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POPULATION DYNAMICS AND EARLY LIFE HISTORY OF MUSKEGON RIVER WALLEYES

By

Robert Marshall Day

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ABSTRACT

POPULATION DYNAMICS AND EARLY LIFE HISTORY OF MUSKEGON RIVER WALLEYES

By

Robert Marshall Day

Spawning walleye populations in the Muskegon River declined from an estimated peak of 139,000 in 1953 to 2500 in 1975. The Michigan Department of Natural Resources initiated a stocking program in 1978 and the spawning population has increased to an estimated 43,000 fish in 1986.

Walleyes tagged in the 1940's and 1950's were more likely to leave the Muskegon River system and ranged farther than walleyes tagged in 1986-87. Fecundity estimates from Muskegon walleyes captured in 1986-87 were usually greater than estimates reported for other populations but were not statistically different from Muskegon walleyes captured in 1947. Average back calculated lengths and weights of Muskegon River walleyes were generally larger at each age than lengths and weights of walleyes from other systems.

Recruitment problems were probably not due to egg survival or hatching success. Potential impacts of alewife and gizzard shad on walleye recruitment are also discussed.

ACKNOWLEDGEMENTS

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INTRODUCTION

Walleye (*Stizostedion vitreum*) populations in Lake Michigan have undergone dramatic changes in the past century. Spawning runs of walleye in the Muskegon River may have been unique indicators of the relative size of walleye populations throughout eastern Lake Michigan because walleyes from the entire eastern coast of Lake Michigan were thought to "home" to this river system (Eschmeyer 1950, Eschmeyer and Crowe 1955, Crowe 1955). The status of this valuable species has been monitored since the late 1920's primarily by observing Muskegon River spawning runs.

Schneider and Leach (1979) speculate that historically, minor populations of walleye were found along the eastern shore of Lake Michigan often associated with river mouths. These populations were at a low in the early 1900's possibly due to the destruction of spawning areas caused by extensive lumbering operations. Walleye stocks increased in the early 1900's after the Newaygo Dam was built on the Muskegon River. The dam served to retain sediment bedloads and improve spawning areas downstream (Schneider and Leach 1979).

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Michigan's Department of Conservation began the Newaygo transfer in 1923 in an effort to improve walleye fishing in the upstream impoundments. The goal of the Newaygo transfer was to capture spawning walleyes below Newaygo Dan and move them to upstream impoundments. Tags were placed on walleyes captured during the Newaygo transfer with the primary focus being to determine movements of walleyes transferred to upstream impoundments (Eschmeyer and Crowe 1955). However, anglers returned tags from walleyes recaptured along the entire east coast of Lake Michigan. Walleyes were captured as far south as Porter Beach, Indiana (approximately 114 miles [183 km] from the mouth of the Muskegon River) and as far north as Good Harbor Bay, approximately 85 miles (137 km) from the mouth of the Muskegon River (Eschmeyer and Crowe 1955). Using this information, Crowe (1955) deduced that walleyes were homing to the Muskegon River to spawn then dispersing widely after spawning was completed. He stated that no walleyes tagged during Muskegon River spawning runs were ever captured outside of the system during spawning season and cited recaptures from Muskegon River spawning runs as indirect evidence for homing to the Muskegon River spawning grounds.

Schneider and Leach (1979) used the absolute number of walleyes captured at the Newaygo transfer to track population trends and determined that walleye populations fluctuated greatly between the late 1920's and the late

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1950's with the largest spawning run occurring in 1933. However, Crowe (1955) estimated that peak walleye runs of 114,000 and 139,000 occurred in 1953 and 1954, respectively.

Using commercial fishing records and Newaygo transfer data, Schneider and Leach (1979) hypothesize that peak populations were supported by strong year classes that appeared to have been produced when adult populations were low and in an approximate 10 year cycle. The spawning population began to decline after strong year classes anticipated in the 1950's did not occur. The Newaygo transfer was discontinued in 1966 due to poor spawning runs and by 1975 the run was estimated to be 2,500 fish (MDNR, Fish. Div., unpublished data). During the years of decline, walleye runs were dominated by larger fish, indicating that recruitment problems caused by poor survival of eggs, larvae or juveniles were probably more important to the demise of the population than was over exploitation or sea lamprey (Petromyzon marinus) predation (Schneider and Leach 1979).

Schneider and Leach (1979) contend that the most likely cause of the decline in recruitment was the introduction and abundance of exotic species. The exotic species of primary concern was the alewife (Alosa pseudoharengus), but gizzard shad (Dorosoma cepedanium) and smelt (Osmerus mordax) also may have contributed to the decline in recruitment. Schneider and Leach (1979) note that larval walleyes drift down to rearing areas in Muskegon Lake and that large popu

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populations of alewives inhabit Muskegon Lake from late spring to early summer. Recruitment was suppressed when alewives and to a lesser extend gizzard shad and smelt preyed upon or competed directly with Young-of-the-Year (YOY) walleyes.

In 1978 the Michigan Department of Natural Resources (MDNR) initiated a program to increase spawning stocks of walleye spawning in the Muskegon River. Adult walleyes were captured during spawning runs and eggs were stripped, fertilized and hatched artificially. The larval walleye were raised in ponds and later planted in the Muskegon River, Muskegon Lake or other suitable areas around the state. Since the start of the program the population has increased substantially although not to the peak levels reported in the early 1950's.

The primary goal of this study was to document any biological or behavioral differences between present populations and walleye populations observed in the 1940's and 1950's. One of the major differences is that the majority of the adult population remains in the Muskegon River system for most of the year as opposed to leaving the river system for Lake Michigan or other tributaries.

