Reprinted from

Journal of the Fisheries Research Board of Canada

Réimpression du

Journal de l'office des recherches sur les pêcheries du Canada

Food Consumption of Walleye (*Stizostedion vitreum vitreum*) and Sauger (*S. canadense*) in Relation to Food Availability and Physical Conditions in Lake of the Woods, Minnesota, Shagawa Lake, and Western Lake Superior

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Volume 34 • Number 10 • 1977

Pages 1643–1654

Environment Canada
Fisheries and Marine Service

Environnement Canada
Service des pêches et des sciences de la mer

Food Consumption of Walleye (*Stizostedion vitreum vitreum*) and Sauger (*S. canadense*) in Relation to Food Availability and Physical Conditions in Lake of the Woods, Minnesota, Shagawa Lake, and Western Lake Superior[1,2]

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SWENSON, W. A. 1977. Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical environmental conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. J. Fish. Res. Board Can. 34: 1643–1654.

Measurement of walleye (*Stizostedion vitreum vitreum*) daily food consumption rates and prey density in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior showed a general relationship exists between the two variables. Daily food consumption increased from 1 to 3% of body weight at prey densities up to 400 mg · m^{-3}. Abundance of age 0 yellow perch (*Perca flavescens*) in Lake of the Woods, Minnesota, and Shagawa Lake resulted in much higher prey densities and daily food consumption to 4% of body weight. In Lake Superior where walleye fed exclusively on rainbow smelt (*Osmerus mordax*), prey density did not exceed 300 mg · m^{-3} and daily food consumption averaged less than 2.5% of body weight.

Hourly food consumption by walleye changed in response to variation in prey availability and light intensity. Night feeding predominated during July and August when walleye fed on pelagic age 0 yellow perch. Feeding appeared to be continuous or crepuscular during June and September when larger demersal prey fish or invertebrates were eaten. Food consumption declined when prey concentrated near aquatic macrophytes and under conditions of high light intensity. Walleye daily food consumption was not influenced by a change in temperature from 20 to 15°C.

Daily food consumption of Lake of the Woods, Minnesota sauger (*Stizostedion canadense*) averaged less than walleye and was influenced by wave activity and prey density. Demersal prey was utilized by sauger throughout the 24 h-day.

Key words: Percidae, food consumption, behavior, feeding, walleye, *Stizostedion vitreum vitreum*, sauger, *S. canadense*, light

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La mesure des taux de consommation quotidienne de nourriture et de densité des proies du doré jaune (*Stizostedion vitreum vitreum*) dans le lac des Bois, Minnesota, le lac Shagawa et le lac Supérieur occidental démontre qu'il existe une relation générale entre ces deux variables. La consommation quotidienne de nourriture augmente de 1 à 3% du poids corporel à des densités de proies allant jusqu'à 400 mg · m^{-3}. L'abondance des perchaudes (*Perca flavescens*) d'âge 0 dans le lac des Bois, Minnesota, et le lac Shagawa a pour résultat des densités de proies beaucoup plus élevées et une consommation quotidienne de nourriture allant jusqu'à 4% du poids corporel. Dans le lac Supérieur, où le doré jaune se nourrit exclusivement d'éperlans arc-en-ciel (*Osmerus mordax*), la densité des proies n'excède pas 300 mg · m^{-3}, et la consommation quotidienne de nourriture est en moyenne inférieure à 2.5% du poids corporel.

La consommation horaire de nourriture par le doré jaune change en réponse à la variation

[1]This paper forms part of the Proceedings of the Percid International Symposium (PERCIS) convened at Quetico Centre, Ontario, September 24–October 5, 1976.

[2]Contribution No. 15, Center for Lake Superior Environmental Studies, University of Wisconsin-Superior, Superior, Wis. 54880, USA.

Printed in Canada (J4582)
Imprimé au Canada (J4582)

dans l'accessibilité des proies et l'intensité lumineuse. L'alimentation nocturne prédomine en juillet et août, alors que le doré jaune se nourrit de perchaudes pélagiques d'âge 0. L'alimentation semble être continue ou crépusculaire en juin et septembre, alors que le doré se nourrit de proies démersales plus grandes, poissons ou invertébrés. La consommation de nourriture diminue quand les proies se concentrent à proximité des macrophytes aquatiques et dans des conditions de forte intensité lumineuse. La consommation quotidienne de nourriture par le doré jaune n'est pas affectée par un changement de température de 20 à 15°C.

La consommation quotidienne de nourriture par le doré noir (*Stizostedion canadense*) du lac des Bois, Minnesota, est en moyenne moindre que celle du doré jaune et est affectée par l'action des vagues et la densité des proies. Le doré noir mange des proies démersales tout au long de la journée de 24 h.

Received September 22, 1976
Accepted March 9, 1977

Reçu le 22 septembre 1976
Accepté le 9 mars 1977

INFORMATION on the feeding behavior of walleye (*Stizostedion vitreum vitreum*) and sauger (*Stizostedion canadense*) is important to our understanding of percid communities and to effective management of these resources. In this investigation estimates of daily and hourly food consumption rates are related to species composition of prey populations, prey density, prey distribution, prey size, utilization of cover by prey, surface light intensity, temperature, and wave activity to measure the influence of these factors on walleye and sauger feeding success and feeding time.

Studies were conducted on Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. Differences in food and physical habitat conditions between the three waters were important to measuring effects on feeding. Swenson and Smith (1976) showed that Lake of the Woods, Minnesota, prey populations are dominated by age 0 yellow perch and prey densities vary between approximately 60–800 $mg \cdot m^{-3}$. Shagawa Lake possesses a comparative similar prey species complex but densities reach much higher levels due to cultural enrichment. Western Lake Superior fish populations are dominated by rainbow smelt (*Osmerus mordax*) occurring at relatively low densities. Erosion of red-clay sediments in western Lake Superior reduces water clarity and light penetration during and after storm winds. Variation in western Lake Superior (Table 1) between the three lakes and diurnal changes provided an opportunity to measure the influence of light penetration on walleye feeding behavior. Large size and regular shoreline of Lake Superior and Lake of the Woods resulted in storm waves and curtailed development of aquatic vegetation which was prevalent in the protected bays of Shagawa Lake (Table 1).

