellunge, thus increasing the time required to forage successfully.

Many studies have shown that piscivorous fishes select prey based on size (Mauck and Coble 1971; Gillen et al. 1981; Deutsch 1986; Juanes 1994), and optimum foraging theory predicts that prey size increases with predator size (Charnov 1976). In this study, muskellunge ate prey fish that ranged from 6% to 47% of their own total length, which is similar to the results of other research. Gillen et al. (1981) found that in aquaria, small (90–170-mm TL) tiger muskellunge (muskellunge × northern pike) selected cyprinids that were about 40% of their own TL and bluegills that were about 30% of their TL; however, in field experiments, tiger muskellunge chose smaller bluegills than predicted. Krska and Applegate (1982) found that muskellunge ate *Lepomis* spp. that ranged from 17% to 31% of their TL and minnows and darters that ranged from 26% to 37% of their TL in a South Dakota reservoir, which are slightly smaller than the sizes predicted by Gillen et al. (1981). Deutsch (1986) found that small (<60-cm) muskellunge ate prey that averaged 17% of their TL and that large (≥60 cm) muskellunge ate prey 36% of their TL. Muskellunge clearly eat larger prey as they grow. When sample sizes were sufficient ($N > 10$), prey TL of most species was positively correlated with muskellunge TL. Darters ($N = 55$) were exceptions, but the narrow range of lengths (i.e., little variation in length) may account for the lack of any relation. However, our study clearly showed that when scaled against body size, muskellunge eat the same size prey in proportion to their own size. Small and large muskellunge both ate fish that averaged 20% of their total length. Muskellunge also broaden the range of prey sizes eaten as they grow; maximum prey size ingested increases, while the minimum size remains constant.

We urge fisheries personnel to carefully consider all ecological and economic factors when managing muskellunge. The results of this study indicate that, if present, yellow perch and catostomids will be a common prey item of muskellunge in Wisconsin water bodies during all open-water seasons. We believe that substantial biomass of yellow perch and catostomids in waters receiving stocked muskellunge would be beneficial to successful muskellunge stocking but that evaluations are clearly need to substantiate this. However, this research did not address prey selectivity. Future studies should critically evaluate muskellunge diet across a suite of lakes composed of different prey fish communities. Particularly important are those lakes that do not have abundant yellow perch or catostomid populations and in which other species comprise the prey base. Ideally, muskellunge fisheries should have an abundant and diverse prey base to avoid inter- and intraspecific competition and to minimize possible predation on sport or protected fish. Moreover, muskellunge should not be managed as a single species but with the goal of maintaining a balanced fish community.

Acknowledgments

We thank D. Coble, F. Copes, and W. LeGrande for reviewing earlier drafts of this manuscript and W. LeGrande, M. Retzer, and T. Cavender for assistance in identification of digested food items using diagnostic fish body parts. We are indebted to the many Wisconsin Department of Natural Resources crews that assisted in this study, particularly Thomas ''Skip'' Sommerfeldt and Terry Margenau. This study was funded by the Wisconsin Department of Natural Resources and the Wisconsin Cooperative Fishery Research Unit.

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