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Feeding Habits of Walleye Larvae and Juveniles: Comparative Laboratory and Field Studies

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Abstract

The feeding habits of larval and juvenile walleyes *Stizostedion vitreum* were examined in the field and laboratory. Walleyes are "strike" feeders and rely on vision to capture food. The mouth, jaws, and teeth are strongly developed by the time feeding begins about 5 days after hatching, but the gill rakers do not develop a filtering function until the juveniles are 20–30 mm long. The preferred food of postlarvae was crustacean zooplankton, about 1.2 mm in total length. Rotifers were not consumed at normal pond densities. Size selection of prey was more important than species selection. During the juvenile stage, walleye food preference shifted from zooplankton to larger, faster prey; first to *Chaoborus* sp. and mayflies, later to *Gammarus lacustris* and fish. The rate of food consumption by juveniles varied with food preference; it was highest with *Chaoborus* sp. and fish, lower with *Daphnia pulex*, and lowest with *Gammarus lacustris*. The food consumption rate was linearly proportional to food density when *Daphnia pulex* was fed at densities less than 100 per liter. In highly turbid ponds, there were three periods of feeding activity per day, separated by 8-hour intervals. The feeding periodicity of smaller walleyes was opposite to that of larger walleyes when both were present together in a pond. Predation on smaller fish (including cannibalism) was first observed when walleyes reached a total length of about 30 mm.

Many stocks of walleye *Stizostedion vitreum* are below historical production levels and thus far there has been no effective way to reverse this trend. Stocking 1–4-month-old juveniles into lakes has been shown to stimulate walleye production (Schweigert et al. 1977), but the success of rearing juveniles often is variable and unpredictable. The purpose of our research is to define the mechanisms of survival and growth of larvae and juveniles. Previously (Li and Mathias 1982, this issue), we examined the relationship between survival and early development. In this paper, we qualitatively and quantitatively analyze the feeding habits of larval and juvenile walleyes.

Methods

Studies were conducted from May to October 1981 at the Canada Department of Fisheries and Oceans' Rockwood Fish Hatchery near Gunton, Manitoba. Li and Mathias (1982, this issue) give detailed descriptions of the source of walleye larvae, holding facilities for the larvae, and the preparation and environmental characteristics of the culture water. For this study, larvae were cultured in 40-, 70-, and 200-liter glass aquaria in the laboratory, in outdoor plastic tanks measuring 25 m² × 0.8 m deep, and in eight earthen ponds measuring 0.2 hectares × 2 m deep.

Food organisms were collected every 2 days from outdoor tanks, hatchery ponds, and nearby farm dugouts. Crustacean zooplankton (mainly *Daphnia pulex* in May and June, but including up to 50% *Cyclops bicuspidatus* by the end of July) as well as *Chaoborus* sp. larvae were collected with a 0.5-m, 73-μm-mesh net; a 53-μm-mesh net was used for rotifers. *Gammarus lacustris*, mayfly nymphs, and juveniles of the brook stickleback *Culea inconstans* were collected with dip nets. Food organisms were held in 75-liter plastic pails with aeration until required.

Walleye larvae kept in laboratory holding tanks were fed daily on plankton of a wide variety of sizes, from rotifers measuring 100 μm in length to adult daphnids measuring 2.7 mm long.

All lengths of walleyes and of their prey are total lengths in this paper.

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Feeding

Five morphological variables related to feeding were measured: maximum width (horizontal opening) and gape (vertical opening) of the mouth: the degree of development and total length of the gut; and the average length of the gill rakers and their filtration area. The gill raker filtration area was the average length of adjacent rakers times the distance between them. All measurements were made on fresh specimens; the mouth and gill rakers of larvae were measured under a microscope with an eyepiece micrometer.

The behaviour of first-feeding larvae (8.9 mm) in well-lighted (50 microeinsteins $m^{-2} \cdot second^{-1}$), 40-liter aquaria was recorded for a total period of 137.5 minutes. Water temperature was 20 C and the density of food (*D. pulex*, size-graded to a range of 1.0–1.3 mm total length) was 100 per liter. The number of orientations to prey, the number of strikes, and the number of successful captures were recorded.

Food Selection

Walleye larvae in laboratory holding tanks and larvae and juveniles from hatchery ponds were sampled to examine food in their guts. Specimens were preserved in 10% formalin and the body wall of larger specimens was slit. Gut contents were easily recognizable. Samples of plankton (and of benthos, in ponds) were taken at the same time and place as the fish for comparison with gut contents. Linear selection indexes L (Strauss 1979) were calculated:

$$L = r_i - p_i;$$

r_i = relative abundance of prey taxon i in the gut;

p_i = relative abundance of prey taxon i in the habitat.

A variety of food organisms (*Daphnia pulex*, *Cyclops bicuspidatus*, *Chaoborus* sp. larvae, *Gammarus lacustris*, mayfly nymphs, and juvenile fish) were introduced in various combinations to walleye larvae and juveniles in 40-liter aquaria. Water temperature was 20 C. The preference of walleyes and rate of consumption for each taxa were recorded. Specific details of each test are given below with the results.

Food Consumption

The rate of food consumption by walleyes in the laboratory was measured by introducing known quantities of prey organisms into aquaria with walleyes, and recording the number remaining after a specified time. Specific details of experimental protocol are given with the results.

The rate of food consumption by walleyes in ponds was calculated according to Baikov (1935) and Pavlovskii and Borutskii (1961):

$$\text{daily ration} = \frac{\begin{array}{c}\text{24-hour average}\\ \text{stomach fullness}\end{array}}{\begin{array}{c}\text{number of hours}\\ \text{to evacuate food}\\ \text{from the stomach}\end{array}} \; 24 \times 10^{-2};$$

$$\begin{array}{c}\text{stomach}\\ \text{fullness index}\end{array} = \frac{\begin{array}{c}\text{weight of food}\\ \text{in stomach}\end{array}}{\text{weight of fish}} \; 10^{4}.$$

The time required to evacuate food from the gut was estimated from observations of walleyes in the laboratory, and from diel feeding dynamics of walleyes in ponds. Detailed methods are given with the results.