Swenson and Smith (1976) failed to identify differences in daily food consumption of Lake of the Woods walleye at temperatures of 14 and 20°C. Samples collected over the same temperature range from Shagawa Lake provided improved precision in measuring the influence of temperature on walleye feeding in this study.

Materials and Methods

Walleye, sauger, and prey fish were collected with a semiballoon trawl, 7.6-m headrope and 2-cm bar mesh with a 0.6-cm bar mesh cod liner. Standard hauls filtered and estimated 3460 m^3 of water in 10 min on Lake Superior, 2600 m^3 in 7 min on Lake of the Woods and 1608 m^3 in 5 min on Shagawa Lake. A smaller trawl with a 5-m headrope and 0.64-cm bar mesh was used on the bottom and at midwater depths to sample prey populations in Lake Superior because age 0 rainbow smelt escaped through the mesh of the larger gear. Standard 10 min hauls filtered approximately 1950 m^3 of water. Trawling speed was maintained at 4.8–5.7 $km \cdot h^{-1}$ (3.0–3.5 $mi \cdot h^{-1}$). Use of trawl catches in defining and comparing prey and predator densities in the three waters was based on the assumption that variation in trawling speed and distance did not influence catchability of prey or predators. Comparison of length–frequency distributions for trawl and gillnet catches from Lake of the Woods suggested that some walleye and sauger exceeding 400 mm TL escaped capture by the trawl (Swenson and Smith 1976). Trawl avoidance by larger walleye probably occurred on Shagawa Lake and Lake Superior as well.

The number of age 0 and older fish captured was recorded for each species. Lengths and weights were taken for walleye and sauger used in the feeding analyses, and representative samples from prey populations. Prey density was estimated from trawl catches as weight of prey per volume of water sampled ($g \cdot m^{-3}$). Trawl catches did not provide an adequate estimate of prey densities during July for Shagawa Lake and from July 1 to mid-August for Lake of the Woods. During these periods pelagic behavior and small size significantly reduced catches of age 0 yellow perch, the dominant prey species in both lakes. Decline in catch demonstrated vulnerability stabilized when age 0 yellow perch reached approximately 40 mm, the approximate size at which Kelso and Ward (1976) and Ney and Smith (1976) found perch become demersal. A minimum estimate of prey density for sampling days occurring during

TABLE 1. Physical data for the three waters studied.

Characteristic	Lake of the Woods, Minnesota	Shagawa Lake	Western Lake Superior Turbid Zone (8.5 ppm)	Western Lake Superior Clear Zone (0.5 ppm)
Latitude	49°00′	47°55′	46°46′	
Longitude	95°00′	91°52′	92°02′	
Surface area (ha)	122,000	925	—	
Depth (m)				
maximum	12	13	12[e]	
mean	7.3	6.7	6[e]	
Temperature range June–September (°C)	11–21	14–23	7–19	5–17
Vegetation (macrophytes)	Sparse, mainly emergent	Dense at 1–3 m in bays	None	None
Light penetration (Depth m, of 1% surface light)	2.2 (July–Sept. 1969)	3.5 (July 1974–75)[b]	2	15
Turbidity	6.5–49 JTU[a]	—	122–10ppm[d]	0–10[d]
pH	7.3[a]	7.2[b]	7.5[d]	7.4[d]
Total alkalinity (ppm)	67[a]	22[c]	40[d]	43[d]
Conductivity (μ ohms)	115[a]	60[c]	101[d]	97[d]
Total phosphorus (ppm)	0.060[a]	0.031[b]	0.067[d]	0.036[d]

[a]National Biocentrics Inc. (1973).
[b]Personal Communication: Paul Smith, Environmental Protection Agency, Shagawa Lake Restoration Project, Ely, Minn.
[c]Larson et al. (1975).
[d]Bahnick (1975).
[e]Maximum at which walleye were captured and mean sampling depth for Western Lake Superior sampling program. Depths given for other waters are lake maximum and means.

the period of changing vulnerability was defined as the sum of the average number of age 0 yellow perch caught during the first 2 sampling days after perch length averaged 40 mm and the calculated consumption of yellow perch by walleye and sauger captured in a standard trawl haul for all days during the intervening period. Catches of other prey species were added to the estimated yellow perch densities in estimating total prey densities.

Water temperature and depth were measured with each trawl on Lake of the Woods and Shagawa Lake, and trawl distance was measured on selected days. On Lake Superior, temperature[3] and transmissometer[4] probes were towed close to the bottom in a Tri-Vane (Swenson unpublished data) which also metered haul distances. Total suspended solid concentration (ppm) was estimated from the relationship between percentage light transmittance and galimetric measurements of total suspended solids (APHA et al. 1971). At Shagawa Lake, surface light was monitored with a radiometer within 3 km of the lake by the U.S. Environmental Protection Agency. An index of light intensity for Lake of the Woods was developed from cloud cover data collected at Kenora, Ontario, by the Canadian Ministry of Atmosphere and Environmental Services. Wind directions and wave heights were estimated during Lake of the Woods sampling. Waves were rated on a scale of 0–4 with a rating of 0 approximating calm conditions and 4 equivalent to a 1 m trough to crest average wave height.

Estimation of daily food consumption by walleye and sauger was based on analysis of stomach content from field collections and laboratory estimates of gastric digestion rates (Swenson and Smith 1973). Stomachs from 2028 Lake of the Woods walleye and sauger collected during 27 days, June–September 1969 and 1970 (Swenson and Smith 1976), 840 Shagawa Lake walleye collected on 17 days, June–September 1974 and 1975, and 88 Lake Superior walleye collected during 5 days, July–September 1973 were analyzed to estimate daily and hourly food consumption rates. It was necessary to subsample from a total of 354 walleye stomachs from Lake Superior to meet the conditions included in the laboratory digestion studies of Swenson and Smith (1973) upon which estimates of food consumption are based. Digestion data were not applicable for most samples collected on 22 days during June–September 1973 because sizes of fish captured, sizes of food eaten, or lake temperatures were not included in the digestion studies. The total sample was used to define Lake Superior walleye diet and effects of suspended solids on feeding.