Another goal of this project was to evaluate some of the factors affecting the survival of larval and juvenile walleyes. A substantial number of larval walleyes was collected as the larvae drifted down the Muskegon River.

However, juvenile walleyes were scarce and it seems that recruitment problems occur after walleyes leave the spawning areas.

Description of the Area

The Muskegon River flows in a southwesterly direction from its origin in Higgins and Houghton lakes (Figure 1). The river is approximately 230 miles (370 km) long and the average rate of fall is 2.5 feet per mile (0.47 m/km) with the greatest rate of fall equaling about 4.4 feet per mile (1.34 m/km) in the 70 miles (113 km) upstream of Newaygo, Michigan. Until 1969 the Muskegon River flowed through a series of five impoundments before entering Muskegon Lake, then Lake Michigan, in Muskegon County, Michigan. The Newaygo Dam at Newaygo, Michigan was the farthest downstream impoundment and was 39 miles (63 Km) from the mouth. When the Newaygo Dam was removed in 1969, Croton Dam, 51 miles (82 km) from the mouth, became the first impasse to any fish moving up the river.

The Muskegon River watershed is 2,634 square miles (6,822 km^2) and is the second largest watershed in Michigan. Soil types range from well drained sandy soils to poorly drained mucks but the watershed is dominated by highly permeable sandy soils. The basin is also characterized by undisturbed woodlands with more than 65% of the area being wooded (Wuycheck 1987).

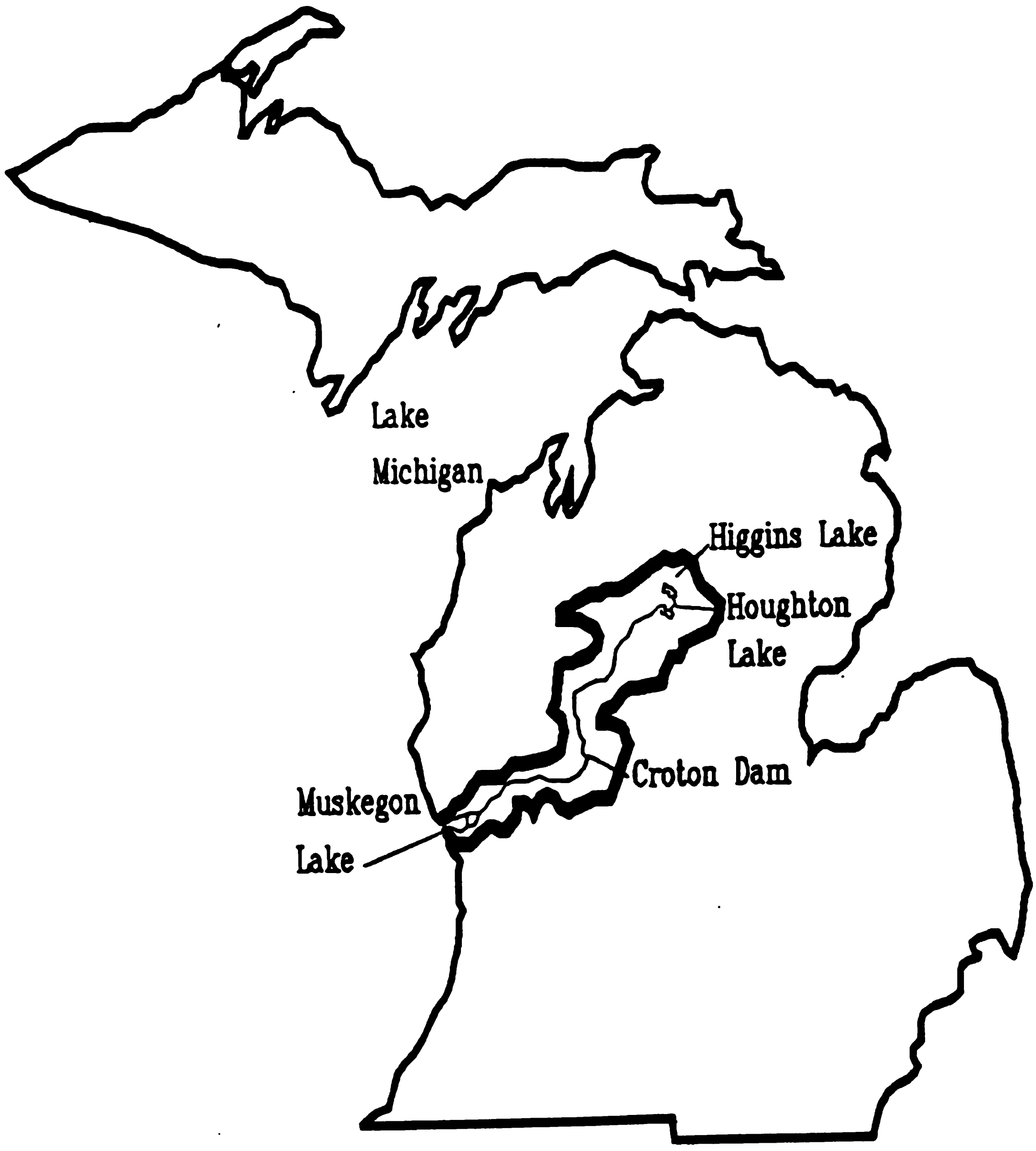

Figure 1. Location of the Muskegon River and the watershed.