Results

Prolarval walleyes, from hatching until disappearance of the yolk (about 5 days at 18–20 C) did not feed. Feeding first began with the postlarval stage at a length of about 8.5 mm. At this time, the mouth of larval walleyes exhibited predator characteristics such as a large gape and well-developed jaws and teeth. The mouth was 0.6–0.8 mm wide, with a gape of 1.4–1.8 mm (Fig. 1). There were 6–10 teeth on each side of the upper and lower jaws. These fish were capable of swallowing daphnids 0.7–1.6 mm long, and could capture and partially swallow siblings of their own size.

The first 5 days of the walleye postlarva period have been functionally termed stage I (Li and Mathias 1982, this issue) because the larvae contain an oil globule, and this is a period of mixed nutrition. At the end of stage I, the larvae are 10–11 mm long (at 18–20 C). The remaining 8 days of the postlarva period have been termed stage II, to distinguish this period as one of solely exogenous nutrition. The larvae were about 16–19 mm at the end of stage II (at 18–20 C).

At the beginning of the postlarva period, the gut was a simple, straight tube with a small, bag-like extension of the intestine (precursory stomach). By the end of the postlarva stage I, the

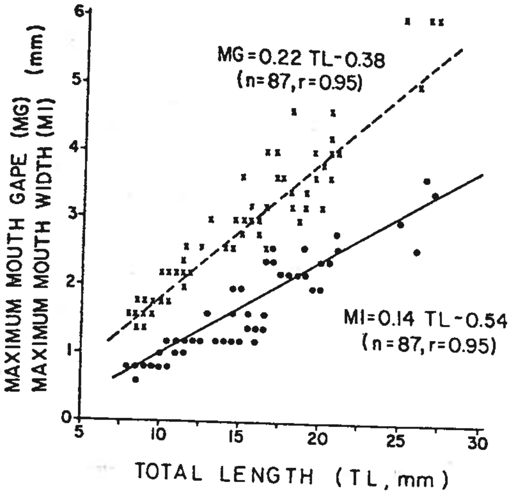

FIGURE 1.—*Relation of maximum mouth gape and width to total length of walleyes. Some points represent more than one observation.*

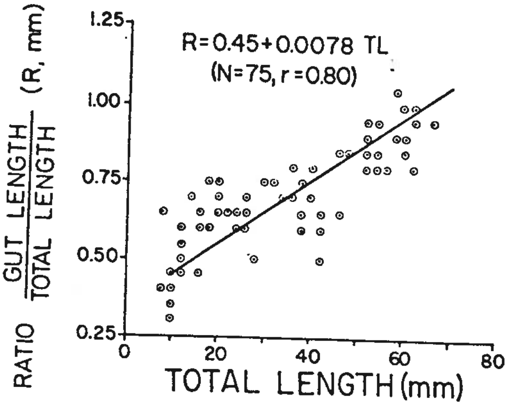

FIGURE 2.—*Ratios of gut length to total body length for walleyes, related to body length. Some points represent more than one observation.*

cells of the stomach had grown in number and size, and a sphincter had developed that divided the gut into intestine and rectum. The first intestinal loop appeared during the postlarva stage II and a second loop appeared during the juvenile stage. Throughout the larva and juvenile stages, the length of the digestive tract increased at a faster rate than body length (Fig. 2).

The gill rakers assumed no filtering function during the larva period, because they did not begin to differentiate until the end of the postlarva stage II. Their growth was linear during the juvenile stage, resulting in an exponential increase in the area filtered (Fig. 3).

First-feeding larvae were "strike" feeders. Making visual contact with a food particle, a larva oriented towards it, bringing it into the visual field of both eyes. Next, the larva slowly approached the particle to within 1.5–3 mm; at this point, the larva either rejected it and swam away, or "struck" using one of two behaviours. The first, which was more common in early

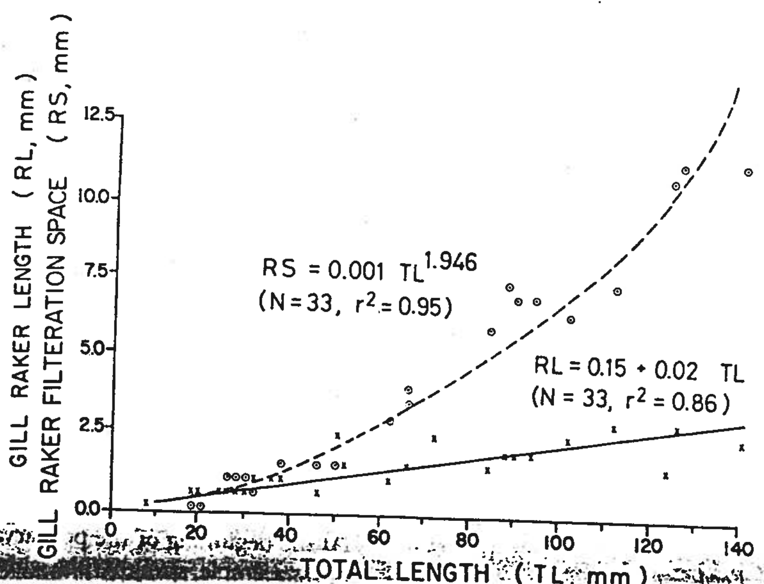

FIGURE 3.—*Relation of gill raker length and functional filtration space to total length of walleyes. Filtration space is the sum of (gill raker length × distance between rakers). Some points represent more than one observation.*

postlarvae, was to curl the trunk into an S shape and lunge forward, at the same time opening the mouth. The second, more common as swimming strength increased, was to dart forward by rapid swimming motions of the trunk and tail. The former behaviour carried the larvae forward about half of a body length; the latter achieved a greater strike distance. When a strike was unsuccessful, successive strikes often followed, as long as the particle remained within the larva's visual field.

During the second day of feeding, 30 larvae were observed for an average of 4.5 minutes each. Each observation began after a strike and ended when the larva swam out of the observer's visual field. The food was *Daphnia pulex*, at a density of 16.7 per liter. The fish density was 20 fish in 30 liters of water. Over the total observation period, larvae approached food particles an average of once every 0.75 minutes (SD 0.65). The ratio of strikes to approaches was 0.73 (SD 0.17). The ratio of successful strikes to total strikes was about 0.04.