Electivity indices (Ivlev 1961) were calculated from the percentage of each prey species in the daily meal and percentages in trawl catches for Lake of the Woods and Shagawa Lake. Lake of the Woods calculations were based on estimates of daily food

[3]Yellowsprings Instrument Co. Model 43TD telethermometer, Yellow Springs, Ohio.

[4]Hydroproducts, Inc. Model 410Br transmissometer, Box 2528, San Diego, Calif.

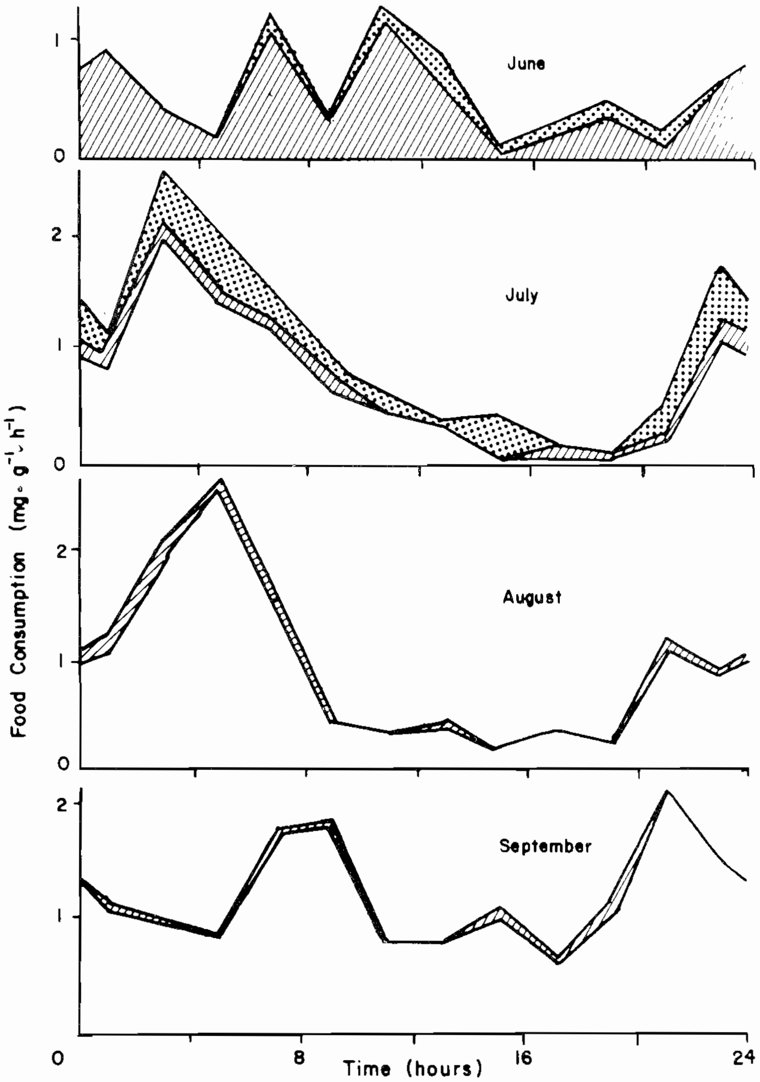

FIG. 1. Hourly food consumption ($mg \cdot g^{-1} \cdot h^{-1}$) of invertebrates (stippled), age 0 yellow perch (open) and other fish (barred) by Lake of the Woods walleye.

consumption and prey density presented by Swenson and Smith (1976). Although biased by trawl selectivity, electivity indices were useful in identifying changes in feeding associated with variation in prey availability.

Factors Influencing Walleye Feeding

Food quality — Invertebrates and fish were eaten primarily during night and twilight hours in both Lake of the Woods and Shagawa Lake (Fig. 1 and 2). Lake of the Woods walleye over 200 mm TL ate an average of 2.5 and 5.6 $mg \cdot g^{-1} \cdot day^{-1}$ of invertebrates, mainly the mayfly *Hexagenia limbata* during June and July, respectively (Table 2). Chironomidae and mayflies were the most common invertebrate items in Shagawa Lake walleye daily meals.

Daily food consumption of walleye was influenced by abundance and location of yellow perch. In Shagawa Lake average daily food consumption for June was highest during 1975 (Table 2) when yearling yellow perch abundance was high (Table 3). In 1974 although June consumption of invertebrates and other prey fish species was high, abundance of yearling perch (Table 3) and total daily food consumption ($mg \cdot g^{-1} \cdot day^{-1}$)

TABLE 2. Total daily food consumption (g·individual^{-1} and mg·g^{-1}) and daily consumption of major forms (numbers of prey consumed daily 100 m^{-3}) by walleye over 200 mm TL in Shagawa Lake, 1974 and 1975 and western Lake Superior, 1973. Comparable data for Lake of the Woods, Minnesota, were given by Swenson and Smith (1976). Values in parenthesis are percentages of the meal.

Month	Sample size (No.)	Mean wt. (g)	Total g·ind^{-1}	Total mg·g^{-1}	*Perca flavescens*	*Percopsis o.*	*Osmerus mordax*	*Notropis hudsonius*	Other Fish	Invert.
					Shagawa Lake					
1974										
June	131	105	1.6	15.0	0(0)	0(3)	—	0.36(30)	(19)	(49)
July	80	145	5.6	38.9	12.10(96)	0(0)	—	0.17(2)	(>1)	(2)
Aug.	111	98	3.1	32.2	1.22(75)	0(0)	—	0.15(9)	(3)	(14)
Sept.	23	135	3.5	26.1	0.96(57)	0(0)	—	0.83(38)	(0)	(4)
1975										
June	101	280	3.4	24.5	0.45(56)	0.02(3)	—	0(0)	(10)	(31)
July	140	177	6.6	39.5	11.94(90)	0(0)	—	0.07(1)	(2)	(6)
Aug.	78	180	6.2	34.3	1.13(88)	0.01(2)	—	0.50(3)	(6)	(>1)
Early Sept.	85	252	7.8	31.0	0.61(69)	0.03(2)	—	0.05(5)	(18)	(7)
Late Sept.	91	265	3.5	13.7	0.16(83)	0(0)	—	0.02(5)	(9)	(4)
					Western Lake Superior					
1973										
July	35	129	3.1	22.8	—	—	0.5(100)	—	—	—
Aug.	31	240	5.1	19.5	—	—	0.6(100)	—	—	—
Sept.	22	148	3.1	21.0	—	—	1.0(100)	—	—	—

TABLE 3. Densities of principal walleye and sauger prey (number 100·m^{-3}) and of total prey (mg·m^{-3}) in the three waters studied. Values in parentheses are for depths greater than 5 m.