The Muskegon River splits into the North Branch and Middle Branch approximately 6.5 miles (10.4 km) upstream of Muskegon Lake and the South Branch of the Muskegon River splits from the Middle Branch approximately 2 miles (3.2 km) upstream of Muskegon Lake (Figure 2). There are extensive wetlands located between the North and Middle branches of the Muskegon River and between the Middle and South branches of the Muskegon River.

Muskegon Lake has a surface area of 4,150 acres (1,680 hectares) and an average and maximum depth of 23 feet (7.1 m) and 69 feet (21 m), respectively The volume of the lake is 97.5 acre ft (12.03 x 10^7 m^3) and the mean hydraulic retention time is about 23 days (U.S.EPA 1975). Muskegon Lake was classified as hypereutrophic with nuisance algal blooms and extensive macrophyte growth, before diversion of industrial and municipal discharges in 1973 (Wuycheck 1987). Recent water quality data indicate mesotrophic to eutrophic conditions with dissolved oxygen depletion occurring during summer stratification (MDNR, Land and Water Mgmt. Div., unpublished data).

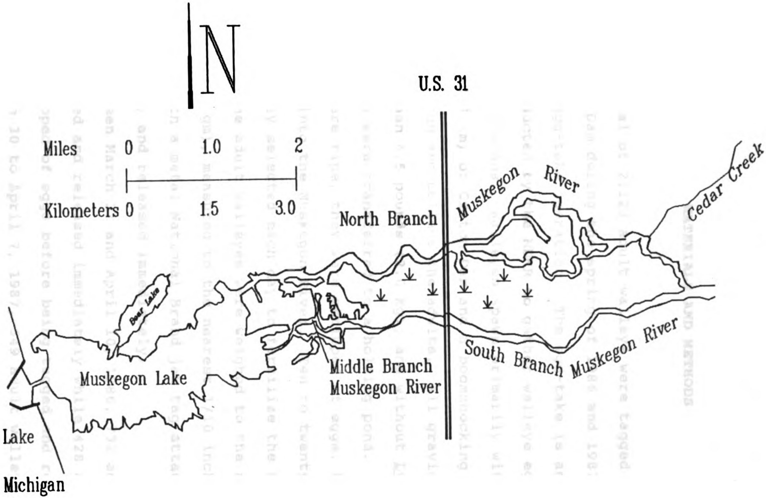

Figure 2. The North, Middle and South branches of the Muskegon River near the mouth at Lake Michigan.

MATERIALS AND METHODS

A total of 2,123 adult walleye were tagged and released at Croton Dam during the spring of 1986 and 1987 as part of the MDNR egg-take operation. The egg-take is an annual event conducted by the MDNR to gather walleye eggs for their hatchery programs. Walleyes spawn primarily within 0.5 miles (0.8 km) of Croton Dam and a boomshocking unit was used to stun and collect the adults. All gravid females greater than 4.5 pounds (2.0 kg), and without Lymphocystis infections were transferred to a holding pond. When the females were ripe, they were stripped of eggs, tagged and released into the Muskegon River. Ten to twenty males were arbitrarily selected each day to fertilize the eggs. The rest of the adult walleyes were weighed to the nearest 1/10 pound (45 gm), measured to the nearest 1/10 inch (2.5 mm), tagged with a metal National Brand jaw tag attached to the lower jaw, and released immediately.

Between March 31 and April 10, 1986, 732 adult walleyes were tagged and released immediately while 428 adult females were stripped of eggs before being tagged and released. From March 30 to April 7, 1987, 549 adult walleyes were tagged and released immediately and 358 adult females were stripped of eggs before being tagged and released. Also, 56 males were tagged and kept for milt before being released.

In 1986 all but twelve of the 1,160 walleyes tagged were larger than Michigan's 15 inch (38 cm) minimum size limit. The smallest walleye tagged was a 12.8 inch (32.5 cm), 0.7 pound (0.32 Kg) male while the largest fish tagged was a 31.2 inch (79.2 cm), 13.0 pound (5.90 Kg) female. The average length and weight of male walleyes tagged in 1986 was 19.7 inches (50.0 cm) and 3.0 pounds (1.4 Kg) while the average length and weight of all female walleyes tagged was 25.2 inches (64.0 cm) and 7.1 pounds (3.2 Kg).

In 1987 all but twenty of the 963 walleyes tagged were larger than 15 inches (38 cm). They ranged in size from a 13.0 inch (33.0 cm), 0.6 pound (1.1 kg) immature fish to a 30.2 inch (76.7), 10.0 pound (4.5 kg) spent female. The average length of males and females tagged in 1987 was 20.7 inches (52.6 cm), 3.2 pounds (1.5 kg) and 25.4 inches (64.5 cm) and 6.3 pounds (2.9 kg), respectively.

Since the largest walleyes tend to be female and the largest females usually yield the most eggs, the larger fish were more actively pursued than smaller fish. Therefore, the average size of tagged walleyes from both years is probably not representative of the average male and female walleyes in the spawning population.

A $3.00 reward was offered for each tag to encourage anglers to return tags. The program was initiated and advertised by MDNR and the Muskegon Sportsfishing Association. During the 1986 and 1987 walleye seasons, bulletins were posted at each public access site from Croton Dam down to and including Muskegon Lake (Appendix 1). Bulletins were taken to bait and tackle shops, marinas and to the headquarters of both state parks in the Muskegon area. Also, bulletins were posted at public access sites along the Grand and White rivers.

Determination of spawning run sex ratios was not made for two reasons. First, selecting the largest fish would bias sex ratio estimates toward females. Second, the sampling strategy would cause the estimated sex ratio to be biased by behavioral differences between the sexes. Based on observations of recaptures of fish tagged earlier in the spawning run it appears that at Croton Dam the males may stay on the spawning grounds longer than females possibly because females tend to spawn in one or two days while males remain ripe several days longer (Priegel 1970, Eschmeyer 1950). If males remain in the spawning area longer, the probability of capturing males would be higher than the probability of capturing females.