Food Selection

Rotifers and Copepod Nauplii

Three tests were made to examine the significance of rotifers and copepod nauplii as food for larval walleyes. The first test was made in four outdoor plastic tanks each containing 20 m^3 of water and stocked with 150 larvae (9 mm) that had just begun to feed. The tanks had been filled with pond water and contained an array of plankton species. Every 4 days, one tank was sampled and food organisms in the plankton were compared to those found in fish guts. The density of rotifers and nauplii found in the 4 tanks, and the number of fish examined were:

Date	Rotifer density (*N*/liter)	Nauplii density (*N*/liter)	Fish examined (*N*)
May 24	9	60	33
May 28	44	33	14
Jun 1	108	171	15
Jun 5	0	56	17

No rotifers or copepod nauplii were found in any of the fish guts.

The second test was made in a light grey plastic tub containing 100 liters of water and about 20,000 larvae that had just begun to feed. Food organisms were added simultaneously at the following densities: rotifers, 43 $liter^{-1}$; copepod nauplii, 92 $liter^{-1}$; *Cyclops bicuspidatus*, 18 $liter^{-1}$; *Daphnia pulex*, 433 $liter^{-1}$. Within one day, 83 larvae with a mean length of 9.1 mm were examined. Only fish showing feeding behaviour were sampled. None of the fish contained nauplii or rotifers in their guts.

The third test was made in two 30-liter aquaria, each containing 300 larvae that had begun to feed the previous day. Rotifers (mean length, 100 μm) were added to the tanks at densities of 159,000 $liter^{-1}$ and 107,500 $liter^{-1}$, and copepod nauplii were added at densities of 5,000 $liter^{-1}$ and 6,000 $liter^{-1}$. Seven hours after food was added, 20 fish (mean length, 9.1 mm) were examined from each tank. None contained nauplii, but 90% of the larvae contained rotifers in their guts. The average gut contained 20 rotifers.

Crustacean Zooplankton

Daphnia pulex and *Cyclops bicuspidatus* were introduced in varying proportions into eight 40-liter aquaria, each containing 20 postlarva walleyes. The proportions ranged from 2% to 99% daphnids, and the total food concentration ranged from 257 $liter^{-1}$ to 900 $liter^{-1}$. The zooplankters were size-graded between 300-μm- and 500-μm-mesh screens and ranged between 1.1 and 1.3 mm long. The fish averaged 10.1 mm long. Their stomachs were analysed after 24 hours. The linear selection index for daphnids remained close to 0.0 over the range of food proportions tested (Fig. 4, solid circles: $L = 0.005 - 0.001$ % *daphnids*; $r^2 = 0.01$; NS), indicating no differential selection for daphnids over the copepods.

The food selection of early postlarvae in the laboratory (above) was compared with food selection of juvenile walleyes in ponds. Samples of fish and zooplankton were taken simultaneously from various ponds:

Date	Zooplankton density (*N*/liter)	Daphnids (%)	Fish (*N*)	Fish length (mm)
Jun	308	91	12	19
	204	74	12	18
	281	79	9	19
Jul	64	44	6	38
	78	67	10	56
	275	68	12	54
	347	53	35	40
Aug	231	15	21	61

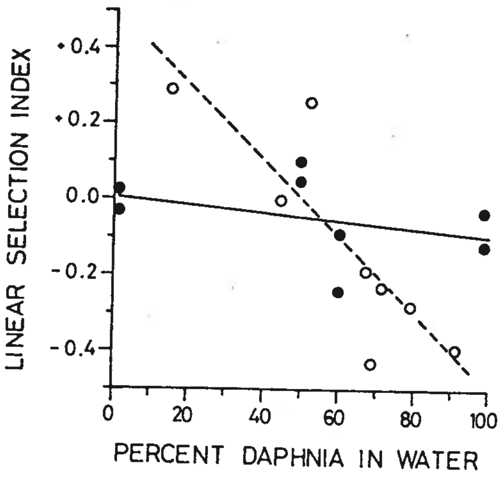

FIGURE 4.—*Selection of daphnids by young walleyes as a function of the percentage of daphnids in the water. Solid circles and solid line, laboratory tests with mixtures of* Daphnia pulex *and* Cyclops bicuspidatus. *Open circles and broken line, field samples. The linear selection index is* $L = r_i - p_i$ *where* r_i *and* p_i *are proportions of daphnids in the gut and water, respectively. Lines are least-squares regressions.*

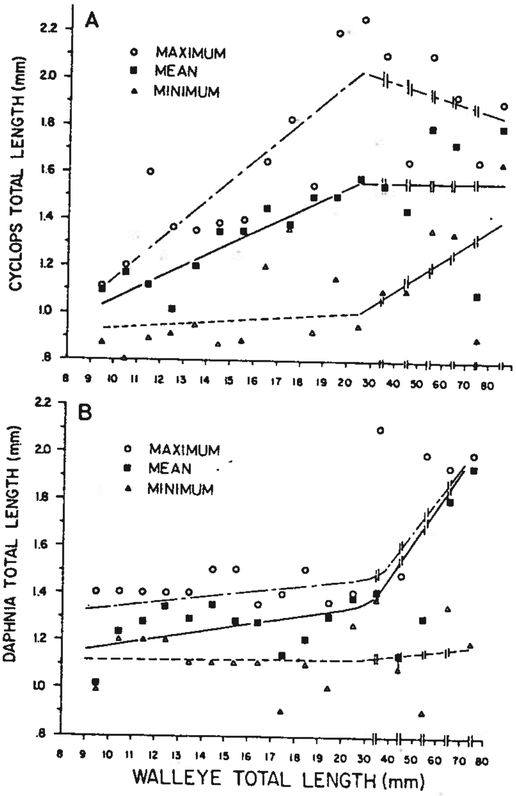

FIGURE 5.—*Relation between walleye size and the minimum, maximum, and mean sizes of zooplankton found in their stomachs. A,* Cyclops bicuspidatus; *B,* Daphnia pulex. *Data are from laboratory and pond populations of walleyes. Lines are least-squares regressions.*

Daphnia pulex and *Cyclops bicuspidatus* made up over 80% of the zooplankton biomass in all ponds. Their relative proportions in fishguts were compared to those in the ponds. The linear selection index for daphnids (Fig. 4, open circles) changed from positive when daphnids were relatively scarce, to negative when they were relatively abundant ($L = 0.484 - 0.010$ % *daphnids*; $r^2 = 0.71$; $P < 0.05$), suggesting that juvenile walleyes selected the relatively least abundant of these two prey taxa when they occurred together.