Month	Days sampled	Net lifts	*Perca flavescens* Age 0	*Osmerus mordax*	*Percopsis omiscomaycus* Age 0+	*Notropis* sp. Age 0+	Total prey density
			Lake of the Woods, Minnesota (1969–70)[a]				
June	15	144(16)	0.1(0.0)	—	2.3(15.8)	0.2(0.0)	100(576)
July	9	106(11)	86 (3.0)[c]	—	3.3(13.5)	0.2(0.1)	374(486)[c]
Aug.	17	128(27)	29.6(5.2)	—	5.6(24.6)	0.9(0.0)	532(698)
Sept.	9	87(20)	21.6(10.9)	—	7.3(30.6)	0.7(0.0)	616(1008)
			Shagawa Lake, Minnesota (1974–75)				
June 1974[b]	2	14(2)	0.0(0.0)	—	4.0(2.7)	2.4(0.2)	132(68)
June 1975[b]	3	20(16)	19.5(0.8)	—	0.3(0.9)	0.7(0.1)	585(40)
July	4	19(21)	500 (23.6)[c]	—	2.7(8.0)	1.5(1.8)	2528(388)[c]
Aug.	4	15(9)	84.7(10.1)	—	16.4(8.0)	14.3(1.1)	2691(439)
Sept.	5	26(17)	24.3(9.7)	—	8.8(6.8)	5.5(4.3)	1715(871)
Oct.	1	6(3)	66.9(1.7)	—	0.5(0.4)	5.5(1.5)	2127(150)
Nov.	1	4(2)	1.8(0.9)	—	0.1(4.7)	0.4(0.1)	117(314)
			Western Lake Superior (1973)				
June	4	6	—	7.4	0.2	—	282
July	4	6	—	8.3	0.3	—	157
Aug.	4	6	—	52.2	0.3	0.2	169
Sept.	4	6	—	46.5	1.6	0.2	317

[a]Information for Lake of the Woods, Minnesota, was converted from Swenson and Smith (1976).
[b]Estimates given separately for the 2 years to illustrate major differences in abundance of yearling yellow perch.
[c]Estimates for water under 5 m are corrected for incomplete vulnerability of age 0 yellow perch to the trawl by procedures described in "Methods."

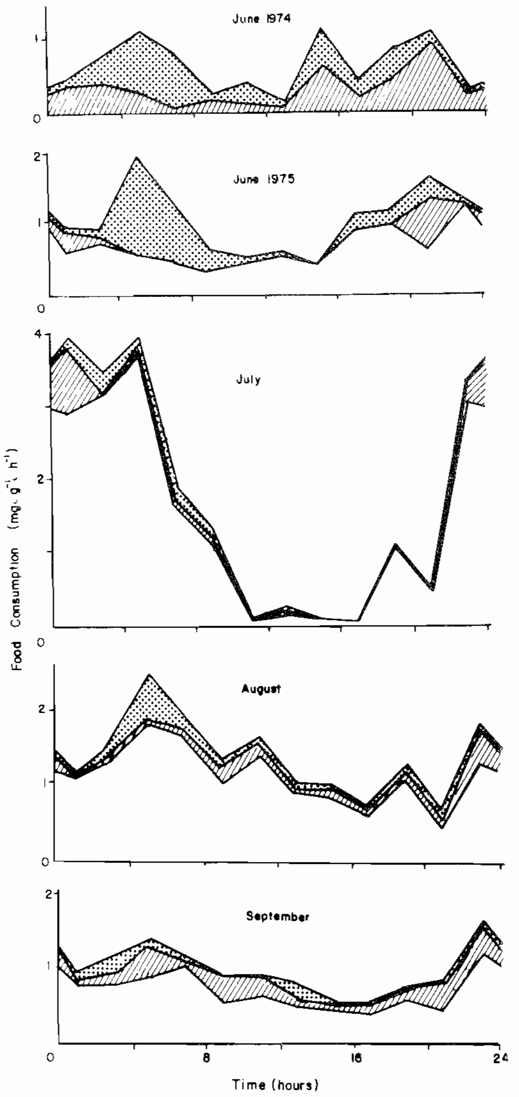

FIG. 2. Hourly food consumption ($mg \cdot g^{-1} \cdot h^{-1}$) of invertebrates (stippled), age 0 yellow perch (open) and other fish (barred) by Shagawa Lake walleye.

was low. June 1975 consumption averaged 24.5 $mg \cdot g^{-1} \cdot day^{-1}$ in comparison with 11.6, 7.5, and 15.0 $mg \cdot g^{-1} \cdot day^{-1}$ for 1969, 1970, and 1974, respectively. Increased abundance of age 0 yellow perch during July in both Lake of the Woods and Shagawa Lake was associated with increased walleye daily food consumption and a change to night feeding (Table 2, Fig. 1 and 2). The highest daily food consumption occurred during July in Shagawa Lake where walleye fed primarily at night and ate approximately 4% of their body weight per day (Fig. 2, Table 2). Prominence of night feeding declined during August in Shagawa Lake and during September in Lake of the Woods. The trend away from night feeding appeared related to a closer association between age 0 yellow perch and the lake bottom.