Scales were collected from 1,139 walleyes captured in 1986 and from 349 walleyes captured in 1987. A number of scales were removed with a dull knife from an area above the lateral line and between the spinous and soft dorsal fins. The age of each fish was determined by placing the scales on a microfiche reader, at 22X magnification, and counting annuli including the outside edge of the scale. Measurements were taken from the focus to each annulus on one scale from each fish. Measurements of the total scale radius were made on as many as eight scales from each fish depending on the number of readable scales available. An average total scale radius was then calculated for each fish.

In 1986 ovaries were taken from 15 green females and 22 ovaries were collected from walleyes captured in 1987. These females ranged in size from 28.0 inches (71.1 cm), and 10.7 pounds (4.9 kg) to 19.6 inches (48.5 cm) and 4.1 pounds (1.9 kg). The ovaries were removed, wrapped in cheesecloth and preserved in a 15% formaldehyde solution. The total number of eggs in each pair of ovaries was determined using a water displacement method described by Brazo (1973). First the total volume of each pair of ovaries was determined by measuring the total volume of ovaries and water and subtracting the known amount of water. Next the ovarian tissue was separated from the eggs and the volume of tissue was determined in the same manner. The volume of ovarian tissue was subtracted from the total volume of the ovaries so that the net difference equaled the volume of the eggs. Ovaries from two walleye were then arbitrarily selected and egg counts were made on ten, 1.0 ml and 5.0 ml aliquots from each set of ovaries. An average and variance were calculated and used with alpha=0.05 and precision (D)= 0.05 (D=precision or standard error expressed as a percentage of the mean) to estimate the number of subsamples needed. Egg counts were made on seven 5.0 ml aliquots on all other sets of ovaries. Estimates of the total number of eggs per walleye could then be determined by the proportion of the average number of eggs per 5.0 ml and the total volume of eggs. Ninety-five percent confidence intervals were calculated and fecundity was related to total length and weight of the walleye.

Larval walleye sampling occurred on April 26 and 27, May 3, and May 9, 1986 at six sites in the Muskegon River between Croton Dam and Maple Island (Figure 3). Sampling was conducted during the day with two drift nets tied to a boat anchored in the river. Each net had a square opening measuring 40 cm on a side and the mesh size was 363 micrometers. One of the nets had floats attached to the top so that it would stay on the surface while the other net was weighted to stay near the bottom. The harness rope for the bottom net was scaled so that the distance from the boat to the net could be recorded and a davit was used to measure the angle between the rope and a line perpendicular to the surface of the water. The depth of the bottom net was calculated using the length of harness rope and the cosine of the measured angle.