The size of crustacean zooplankton eaten by walleyes was examined in relation to fish body length. Fish were held in 100-liter holding tubs and in 170-liter observation aquaria for 2.5 months. They were fed daily with the complete size range of zooplankton taken from ponds and dugouts. *Cyclops bicuspidatus* were 0.7–2.2 mm, and *Daphnia pulex* 0.8–2.4 mm, long. Ten fish were removed from the tanks at intervals, and their total lengths and the size distributions of prey in their guts were measured. Fish larger than 20 mm were collected from ponds and treated similarly. Altogether, 187 fish were examined. The maximum, the minimum, and the mean size of prey found in the guts of the sampled fish were averaged, and plotted in relation to mean fish length (Fig. 5).

The average maximum size of *Cyclops bicuspidatus* eaten increased rapidly until fish reached the end of the postlarva stage (about 19.9 mm), after which there was no further change (see Table 1 for regression statistics). The average minimum size eaten increased slightly, but significantly, over the total range of fish sizes. The mean size of *C. bicuspidatus* eaten remained approximately intermediate between the maximum and minimum throughout the larval stage, and remained constant during the juvenile stage.

A different pattern was evident for *Daphnia pulex* prey. Despite a rapid increase in mouth size of the fish (Fig. 1), the maximum and the mean size of daphnids eaten increased slowly, showing almost no change during the larva stage. For example, at 20 mm, the fish had a

TABLE 1.—*Linear-regression statistics for body lengths of prey (dependent variable) versus those of walleyes, based on data in Fig. 5. Intercepts (prey length, mm) are extrapolations to zero walleye length. Asterisks ** denote* $P < 0.01$*; NS means not significant.*

Prey and body-length measure	Intercept	Slope	r^2
8.5-mm larval–80-mm juvenile walleyes			
Daphnia pulex			
Maximum	1.230	0.012	0.384**
Mean	1.013	0.017	0.672**
Minimum	1.109	0.001	0.000 NS
Cyclops bicuspidata			
Minimum	0.877	0.007	0.409**
8.5–19.5-mm larval walleyes			
Cyclops bicuspidata			
Maximum	0.379	0.085	0.720**
Mean	0.654	0.047	0.856**
20–70-mm juvenile walleyes			
Cyclops bicuspidata			
Maximum	2.055	−0.003	0.095 NS
Mean	1.553	0.000	0.000 NS

mouth gape of 4.02 mm and width of 2.26 mm, yet the preferred size of daphnids was only 1.35 mm (Fig. 5). The minimum size of daphnids taken did not change significantly throughout the entire range of fish size.

The preference of walleyes for smaller daphnids was tested further experimentally. *Daphnia pulex* were sorted into three size distributions (Fig. 6A) and introduced into three pairs of aquaria, each aquarium containing 12 walleyes of 20 mm mean length. The walleyes tended to choose daphnids in the range 1.1 to 1.5 mm except when this category was least abundant, or not available. Daphnids longer than 2.0 mm were rejected totally.

The selection for smaller prey sizes also was confirmed in a pond with calanoid copepods as prey (Fig. 6B). Eight fish were caught, ranging from 38 to 61 mm long. The size of calanoids in their guts was less than 1.2 mm total length, corresponding to the fraction that passed through a 210-μm-mesh screen. Larger calanoids were present in the pond (Fig. 6B), although their lengths were not measured.

Macroplankton and Benthos

Fish samples were taken from four ponds on June 12, July 23, August 23, and September 29–October 22, 1980. Fish stomach contents were examined ($N = 67$, 74, 70, and 370 for the above dates, respectively) and compared to the composition of the pond biota on the same dates with the linear selection index.

Young juveniles (54 mm long) selected *Chaoborus* sp. larvae and mayfly nymphs more strongly than crustacean zooplankton (Fig. 7), and the latter more strongly than *Gammarus lacustris*. As juveniles grew larger, however, gammarids and mayflies were selected and zooplankton became less important in the diet.

The food preferences of young juveniles were examined more closely in the laboratory. Food consisting of 100 *Chaoborus* sp., 100 *Gammarus lacustris*, and 100 *Daphnia pulex*, together and in

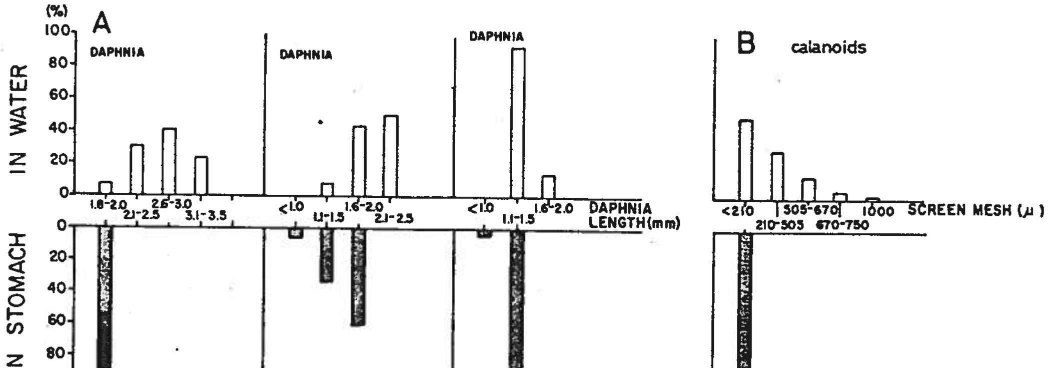

FIGURE 6.—*Size frequencies of zooplankton in the water (open bars) compared to the size frequencies of zooplankton in walleye stomachs (solid bars). A, three paired laboratory tests with different size spectra of* Daphnia pulex. *B, field observations with calanoid copepods in a hatchery pond, August 1981.*

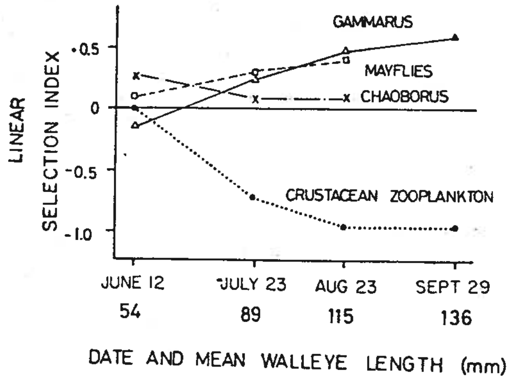

FIGURE 7.—*Selectivity of walleyes for various prey organisms in ponds in relation to time and predator size. Linear selection index is* $L = r_i - p_i$, *where* r_i *and* p_i *are proportions of each taxon in the gut and in the habitat, respectively.*

paired combinations, was introduced into a 40-liter aquarium containing 12 walleyes (34 mm mean length). Food organisms remaining in the aquarium were counted periodically. The walleyes showed very strong selection for *Chaoborus* sp. first, then daphnids, and finally gammarids (Fig. 8A). The chaoborids were consumed entirely before daphnids were considered (Fig. 8B), and gammarids were not taken while daphnids remained (Fig. 8C).