Trout-perch (*Percopsis omiscomaycus*) were the second most abundant prey in the three waters (Table 3) but were uncommon in the daily meals of walleye (Table 2; Swenson and Smith 1976). For both Lake of the Woods and Shagawa Lake electivity of trout-perch was strongly negative (Table 4) during all sampling months suggesting that trout-perch are avoided or are not available. Electivity indices for *Notropis* sp., which were common in Lake of the Woods and Shagawa Lake, were positive or zero during periods of reduced age 0 yellow perch abundance but became negative during periods of high perch abundance. Shagawa Lake walleye appeared to positively select age 0 black crappie (*Pomoxis nigromaculatus*).

Lake Superior walleye fed only on rainbow smelt, which comprised 95% by weight of the prey-sized fish in trawl catches. The data suggested that western Lake Superior walleye utilize rainbow smelt in approximate proportion to their abundance.

Prey density — Monthly averages of Lake of the Woods walleye daily food consumption estimates increased with prey densities up to 300 $mg \cdot m^{-3}$ but averaged approximately 3% of body weight at prey densities of 300–800 $mg \cdot m^{-3}$ (Swenson and Smith 1976). Daily food consumption by Shagawa Lake walleye approximated 4% of body weight during July and August, when prey densities exceeded the maximum encountered in Lake of the Woods. Observations for the three waters were combined to determine if a general relationship could be identified between monthly averages of daily food consumption and prey density. For this analysis, prey densities were estimated from trawl catches in water shallower than 5 m except during late September when prey and predator concentrated at greater depths in Shagawa Lake and data for all sampling depths was combined. Trout-perch were not included in estimates of prey density because of low utilization by walleye in all three lakes.

Daily food consumption increased with prey densities between 10 $mg \cdot m^{-3}$ and 3500 $mg \cdot m^{-3}$ with the greatest increase occurring at densities from 10 to 400 $mg \cdot m^{-3}$ (Fig. 3). Daily food consumption averaged between 3–4% of body weight over the 400–3500 mg m^3 range of prey densities. Differences between July feeding rates in Lake of the Woods and Shagawa Lake were large (Fig. 3) and resulted from major differences in

TABLE 4. Electivity indices (Ivlev 1961) of major prey consumed by walleye over 200 mm in Lake of the Woods, Minnesota, and Shagawa Lake.

Month	*Perca flavescens*	*Percopsis omiscomaycus*	*Notropis* sp.	*Pomoxis nigromaculatus*
		Lake of the Woods, Minnesota		
Walleye				
June	0.0	−0.6	+0.6	—
July	+0.2	−1.0	+0.2	—
Aug.	+0.3	−1.0	−0.1	—
Sept.	+0.2	−1.0	−0.7	—
Sauger				
June	−1.0	0.0	−0.2	—
July	−0.3	+0.4	−1.0	—
Aug.	+0.1	−0.2	−0.1	—
Sept.	−0.4	+0.2	+0.5	—
		Shagawa Lake		
Walleye				
June	0.0	−0.7	0.0	—
July	+0.3	−0.8	−0.9	+1.0
Aug.	+0.3	−0.9	−0.4	−0.6
Sept.	+0.3	−1.0	−0.2	+0.7

abundance and growth of age 0 yellow perch. In Shagawa Lake age 0 yellow perch averaged 35 mm by the middle of July, in comparison with 30 mm in Lake of the Woods. High abundance of yearling yellow perch during June 1975 also resulted in higher June consumption rates in Shagawa Lake (Fig. 3, Table 2). Low prey density in Lake Superior (Table 3) limited daily consumption to an average of approximately 2% of body weight (Fig. 3).

Physical conditions — Walleye consumption of age 0 yellow perch was greatly restricted during late September 1975 (Table 2, Fig. 3) when perch availability in open water was below 200 $mg \cdot m^{-3}$ but exceeded 1000 $mg \cdot m^{-3}$ in areas of aquatic macrophytes. Vegetation appears to reduce food availability to walleye by providing cover for some prey species which concentrate in these areas where walleye density is low. Shagawa Lake walleye catches in areas with aquatic macrophytes were low but catches on age 0 Centrarchidae were highest in these areas throughout most of the growing season.

Daily food consumption rate did not change with water temperature during periods when food abundance exceeded 400 $mg \cdot m^{-3}$ in Lake of the Woods and Shagawa Lake. Daily food consumption at 14–15.5°C (11 days during June and late September) and at 20–22°C (10 days during August and early September) averaged 30.0 and 29.1 $mg \cdot g^{-1} \cdot day^{-1}$, respectively. Higher stomach volumes occurred during the lower temperature periods (t-test; $P < 0.01$). Laboratory digestion studies show a positive relationship between stomach volume and food digested h^{-1} (Fig. 4). Because more food can be processed through the digestive system at higher stomach volumes, the results show that for the range of temperatures tested, limiting effects of low temperature on digestion are compensated by increased stomach volumes. By feeding throughout the day during periods of reduced temperature and high food availability, walleye maintained high stomach volumes, digestion rates, and food consumption rates.

Predominance of night and twilight feeding by Lake of the Woods and Shagawa Lake walleye indicates high light intensity may be a significant factor influencing daily food consumption. Midday feeding was greatest during June and September when walleye ate more demersal prey. Light intensity and the percentage of the total meal consumed between 08:00–18:00 CST for Shagawa Lake walleye were ranked for six periods during which a minimum of two estimates of food consumption were available for days characterized by similar prey densities. The ranks were negatively correlated ($r_\rho = -0.89$; $P < 0.05$) demonstrating walleye food consumption during daylight hours is limited by high light intensity. A negative but insignificant correlation was found from a similar analysis of Lake of the Woods data ($r_\rho = -0.15$; $P > 0.05$).