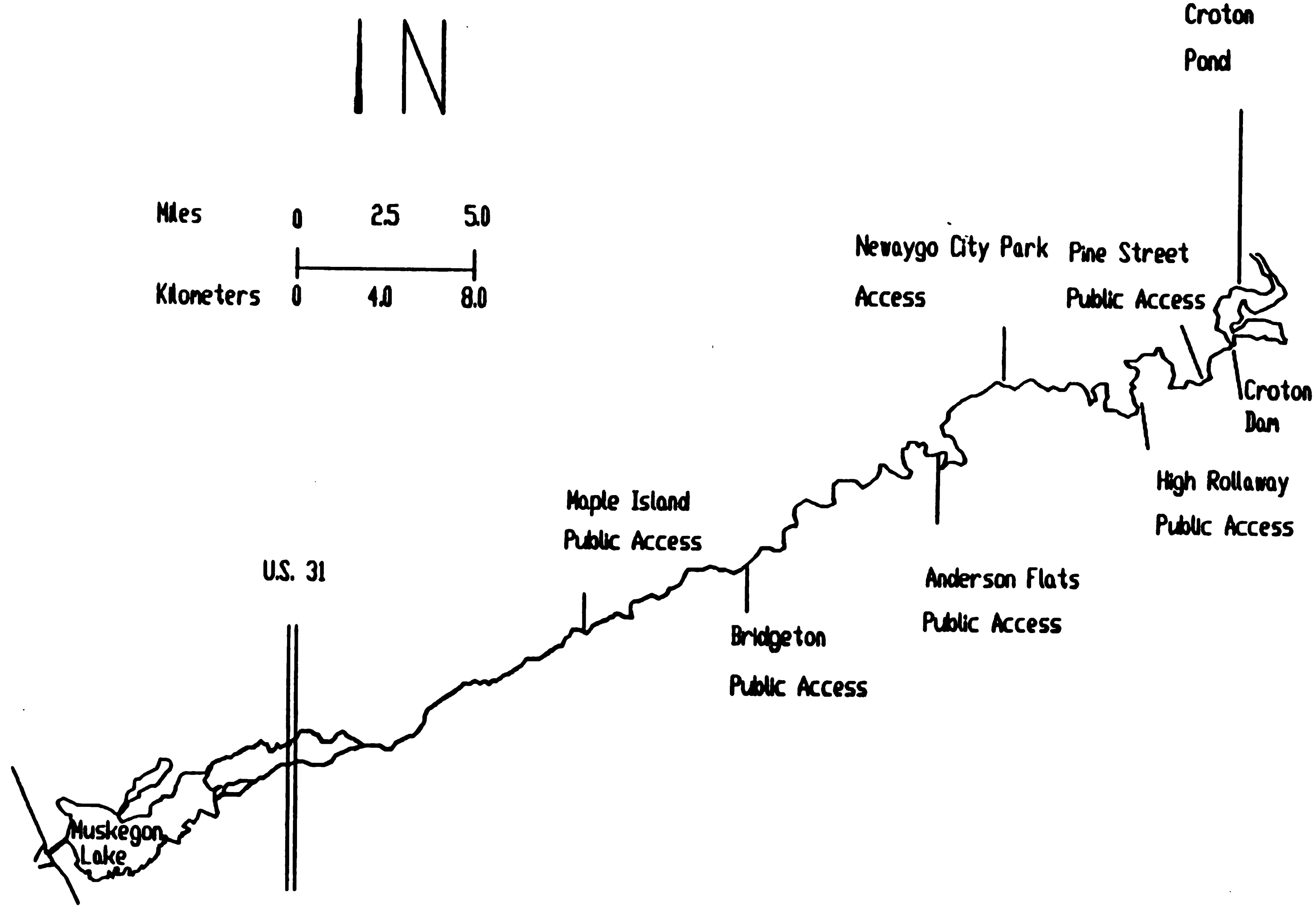

Figure 3. Location of larval fish sampling sites.

The nets were placed in the current for approximately 10 minutes and had flow meters attached to the front so that the volume of water entering the net could be calculated. Larval walleye densities were calculated using the total number of larvae captured and the volume of water filtered.

Juvenile walleye sampling started in mid-April and lasted until late November of 1986. Efforts were concentrated in, but not limited to, Muskegon Lake and the lower river system from U.S. 31 eastward. Starting in May, a boat shocker and beach seine were used to sample backwater areas of the Muskegon River as well as littoral areas of Muskegon Lake. In June, a two-meter diameter drift net was tied to a boat anchored in the lower Muskegon River in an attempt to catch juvenile walleyes as they moved to the lake. A number of juvenile white suckers (Catostomus commersonii) drifted into the net; however, no walleyes were captured. This method was discontinued because large amounts of sand drifted into the net making retrieval difficult.

Beginning in June, small mesh trap nets were used along with electroshocking and seining. The trap nets had 50-foot leads and 1/4-inch bar mesh and were fished 4 days a week, without bait, until mid-September. Typically the nets were set on Monday, left in place for 48 hours, moved on Wednesday and then pulled out on Friday. The pots were checked and all fish removed every 24 hours. All fish were measured and a subsample was preserved for stomach content analysis or for classroom work.

Adult brown bullheads (Ictalurus nebulosus) and bowfin (Amia calva) were commonly caught in the trap nets and were found to feed heavily on other small fish in the nets. Therefore, stomachs were removed from these species and preserved in 10% formaldehyde. Gizzard shad and alewife also were collected for stomach samples in an effort to document suspected predation or competition with larval and juvenile walleyes. Gizzard shad stomachs were removed in the field and preserved in 10% formaldehyde while alewife were preserved in 10% formaldehyde and the stomachs removed in the laboratory. All organisms were identified using the keys of Eddy and Underhill (1978), Scott and Crossman (1973), Pennak (1978) and Merritt and Cummins (1984).

In August, a 16-foot bottom trawl was used in Muskegon Lake. Initially it was felt that trawling would not be effective due to the history of Muskegon Lake as a timber holding area and the potential for a large number of snags on the bottom of the lake. However, a series of trawls were conducted on Muskegon Lake, at carefully selected sites, on five occasions between August and November. Four of these trawls were done at night while the first trawl was done during the day.

RESULTS AND DISCUSSION

Angler Returns

Anglers returned 89 jaw tags (7.7%) during the 1986 fishing season while an additional twelve tags were taken from walleyes tagged during the 1986 spawning run and recaptured during the 1987 fishing season. The two year total of tag returns from walleyes captured in 1986 was 103 (8.9%) including two tags that came from walleyes that were found dead in 1986. Anglers returned 52 tags (5.4%) from walleyes captured during the 1987 spawning run including one from a walleye found dead.

Anglers returned a disproportionately smaller number of tags from walleyes kept for eggs than from walleye tagged and released immediately. In 1986, seven tags were returned from the 428 walleyes kept for eggs (1.6%) while 82 tags were returned from the 732 walleyes released immediately after tagging (11.2%). During the 1987 fishing season anglers returned one tag (0.2%) from fish kept for eggs in 1986 and eleven (1.5%) tags from fish tagged in 1986 and released immediately. The two-year total percentage of tags returned from fish tagged and released immediately in 1986 was 12.7% while there was a 1.9% return of fish held for eggs.

The same trend appears in returns from walleyes tagged in 1987. Anglers returned 47 tags from the 549 walleyes released immediately after tagging (8.6%) while returning four tags from the 414 walleyes held for eggs or milt (1.0%). The difference in these percentages of tag returns suggests that the mortality of walleyes kept for eggs was higher than the mortality of walleyes tagged and released immediately.

Population Estimates

A total of 988 walleyes were captured and inspected for tags during the 1987 egg-take. Twelve of these fish were tagged in 1986. The following adjusted Peterson formula was used to calculate a 1986 population estimate and 95% confidence interval (Everhart and Youngs 1981):

$$N = (M+1)*(C+1)/(R+1) \pm 1.96*((N^2*(C-R))/(C+1)*(R+1))^{1/2}$$

Where:

N = population estimate
M = Number of marked fish (1,160 fish marked and released minus 91 tags returned by anglers = 1,069)
C = 988 fish captured in 1987
R = 12 fish recaptured at the egg-take in 1987

N = 81,402 +/- 43,959

This population estimate may be biased since at least two and possibly three assumptions of mark-recapture studies were violated. One assumption is that there was no differential mortality between marked and unmarked fish.