Food Consumption

Food Concentration

The dependence of food consumption by early juvenile walleyes upon food density was measured with *Daphnia pulex*. In one test, daphnids were size-graded to a mean weight of 53 μg and added to 20-liter aquaria at densities of 15, 30, 45, 60, 75, and 90 per liter. Each aquarium contained six walleyes with a mean length of 19 mm and wet weight of 74 mg. Water temperature was 21 C. The fish were allowed to feed for sufficient time to produce significant changes (20–30%) in food density. All daphnids were hand-counted into and out of aquaria. In a second test, zooplankton were hand-counted into three 20-liter aquaria at densities of 50, 100, and 200 per liter. *Daphnia pulex* (mean size, 53 μg) made up 90% of the organisms; the remainder was *Cyclops bicuspidatus*. Each aquarium contained six fish with a mean length of about 30 mm and weight of 215 mg. Water temperature was 21–22 C.

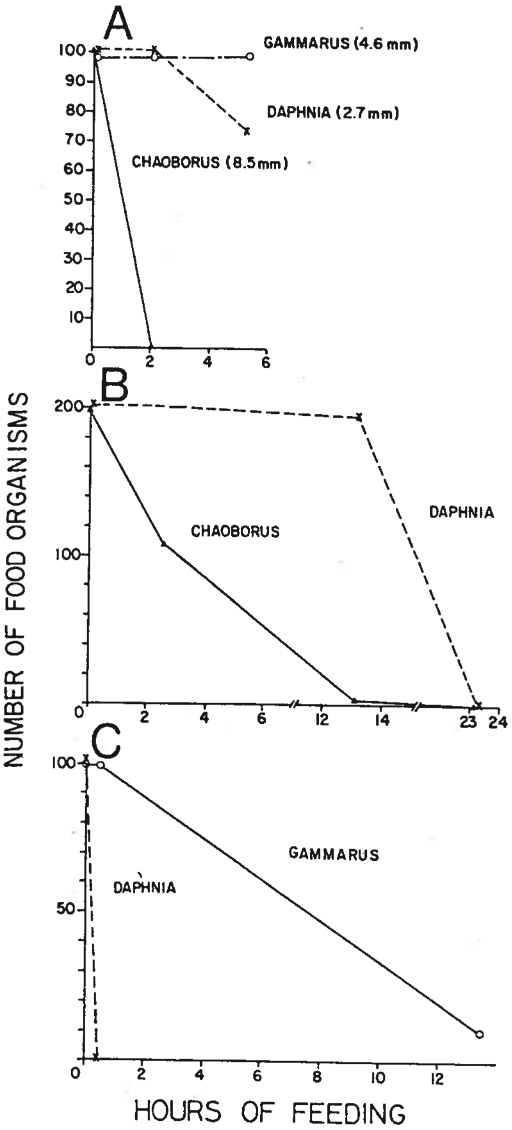

FIGURE 8.—*Prey remaining in aquaria through time during feeding by walleyes given various prey organisms simultaneously. A,* Gammarus lacustris, Daphnia pulex, *and* Chaoborus *sp.; B,* Chaoborus *sp. and* Daphnia pulex; *C,* Daphnia pulex *and* Gammarus lacustris.

The rate *Daphnia pulex* were consumed was approximately linear up to about 100 daphnids per liter, but tended towards an asymptote between 50 and 60 daphnids·fish^{-1}·hour^{-1} at higher densities (Fig. 9). Four tests in which fish were fed at 400 and 500 daphnids per liter (unpublished data) gave extremely variable results

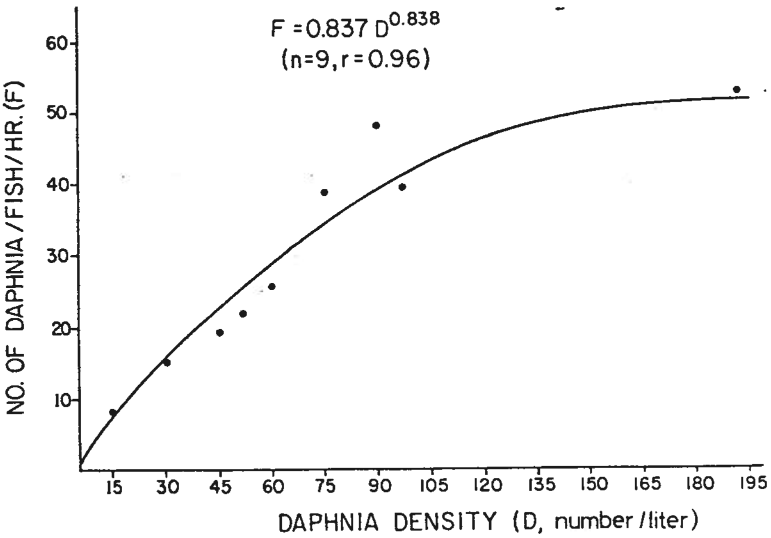

FIGURE 9.—*Relationship between walleye feeding rate and prey density.*

because daphnid counts were estimated by subsampling. Nevertheless, the mean food consumption rate in the tests was 53 daphnids·fish^{-1}·hour^{-1}, reinforcing the suggestion of an asymptote.

Food Type

The effect of food type upon walleye food consumption was measured with four test species: *Chaoborus* sp., *Daphnia pulex*, *Gammarus lacustris*, and brook stickleback. Food was introduced to 7–15 juvenile walleyes in 40 liters of water. The food items were size-graded to produce a narrow size distribution in each test, and were counted before and after the 24-hour test period. Uneaten food always remained after a test. Water temperature was 20–21 C.