Red-clay turbidity and inshore walleye densities in Lake Superior were positively correlated ($R = 0.69$; $P < 0.01$). Light penetration is reduced by red-clay turbidity (Table 1) indicating

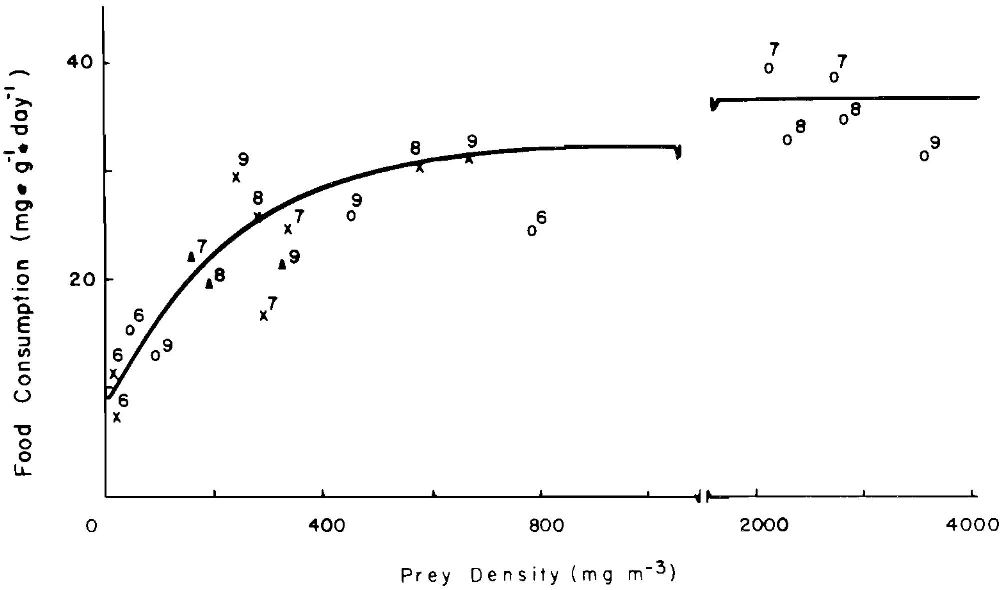

FIG. 3. Relations between monthly averages of walleye daily food consumption rates and prey densities for Shagawa Lake (○), Lake of the Woods, Minnesota (×) and western Lake Superior (▲). Numerals indicate calendar month.

the relationship to turbidity may be in response to changes in light levels. Stomach volume of Lake Superior walleye appeared to increase with turbidity but differences were not significant ($P > 0.05$).

Factors Influencing Sauger Feeding

Lake of the Woods sauger daily meals included a smaller percentage of invertebrates during June than walleye (Fig. 5) and larger quantities of trout-perch (Swenson and Smith 1976). Trout-perch comprised 85% of the food consumed by sauger during June (Swenson and Smith 1976) when midday feeding predominated (Fig. 5). Electivity indices suggested that trout-perch are eaten in approximate proportion to their relative abundance in prey fish populations (Table 4). Although percentages of age 0 yellow perch increased to 33 and 63% in July and August sauger meals, as a result of increased night active feeding on perch (Fig. 5), electivity indices continued to suggest preference or higher availability of trout-perch (Table 4).

Rank correlations suggested high light intensity associated with reduced cloud cover lowered daily food consumption of sauger during midday (08:00–18:00 CST; $r_c = -0.37$) but the relationship was not significant ($P > 0.05$).

Regression analysis showed that daily food consumption by sauger increased with wave activity on Lake of the Woods ($P < 0.01$). The association between daily food consumption and wave activity ratings could result from reduced light penetration during periods of increased wave action.

In contrast to the findings of Swenson and Smith (1976) which did not consider wave intensity, a significant relationship (Fig. 6; $P < 0.05$) between daily food consumption of Lake of the Woods sauger and prey density was observed. Variability between daily food consumption estimates was controlled by omission of data collected during days of extremely low or high wave activity (ratings 1 and 4).

Discussion

Predominance of nocturnal feeding, low percentage of trout-perch and relatively high percentages of age 0 yellow perch, rainbow smelt, and *Notropis* sp. in their daily meals showed that walleye utilize pelagic prey particularly during July and August. Pelagic behavior has been identified for smelt in turbid waters of Lake Superior (Swenson unpublished data), for age 0 yellow perch (Forney 1971; Kelso and Ward 1976) and for spottail shiners (Smith and Kramer 1964). Absence of trout-perch from midwater trawl catches in Lake Superior (Swenson unpublished data) and their food habits (Anderson and Smith 1971) indicate a close association with the