Olson (1958) felt that no differential mortality occurred due to handling and marking (with fin clips) walleyes in Many Points Lake, Minnesota. Although there may not have been differential mortality of Muskegon walleyes tagged and released immediately, it is likely that walleyes kept for eggs or milt suffered higher mortality.

In order to compensate for what appears to be differential mortality based on treatment at Croton Dam all marks and recaptures associated with those fish kept for eggs were disregarded. A new population estimate was calculated based on the following numbers.

M = 1,160 marked - 428 kept for eggs - 84 tags returned by anglers = 648
C = 988
R = 10 walleye recaptured that were not kept for eggs

N = 58,351 +/- 34,290

Another assumption is that there is no recruitment diluting the proportion of tagged to untagged fish in the population which would cause the population estimate to be inflated. Ideally only 1986 age IV fish and older would have been counted as marks and only 1987 age V fish and older counted as census fish. This would have eliminated all of the recruitment except for immature 1986 age IV fish that became mature 1987 age V fish. Unfortunately a complete scale record is not available for 1987. In order to correct for recruitment the average length of age V fish in 1987 was estimated and using scale and length data from these age V fish an average length of these fish as age IV fish in 1986 was calculated. In 1986 the back calculated average length of age IV males was 16.8 inches (42.7 cm) and females were 20.4 inches (51.8 cm). In 1987 the average age V male and female was 18.5 inches (47.0 cm) and 22.1 inches (56.1 cm), respectively. These lengths were arbitrarily selected as cutoff points. In 1986 any male less than 16.8 inches (42.7 cm) or female less than 20.4 inches (51.8 cm) was excluded from the number of fish marked. In 1987 any male less than 18.5 inches (42.7 cm) or female less than 22.1 inches (56.1 cm) was excluded from the 1987 census. Again, this was an arbitrary way to correct for recruitment and although some of the assumptions made may not be exactly correct this method should be better than simply ignoring the problem of recruitment. The population after correcting for recruitment was calculated using the following values:

$M = 576$
$C = 823$
$R = 10$

$N = 43{,}222 \pm 25{,}372$

Another assumption is that there is no immigration of fish into the system. Immigration of unmarked fish will have the same effect as recruitment. Also, emigration of tagged fish will dilute the proportion of marked to unmarked fish if a higher proportion of marked fish leave the system. Again, diluting the proportion of marked to unmarked fish will cause the population estimate to be inflated.

It appears that a small percentage of walleye did leave the system. If these fish come back to the Muskegon River system each spring to spawn, as some investigators believe, and the mortality of marked and unmarked fish is the same outside the Muskegon River system, then no bias will be introduced. However, if tagged fish are differentially leaving and never coming back, suffering higher mortality rates in other systems before coming back or being replaced by unmarked walleyes then the above is an underestimate of the actual size of the population.

In 1986 approximately 4.5% of returns (4 of 89 returns excluding tags from two dead walleyes) were from fish caught outside of the Muskegon River system. If it is assumed that 4.5% of the adult population left the Muskegon River system there would still be no way to quantify immigration and thus no way to determine net movement into or out of the system. In addition, the 4.5% emigration cannot be extrapolated to the whole population because in this study larger fish were more likely to be tagged and larger walleyes are more apt to travel further. Liston et al. (1986) found that small walleyes (<460 mm) traveled shorter post spawning distances averaging 10 km while larger walleyes (>460 mm) averaged 28 km. Muskegon River sampling was biased toward larger members of the population and there was no way to quantify the effects of differential emigration. Therefore population estimates were not corrected for emigration or immigration. The estimate of 43,222 +/- 25,372 is likely the best estimate.

Post Spawning Movements

The results of previous Muskegon River walleye tagging studies are discussed below in order to compare post spawning movements observed in the 1940's and 1950's to those observed in this study. A total of 5,043 walleye were tagged and released in the Muskegon River system from 1939 to 1952 (Eschmeyer and Crowe 1955). Of these, 850 (16.9%) were recaptured by the end of 1953. Most of the tagged walleyes (3,371) were tagged from 1947-1952 during the Newaygo transfer when migrating walleyes were captured below Newaygo Dam and transferred to upstream impoundments. The Newaygo transfer began in 1928 and the number of fish transferred to upstream impoundments ranged from 469 in 1928 to 43,088 in 1933 with the average being 8,683 per year from 1928-1953. Eschmeyer and Crowe (1955) concluded that walleyes transferred to the upriver impoundments tended to move downstream through or over the impoundments. Mortality increased with the size of the dam and with the number of dams passed. Therefore this historical data set is not directly comparable to the more recent tagging information. However, some of the tagged walleye were released below Newaygo Dam. Although Newaygo Dam has since washed out and opened up an additional 13.5 miles (21.8 km) of river up to

Croton Dam these fish are probably the most historically comparable.

In 1948, 292 walleye were tagged and released below Newaygo Dam. Anglers returned 32 tags (11.0%) in the first year; 13 tags (4.5%) in the second year; one tag in each of the third, fourth and fifth years (0.3%) and two tags (0.6%) in the sixth year. In 1950, 473 walleyes were tagged and released below Newaygo Dam. Anglers returned tags from 11 walleyes (2.3%) in the first year; 21 (4.4%) in the second year; six (1.3%) in the third year and eight (1.7%) in the fourth year. The total returns from 1948 and 1950 were 50 (17.1%) and 46 (9.7%), respectively.