The rate of food consumption (Table 2) was related to food preference (Fig. 8). The mean rates (mg·g^{-1}·hour^{-1}) were 23–24 with juvenile brook sticklebacks and *Chaoborus* sp., 8–13 with daphnids, and 4 with gammarids.

Diel Feeding Dynamics

The daily pattern of feeding activity was examined by removing samples of fish from a hatchery pond (Secchi disc transparency, 1–1.5 m) every 3 hours over a 24-hour period on July 16–17 and August 13–14, 1981. Stomach contents were examined separately for "large" fish, which had been stocked on May 20, and "small" fish, which had been stocked on June 18.

The average feeding intensity for all groups peaked at dusk and was lowest at dawn (Fig.

TABLE 2.—*The relationship between food consumption by juvenile walleyes and food type.*

Food		Walleye					Consumption (mg·g^{-1}·hour^{-1})	
Item	Mean wet weight (mg)	Number	Mean wet weight (mg)	Mean total length (mm)	Temperature (C)	Replications	Range	Mean
Chaoborus sp.	2.4	15	230	31	20	4	22–28	24
Daphnia pulex	1.3	15	265	32	21	2	12–13	13
	0.53	7	734	45	23.5	2	7–8	8
Gammarus lacustris	2.4	12	360	36	21	2	3–4	4
Brook stickleback	24	10	410	37	21	2	16–29	23

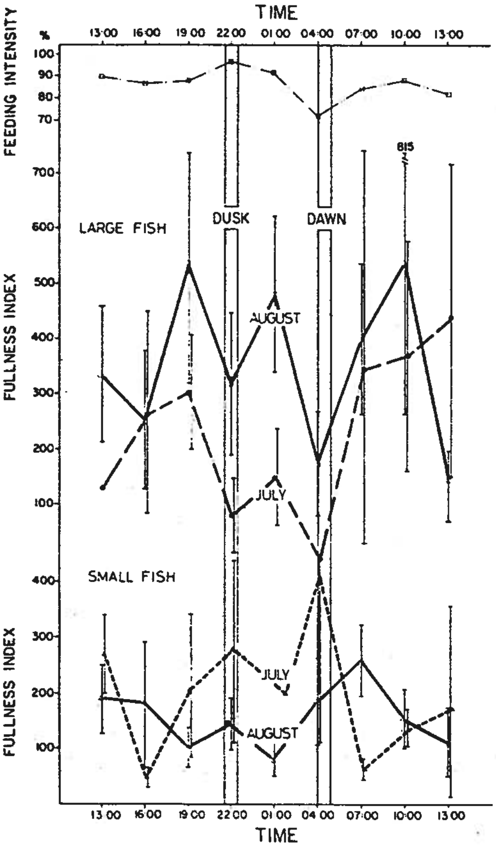

FIGURE 10.—*Diel pattern of feeding intensity and stomach fullness for walleyes in ponds. Large fish were stocked in May and sampled in July (N = 38; mean length = 74 mm) and August (N = 81; mean length = 102 mm). Small fish were stocked in June and sampled in July (N = 93; mean length = 40 mm) and August (N = 323; mean length = 75 mm). Vertical lines indicate 95% confidence limits. The average feeding intensity (percent of all fish with food in stomach) is shown for all groups combined.*

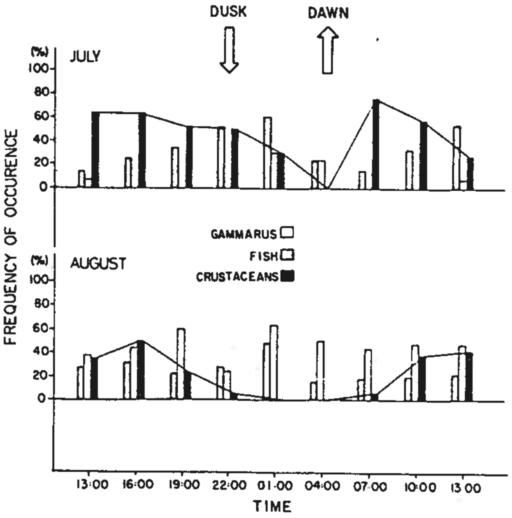

FIGURE 11.—*Diel changes in the frequency of various food organisms in walleye stomachs. "Crustaceans" refers to cladoceran and copepod zooplankton. Solid line emphasizes the change in frequency of zooplankton.*

10). Large fish had a similar feeding pattern whether they were sampled in July or in August, and the pattern was opposite from that of smaller fish. The larger fish had three distinct feeding peaks: one before dusk, one after dusk, and one at midmorning. Smaller fish also had three feeding peaks per day, but these generally coincided with the feeding "lows" of the larger fish. The diel variation in the frequency of food items found in the guts varied for different food groups (Fig. 11). Zooplankton were eaten commonly during daylight, but their occurrence in stomachs decreased during the night and became zero just before dawn. This suggests that walleyes depend upon vision when feeding on zooplankton, but also reflects the availability of alternative prey; fish and gammarids avoid walleyes more effectively during the day.

Daily Ration

The rate of digestion must be known in order to calculate daily ration. The digestion rate of early juvenile walleyes (21 mm mean length) was estimated by feeding ten of them in a 200-liter aquarium on *Cyclops bicuspidatus* until their guts were full, and then removing them to a 40-liter aquarium with filtered water at 22 C. Stomach contents could be observed in situ through the semitransparent abdomen, and the time for evacuation of visual food material was recorded for each fish. Average evacuation time was 7 hours 14 minutes (±78 minutes, 95% confidence limits). This estimate was approximate, and the test temperature was a little higher than field temperatures. However, the daily feeding dynamics also showed independently that walleyes generally have 3 meals per day, with intervals of about 6–9 hours between meals. Therefore, we believe that 7–8 hours is a reliable estimate of digestion rate for larval and juvenile walleyes, and assume that 8 hours would

TABLE 3.—*Estimated daily ration of walleyes in ponds.*

Date	Mean fish size (mm)	Temperature (C)	Fullness index	Estimated daily ration (% of body weight·day⁻¹)
Based on stomach fullness index, and 8-hour digestion rate				
1980[a]				
Jun 12	36	20.2	47.8	1.4
Jul 23	96	21.9	155.4	4.7
Aug 21	127	19.7	93.1	2.8
1981[b]				
Jul 7	71	20.0	167	5.0
Aug 10	120	19.0	170	5.1
Aug 23	138	23.0	130	3.9
Based on diel feeding dynamics				
Jul 16–17, 1981	40 74	17.8		5.8 4.8
Aug 13–14, 1981	75 102	21.4		2.2 8.2

[a] 1980 data were averaged over four ponds.