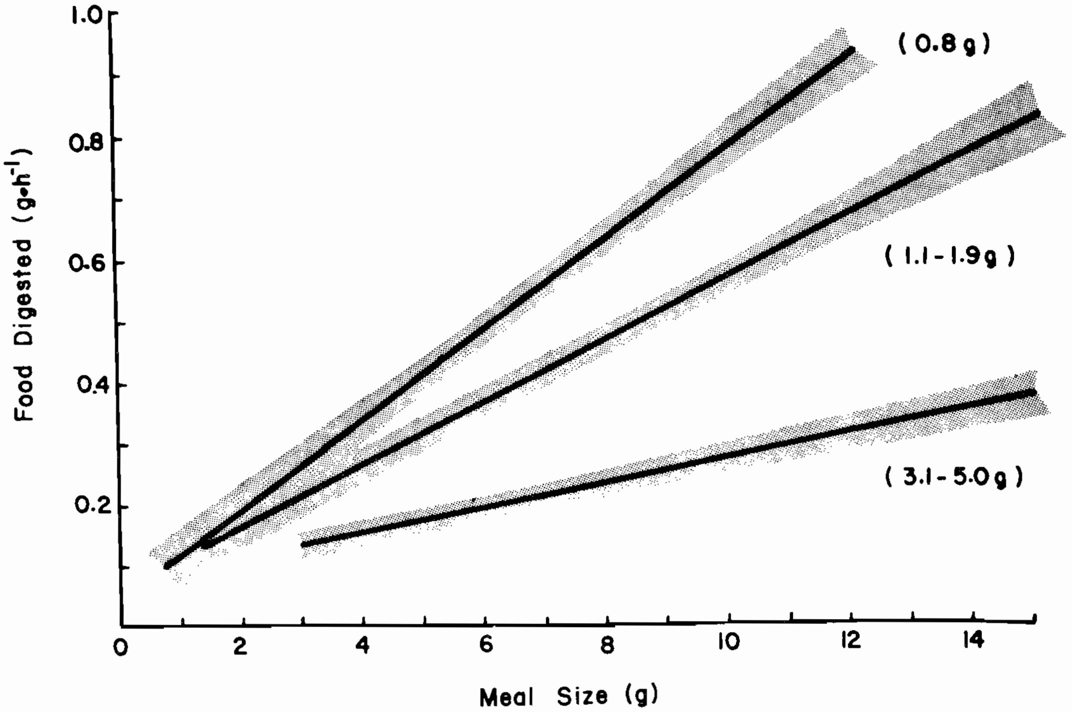

FIG. 4. Relations between walleye and sauger digestion rate and meal size in laboratory experiments including 1.1–1.9 g and 3.1–5.0 g prey at 14.5°C and 0.8 g prey at 20°C. Estimates are based on methods and 371 observations described by Swenson and Smith (1973). Shaded areas include 95% confidence limits.

bottom. Low daily food consumption (1–2 $mg \cdot g^{-1} \cdot day^{-1}$) of Lake of the Woods walleye during June, when trout-perch densities exceeded 400 $mg \cdot m^{-3}$, and by Shagawa Lake walleye when age 0 yellow perch concentrated near aquatic macrophytes shows that walleye required prey in open water to maintain daily food consumption between 3–4% of body weight.

In contrast to walleye, sauger relied primarily on trout-perch as an energy source, indicating a closer association with the bottom. Relative low food consumption rates, limited variation in feeding activity during the 24-h day and predation on trout-perch, a species associated with the cover provided by the lake bottom, suggests that rate of prey capture required to maintain food search behavior is lower for sauger than for walleye. Evidence that food search behavior is dependant on capture success has been provided by Ware (1972) who found rainbow trout (*Salmo gairdneri*) feeding success was limited by cover conditions and food searching waned if rate of prey capture declined below a critical level. Ali and Anctil (1968) found differences in the structure of the retina provide sauger with improved vision under reduced light conditions. This physiological difference would increase the probability for selection of feeding behavior in sauger effective in capturing demersal prey. Differences in feeding behavior identified by this study would appear to be important to the coexistence of walleye and sauger in freshwater communities.

Available information suggests walleye are adapted to maintain daily food consumption between 3–4% of body weight and this level of feeding results in increased food availability, annual consumption, survival, and food conversion efficiency. Crepuscular and night active feeding resulted in daily food consumption between 3–4% of body weight during July and August when prey density and temperature were not limiting and day-active feeding would have resulted in higher feeding rates. However, increased predation during July or early August would reduce age 0 yellow perch population densities. In Shagawa Lake (Table 3), Lake of the Woods (Swenson and Smith 1976), and Oneida Lake (Forney 1974) predation by walleye or sauger was the principal factor limiting prey survival and the greatest effects occurred during early summer when they fed on small size prey. Cannibalism occurred in Shagawa Lake and Oneida Lake

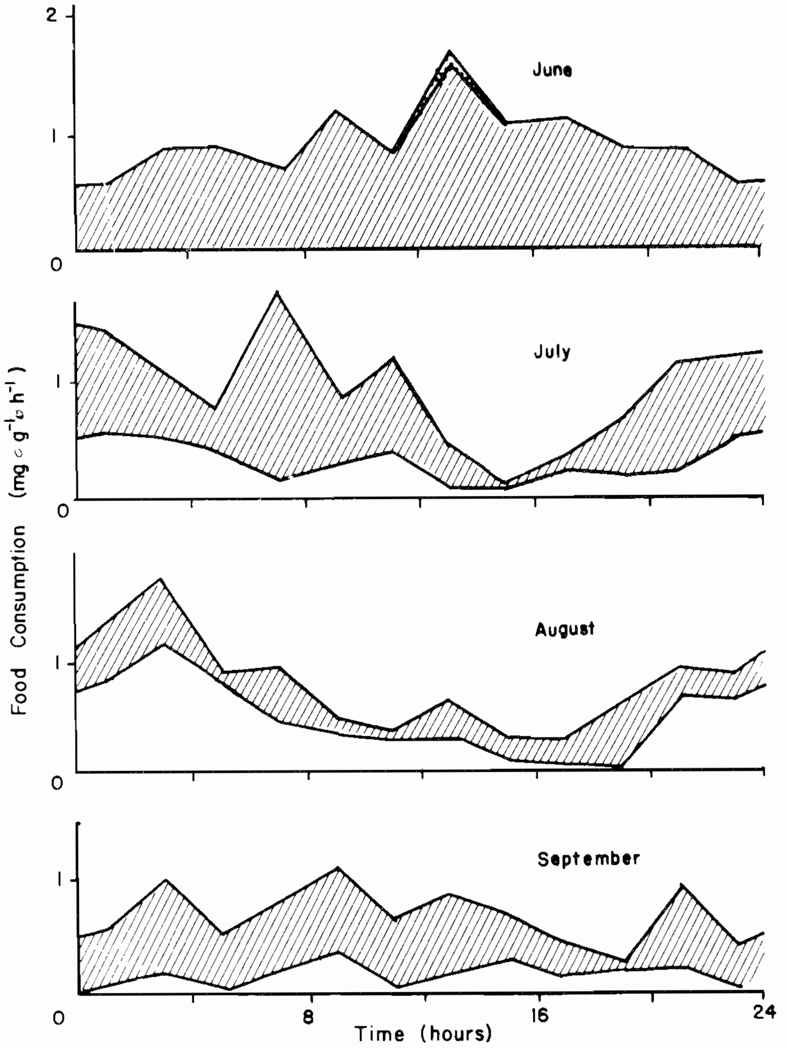

FIG. 5. Hourly food consumption ($mg \cdot g^{-1} \cdot h^{-1}$) of invertebrates (stippled), age 0 yellow perch (open) and other fish (barred) by Lake of the Woods sauger.