First year returns from walleye tagged below Croton Dam in 1986 and 1987 and released immediately were 11.2% and 8.6%, respectively, compared to 11.0% and 2.3% in 1948 and 1950, respectively. Of the fish tagged in 1950 nearly twice as many were returned in the second year as in the first year while first-year rates of return from 1948, 1986 and 1987 all appear to be relatively close.

However, a more interesting difference between the 1948-1950 tag returns and the 1986-1987 tag returns is the number of walleyes recaptured outside of the Muskegon River system and the time of year when the walleyes were recaptured. Of the 96 walleyes recaptured from 1948 and 1950 studies, 42 (44%) were caught in the river, 16 (17%) were caught in Muskegon Lake and 38 (40%) were recaptured outside of the Muskegon river system. The farthest southern movement was roughly 115 miles (185 km) with three walleyes recaptured in Lake Michigan near the mouth of the St. Joseph River. In addition, four walleyes were recaptured at the mouth of the Kalamazoo River [app. 75 miles (121 km)], six were recaptured in Lake Michigan at the mouth of the Grand River [app. 50 miles (80 km)] and twelve were recaptured in Lake Michigan at the mouth of the Muskegon River [app. 39 miles (63 km)] (Eschmeyer and Crowe 1955). The furthest northern movement was roughly 175 miles (282 km) with one walleye recaptured in Lake Michigan near Good Harbor Bay. In addition, one walleye was recaptured in Lake Michigan near Betsie Bay [app. 140 miles (225 km)], another walleye was recaptured near the Manistee River [app. 117 miles (188 km)], three were recaptured near the Pere Marquette River [app. 85 miles (137 km)], two were recaptured near the Pentwater River [app. 70 miles (113 km)] and six more were recaptured at the mouth or immediately north of the White River [app. 50 miles (80 km)].

Also, walleyes tagged below Newaygo Dam in 1948 were quick to leave the Muskegon River System. The 292 walleyes that were tagged and released at a point one-half mile below Newaygo Dam were released from April 17-22 and there were no first-year returns from walleyes recaptured in the Muskegon River system after June 1, 1948 except for one that came from a walleye recaptured at the river mouth in August.

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One tag was recovered from a walleye recaptured at the mouth of the St. Joseph River on May 31, 1948. This fish had moved a distance of 115 miles (185 km) within 39 days for an average of three miles per day. Creel census data indicated that large numbers of unmarked walleyes were captured in the Muskegon River system in April and May but not after June (Eschmeyer and Crowe 1955). Other investigators have observed that walleyes were quick to leave spawning areas. Ryder (1968) found that walleyes in Nipigon Bay, Lake Superior were widely distributed by June and Forney (1963) found the same for walleyes in Lake Oneida, New York.

In contrast, of the 2,123 walleyes tagged and released below Croton Dam in 1986 and 1987, 80.3% of the tag returns were from walleyes recaptured in the Muskegon River, 15.8% were from walleyes recaptured in Muskegon Lake and 3.3% were from walleyes caught outside of the Muskegon River system (Table 1). Also, only 30 of the 146 (20.5%) tags returned from walleyes caught in the Muskegon River system, from both years, were caught after spawning and before June first.

Walleyes tagged in 1986 and 1987 appeared to be less mobile than those tagged in 1948 and 1950. Of the walleyes recaptured outside of the Muskegon river system, four were females and one was a male. All four of the females were tagged in 1986 and recaptured in 1986 in the Grand River or a tributary of the Grand. Two of the females were tagged and released immediately and measured 27.5 inches (69.9 cm), Table

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Table 1. Actual numbers and percentages of tagged walleyes captured in the Muskegon River, Muskegon Lake and outside the Muskegon River system (excluding three tagged fish found dead and one captured at an unknown location).

Category	Musk. Riv.		Musk. Lk.		Outside		Total
1986							
imature/undet.	6	100%					6
small males*	27	90%	3	10%			30
large males**	18	72%	6	24%	1	4%	25
females <4.5 lbs.	8	89%	1	11%			9
females >4.5 lbs.	18	78%	3	13%	2	9%	23
fem. kept for eggs	4	50%	2	25%	2	25%	8
1987							
imature/undet.			1	100%			1
small males*	22	92%	2	8%			24
large males**	8	73%	3	27%			11
females <4.5 lbs.	4	100%					4
females >4.5 lbs.	4	67%	2	33%			6
fem. kept for eggs	2	67%	1	33%			3
Total	122	81%	24	15%	5	3%	151

* Males less than the median length of all males tagged that year
** Males greater than the median length of all males tagged that year

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7.4 pounds (3.4 kg) and 26.5 inches (67.3 cm) 7.8 pounds (3.5 kg) respectively. One of these females was caught on July 29, 1986 in the Grand River at sixth street in Grand Rapids and had traveled approximately 107 miles (172 km). the other was caught in August of 1986 in the Grand River, at Johnson Park, near Grandville, Michigan and had traveled 100 miles (161 km). The other two angler returns came from females kept for eggs. At the time they were tagged they measured 26.9 inches (68.3 cm), 8.0 pounds (3.6 kg) and 26.8 inches (68.1 cm) and 9.1 pounds (4.1 kg), respectively. One was recaptured on June 20, 1986 in the Grand River, at River Park, in Ottawa County, and had traveled approximately 79 miles (127 km). The other was recaptured on May 15, 1986 in Buck Creek, a tributary of the Grand River and had traveled roughly 99 miles (159 km) in 43 days for an average of 2.3 miles per day (3.9 km per day). The only tag return from a male walleye caught outside the Muskegon River system came from a 23.4 inch (59.4 cm), 5.0 pound (2.3 kg) fish tagged in 1986 and recaptured in White Lake on July 20, 1987, approximately 63 miles (101 km) from Croton Dam.