[b] 1981 data were averaged over seven ponds.

be an acceptable digestion rate to apply in the field at temperatures around 20 C.

Digestion rate was combined with pond measurements of mean stomach fullness to estimate daily ration under field conditions as a % of body weight. A second estimate of daily ration was calculated from the diel feeding dynamics (Fig. 10) by summing the positive changes in stomach fullness measured over 24 hours. Both approaches gave similar results (Table 3), which suggest that the daily ration of walleyes ranges between 1.4 and 8.2% of body weight per day, and averages 4.4% per day.

Discussion

Feeding and Food Selection

Our observations on feeding morphology and behaviour indicate that from the time of first feeding, walleyes are selective "strike" feeders, similar to esocids, rather than "pump" feeders like silver carp *Hypophthalmicthys molitrix* or "collectors" like suckers *Catostomus* spp. Their feeding success depends upon vision and their ability to pursue and catch prey, as well as on the prey's size and ability to escape.

Controversy exists concerning the feeding of walleyes on rotifers. Smith and Moyle (1945) reported that walleye fry in Minnesota rearing ponds began feeding on rotifers and nauplii, and Johnson (1969) also reported rotifers in the stomach of newly hatched walleyes in Little Culfoot Sioux Lakes, Minnesota. But Bulkley et al. (1976) reported that cladocerans and copepods were the initial food of walleye fry in Clear Lake, Iowa, and no rotifers and few copepod nauplii were found in fish stomachs even though they were abundant in the lake.

We think that under normal conditions, rotifers and nauplii are too small for walleye larvae to see and catch. In the one test where rotifers were consumed by walleye, the experimental density of rotifers was about six hundred times higher than average pond densities (our unpublished data), and fifty times higher than the maximum density we observed throughout the summer in any of our ponds. Although 90% of the fish in this test contained rotifers, an absence of searching or seizing behaviour by the fish suggests that rotifers were merely inhaled with the respiratory current. In all cases of walleyes feeding on zooplankton or larger food items, predatory behaviour was always observed.

Except for cohort-cannibalism (Li and Mathias 1982, this issue), postlarval walleyes restricted their feeding almost entirely to planktonic crustaceans. Within this food category there is also a trend towards consumption of the smallest crustaceans (Figs. 5 and 6). Three general concepts have been used to explain this type of food selection.

(1) Morphology-limited feeding. Size-selective predation by planktivorous fish occurs within the morphological limits set by mouth size and gill raker spacing (Wankowsky 1979). We have shown that the mouth size of 10-mm postlarvae is only slightly larger (1.8 mm gape, 0.9 mm width) than the total length of preferred zooplankton (1.2 mm). This hypothesis might, therefore, explain the prey selectivity of postlarval walleyes. Indeed, the rate of increase in mouth width as walleyes grow from 10 mm to 20 mm (Fig. 1) coincides with the rate of increase in the average maximum size of cyclopoids taken as prey (Fig. 5A). However, this hypothesis does not explain why the preferred size of *Daphnia pulex* varies only slightly within the range of fish length from 8 to 30 mm. Some further explanation must be given for cladocerans.

(3) Attack ability of the planktivore and eva-

sion ability of the zooplankter. These abilities modify the outcome of a predator–prey encounter (O'Brien 1979). Our observations of postlarvae feeding on 1.2-mm daphnids show a capture-success rate less than 5%. The limited swimming speed and food-capture ability of walleye postlarvae might account for the selection of small zooplankters, but this hypothesis does not apply to juveniles, because at a length of only 30 mm, they already are capable of catching small fish larvae.

(3) Prey selection influenced by predator experience. Brooks (1968) found that a planktivore may continue to select small prey even after a larger prey type becomes more abundant. Hansen and Wahl (1981), summarizing previous work, suggested that prior experience might induce continued utilization of smaller, more familiar prey size classes even though the predator's morphological capability to consume larger prey sizes increased with growth. Although experience may modify the food preference of walleyes for small zooplankton over a short time, it does not explain the phenomenon during the change from postlarva to juvenile. For example, we observed that 25-mm juveniles that previously had been exposed only to crustacean zooplanktors could switch very rapidly and completely to *Chaoborus* sp. when these were available. In these experiments (Fig. 8), *Daphnia pulex* were not consumed until all chaoborids were eaten, yet smaller daphnids still were preferred over larger ones. Several observations of 30-mm walleye feeding on large daphnids (2.2 mm) suggested that walleyes experience difficulty handling this prey in the mouth. Frequently, a fish, after seizing a large daphnid, opened and closed its mouth and opercula rapidly until the zooplankter was expelled. Apart from these scant observations, the reason young walleyes select smaller crustaceans remains unresolved.

As walleyes grow from postlarvae to juveniles, their prey-capture ability becomes much stronger and they shift from smaller, slower prey to larger, faster organisms. In contrast to postlarvae, for which selection may be restricted by morphological considerations and swimming speed, juveniles in ponds show a remarkable change in food selectivity, shifting from zooplankton to chaoborids and mayflies, and finally to gammarids and forage fish as they grow. The significance of this shift in the trophic niche is related to the productivity at each level of the pond food chain. The decrease in yield from walleye rearing ponds that becomes evident after midsummer (Li and Ayles 1981) has, in addition to other causes, a fundamental ecological basis, namely an increase in the length and complexity of the food chain that leads to walleye.

Food Consumption

The rate of food consumption by walleyes is a function of several factors, of which we have data on food density and food preference. Swenson (1977) found that the rate of food consumption of 180-g walleyes was proportional to food density up to about 0.4 g food$\cdot$m^{-3}, and was roughly constant above 0.8 g food$\cdot$m^{-3}. For walleyes that were more than three orders of magnitude smaller (0.074 g, this study), the proportionality continued up to a food density of 5.3 g food$\cdot$m^{-3} and was roughly constant above 10 g food$\cdot$m^{-3}; the density allowing maximum food consumption was roughly an order of magnitude higher for small fish. The maximum food consumption rate of the smaller fish was more than an order of magnitude higher, about 850 mg$\cdot$g$^{-1}\cdot$day^{-1} compared to 30 mg$\cdot$g$^{-1}\cdot$day^{-1} for the larger fish studied by Swenson.