(Forney 1976) during late summer if prey density was low. If prey densities were high, cannibalism was limited (Forney 1976) and food consumption was maintained between 3–4% of body weight even at lower late September temperatures. During late September feeding throughout the day resulted in higher stomach volumes, high digestion efficiency, and maintenance of food consumption between 3–4% of body weight. Kelso (1972) found food consumption by walleye in the laboratory was reduced to maintenance levels at 12°C, the temperature at which food consumption must be temperature limited. Gross food-conversion efficiency of Lake of the Woods walleye was 22% with rations approximating 3% of body weight and 17% at lower June rations of 1% of body weight (Swenson and Smith 1973). Thompson (1941) showed consumption rates between 3–4% of body weight resulted in maximum conversion efficiency in largemouth bass (*Micropterus salmoides*).

Aquatic vegetation appeared to reduce availability of prey in Shagawa Lake. Lower daily food consumption occurred during September when age 0 yellow perch were abundant but associated with aquatic macrophytes. Age 0 walleye moved into deep water with older age groups in both Lake of the Woods and Shagawa Lake at

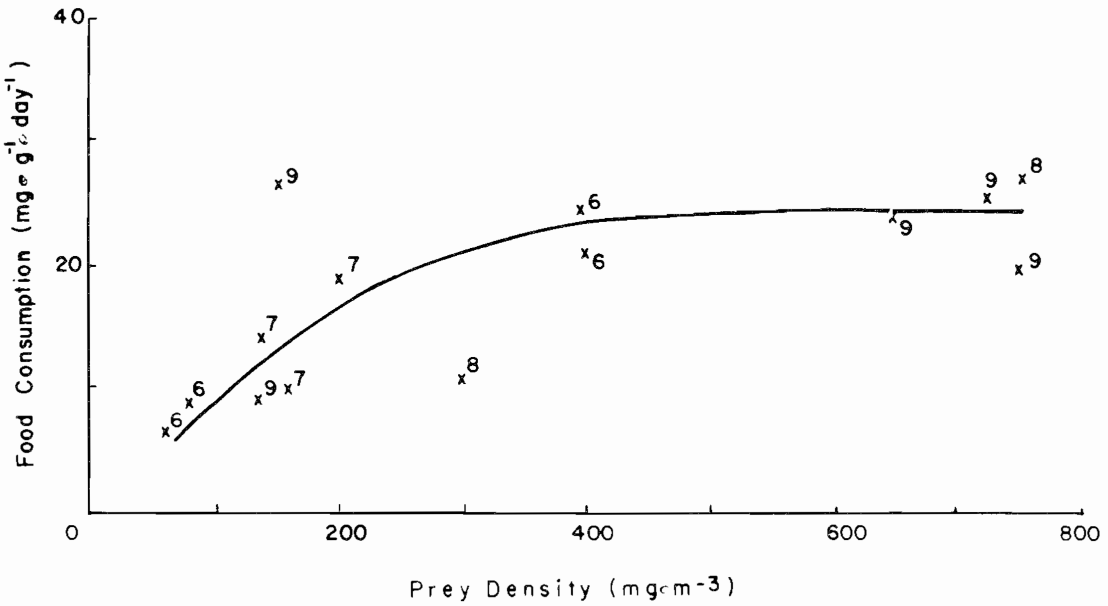

FIG. 6. Relations between daily food consumption rate of Lake of the Woods sauger and prey density during periods of moderate wave action. Numerals indicate calendar months.

this time. Cannibalism by walleye occurred only in open water areas of Shagawa Lake where density of yellow perch was lower. Observations from Shagawa Lake suggest aquatic macrophytes may also be a major factor limiting predation by walleye on Centrarchidae.

Midday feeding activity was reduced by high light intensity. In lakes where prey densities would not result in daily food consumption between 3–4% of body weight through crepuscular and night feeding activity, light limited feeding could restrict growth. The increased water clarity of Shagawa Lake associated with tertiary treatment of sewage since 1973 appears to limit midday feeding as a result of increased light penetration and to reduce food availability as a result of expanded macrophyte distribution. However, daily food consumption was maintained at high levels due to high prey density during most of the growing season. If prey fish populations decline, major changes in daily food consumption, growth, and survival would occur. Walleye abundance was low in the clear water of Lake Superior but increased with red-clay turbidity. High light intensity related to clear water conditions restricted the distribution of Lake Superior walleye and their use of a major food resource.

Figure 3 appears to represent a general relationship between walleye daily food consumption and prey density for a variety of lake systems and could be used to estimate food consumption of walleye in other lakes. Information provided herein on the factors influencing prey availability could be applied in measuring density of available prey from trawl catches for other waters. Food consumption rates could then be estimated from the prey density measurements and the relationship between daily food consumption and prey density developed for the three study waters (Fig. 3). Although estimates of food consumption derived in this manner may lack precision, they could be obtained with limited effort and should be valuable to lake management. Lakes with prey densities high enough to support daily food consumption rates between 3–4% of body weight throughout most of the growing season could be managed to their high production potential. Management of lakes with low food availability should be directed at increasing food availability rather than walleye population numbers because this study and others (Forney 1976; Swenson and Smith 1976) have shown that cannibalism or predation will limit walleye populations in lakes with limited food resources. Lakes characterized by low prey density may be best managed for another species.

Acknowledgments

Research on Lake of the Woods, Minnesota, was supported through the Minnesota Department of Natural Resources, University of Minnesota Agricultural Experimentation Station and U.S. National Marine Fishery Service Project 4-39-R. Projects on Shagawa Lake and Lake Superior were supported through the

U.S. Environmental Protection Agency, Grant Numbers R-803673 and R-802455, respectively and by the University of Wisconsin-Superior Center for Lake Superior Environmental Studies. The contents do not necessarily reflect the views and policies of the supporting agencies nor does mention of trade names or commercial products constitute endorsement or recommendation for use. I wish to thank Mr L. Brooke of the University of Wisconsin-Superior, Center for Lake Superior Environmental Studies, for assistance with the Shagawa Lake research and helpful criticism of the manuscript.

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