The maximum feeding rate of the smallest juvenile walleyes (0.074 g) was equivalent to a daily ration of 85% of body weight per day. This is consistent with the daily ration we measured for slightly larger fish, also feeding on daphnids (58%$\cdot$day^{-1} for 0.23 g fish, and 31%$\cdot$day^{-1} for 0.26 g fish, Table 2). The reason for these high estimates of daily ration is not yet clear, but the explanation may lie in the extremely low efficiency of assimilation; at the high feeding rates we measured, most daphnids were minimally digested. After passing through the fish gut, many daphnids remained intact, though crumpled, with some "blurring" (presumably dissolution) of the internal organs. Our results emphasize the danger of equating daily ration with daily food consumption, unless the efficiency of assimilation is known. They also suggest that small fish can exert a powerful influence on the zooplankton community in relation to their biomass.

In the estimation of feeding rates for fishes, the influence of food preference rarely is taken into account. Nevertheless, we found that the short-term feeding rates (6–24 hours) of juvenile walleyes were strongly related to food preference. Food consumption rates for chaoborids, brook sticklebacks, daphnids, and gammarids were 24, 23, 8–13, and 4 mg food per g walleye per hour, respectively, and each food item in the above list was not eaten until the one preceding it was totally consumed (Fig. 8). The importance of food preference to feeding rate may have some significance in pond culture, where some control may be exerted over the composition of the prey community.

Our study indicated walleyes have a diel feeding rhythm with three feeding peaks, the two major ones being in late evening and midmorning for larger juveniles. A third feeding peak takes place just after dusk. Both stomach fullness and feeding intensity drop to their lowest levels around 0400 hours. A small group of large fish in a pond caused a temporal shift in feeding by smaller fish.

Bailey and Harrison (1945), Reed (1962), Swenson and Smith (1973), and Swenson (1977) reported walleye feeding periodicity in Clear Lake, Iowa, the Saskatchewan River, Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. In contrast to our results, walleyes in these studies fed mainly from evening to early morning. For example, according to Swenson and Smith (1973), the food consumption rate at midday was about half that at night under low light conditions in Lake of the Woods. But Ryder (1977) has found that walleyes feed during the day in turbid lakes and that the optimum for feeding occurs when a surface light intensity of 1,500 lux is reached. He thought that the rate of change of illumination was critical once suitably low light levels were reached. Swenson (1977) reported midday feeding was greatest during June and September when walleyes ate more demersal prey, and thought food consumption could be limited by high light intensity. Li et al. (1980) noted that change of illumination might be a stimulus affecting fish feeding directly, and also indirectly by altering water temperature and dissolved oxygen.

We interpret the contrast between our results and those of other studies to be due to differences in light levels. Although our ponds were shallow, light transparency was very reduced and Secchi depths ranged from 1.0 to 1.5 m during feeding studies. This freed the walleyes from light constraints and the periodic feeding rhythm largely was unrelated to diel light conditions. Lower light intensity at night did, however, reduce visibility, and walleyes were not able to feed upon crustacean zooplankton at that time.

The strong interaction between walleyes of different size groups in the same pond is probably a result of predation. From the relative representation of the two groups in seine hauls, we estimated the group of large fish constituted only 5% of the total walleye population, yet they not only caused a phase change in the temporal feeding pattern of small fish, but also probably suppressed feeding by small fish to a significant degree. In August, the mean daily stomach fullness index of large fish was 353, whereas that of small fish was only 156. In July, the corresponding difference was 233 compared to 197. This result suggests that periodic size-grading in walleye ponds may be a useful means for achieving higher overall fish production.

Piscivorous behaviour of walleyes begins with cohort-cannibalism (feeding upon like-size siblings: Li and Mathias 1982, this issue) from 6 to 7 days after hatching until the end of postlarva stage II at about 16 days. The frequency of cohort-cannibalism during this time depends on the density of fish, their age, and the degree of starvation (Li and Mathias 1982, this issue). Cohort-cannibalism may cease after the larva stage (16–18 days) when the fish are about 19 mm long, but from this size until about 30 mm the fish are difficult to capture in lakes and ponds, and no data exist on piscivorous behaviour.

We observed piscivory in ponds when walleyes were 34 mm long. The prey were brook stickleback larvae. Smith and Pycha (1960) found that walleyes did not start to feed on yellow perch *Perca flavescans* until they were over 50 mm in Red Lake, Minnesota. Walker and Applegate (1976) reported that 62 mm was the size at which walleyes began to feed on fathead minnows *Pimephales promelas*. Smith and Moyle (1945) reported that 60–80 mm walleyes began to eat fish in ponds. Li and Ayles (1981) reported that piscivory by walleyes could be delayed until 100 mm if abundant, alternative food was available in ponds. Piscivory by walleyes probably is related less to walleye size than to the abundance of prey fish in a suitable size range (up to 50% of predator length) and the relative abundance of alternative food.

Cannibalism among juveniles also was first observed in our ponds at a walleye length of 34 mm. We believe it normally does not occur during the juvenile stage until the fish reach a length of 30 mm, because until then there is not sufficient size differentiation within the cohort. In our ponds in July, the frequency of piscivory by 60–88 mm walleyes was 94%, whereas the frequency of cannibalism was 7%. Among smaller fish (27–51 mm), 18% were piscivorous and none were cannibalistic. In August, the frequency of piscivory by 80–148 mm walleyes was 68% and that for cannibalism was 6%; among smaller fish (39–75 mm), 9% were piscivorous and none were cannibalistic. In lakes, the incidence of cannibalism is lower than this. Chevalier (1973) noted that in Oneida Lake the cannibalism rate for adult fish ranged from 4.4% in summer to 0.9% in winter. Rawson (1957) found a 0.1% rate in Lac La Ronge, and Eschmeyer (1950) reported a 2.2% rate in several Michigan waters. Although these rates are low, they may be important because they are instantaneous rates and may operate over long periods of time.

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