As previously noted, Liston et al. (1986) found that in the St. Marys River system, larger walleyes tended to move greater distances than smaller walleyes. The four females and one male recaptured outside of the Muskegon River system were relatively large members of the cohort tagged. Also, smaller males and females were more likely to be

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be recaptured in the Muskegon River than in Muskegon Lake or outside of the Muskegon River system (Table 1). Neither Eschmeyer (1950) nor Eschmeyer and Crowe (1955) presented a summary of the sizes of the walleye tagged.

Crowe (1955) estimated spawning runs of 114,000 walleyes in 1953 and 139,000 in 1954. Population estimates were nearly triple recent estimates and the larger percentage of tag returns from outside of the Muskegon River system could have indicated emigration from a more densely populated system. Current population densities are not as high and as a result walleyes in the Muskegon River system may be behaving differently. In addition, if earlier tagging studies were also biased towards larger fish, it is possible that the estimate of 40% of the tagged population leaving the Muskegon River System could be disproportionately large.

Another reason for the apparent change in post spawning movements could be that Lake Michigan walleye are not as heavily exploited as they were in the early 1950's. Commercial fishermen returned a large number of tags during the late 1940's and early 1950's but no longer target walleyes in Eastern Lake Michigan. Also, since the introduction of Pacific Salmon in the late 1960's, combined with the decline of walleye populations throughout eastern Lake Michigan (Schneider and Leach 1979), sport anglers target salmon and trout more than walleyes.

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Although they are not being targeted, there is evidence that walleyes are utilizing Lake Michigan, especially reef areas. Divers from the MDNR have identified walleyes on a man-made reef south of the Muskegon Lake channel (MDNR unpublished data). In addition, walleyes have been collected in nets along breakwalls south of Ludington (John Gulvas, Consumers Power, personal communication).

Both of these post spawning movement studies rely on angler returns to "sample" tagged fish. Therefore differences in sampling methods may give the appearance of different results. However, it does not seem that temporal and spatial differences between tags returned from historical walleye populations and present populations can be attributed entirely to a difference in methods.

Spawning Migrations and Homing Behavior

Homing behavior is defined here as the annual return to a particular spawning area rather than seeking any suitable spawning site. Some investigators have concluded that walleyes home to particular spawning sites while others have observed no homing behavior. Crowe (1962) stated that walleyes home to the same spawning areas in the Muskegon River system, the Inland Waterway (northern lower peninsula of Michigan) and Bay de Noc in northern Lake Michigan. Todd (1990) analyzed genetic differences in Lake Erie and Lake St. Clair walleyes and determined that discrete stocks homed to t

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to their natal spawning sites and did not interbreed with other stocks in these lakes. Ryder (1968) found that walleye stocks in Black Bay and Nipigon Bay, Lake Superior, home to particular spawning sites. Forney (1963) found that stocks of walleyes in Oneida Lake tributaries homed to specific spawning areas. In contrast, Smith (1977) conducted tagging studies and found no evidence of homing to spawning areas in streams tributary to the Red Lakes, Minnesota.

Olson and Scidmore (1962) attempted to document homing behavior in walleyes in Many Points Lake, Minnesota. Many Points Lake has several areas where walleyes have been observed spawning. These areas include the Ottertail River as well as extensive shoal areas in the lake. During a mark and recapture study all of the walleyes entering the Ottertail River inlet were captured, marked and released. The results of their study indicate that some of the Many Points Lake walleyes returned to Ottertail river every year while some showed an inconsistent pattern of return. They concluded that while some of the walleyes showed a consistent pattern of return, homing behavior was not evidenced to the same degree by all fish.

Crowe (1955) stated that the Muskegon River spawning run was composed entirely of mature fish from Lake Michigan. Based on data gathered in the Muskegon River system Crowe (1962) hypothesized that walleyes from all parts of the

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Muskegon River system and the eastern shore of Lake Michigan could be expected to appear below Newaygo Dam in April. He reported that no walleyes tagged in the Muskegon River system had been recaptured in other areas during the spawning season while fish tagged in the Muskegon River were recaptured there during spawning runs in following years.

Eschmeyer (1950) also felt that the population of resident walleyes in the Muskegon River was not large and that most of the spawning run was made up of fish from Lake Michigan. He presumed that three walleyes tagged in 1947 and captured at Newaygo Dam during the 1948 spawning run had migrated downstream to Lake Michigan during the year and returned upstream to spawn. He felt that tagging studies conducted on fish transferred to upper impoundments proved that walleyes were able to negotiate each of the power dams and returned to Lake Michigan after being transferred to upstream impoundments.

Schneider and Crowe (1977) analyzed data from walleyes tagged and moved to Hamlin Lake, Michigan during the years when the Newaygo transfer was still being conducted. Hamlin Lake is an impoundment on the Big Sable River about 1/2 mile (0.8 km) upstream from the eastern shore of Lake Michigan near Ludington, Michigan. The dam prevented upstream movement of a "modest" number of walleyes. Between 1929 and 1955 as many as 307 walleyes were netted annually and transferred into Hamlin Lake. One walleye tagged during the

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spring spawning run up the Big Sable River reappeared one year later in the Muskegon River during the spawning run. Another was recaptured 160 miles (257 km) away, off Brevort in northern Lake Michigan, 14 months after being tagged. In addition, eighteen walleyes captured in Lake Michigan near Ludington in mid summer were transferred to Hamlin Lake, and recaptured in Lake Michigan "or had passed through it on there way to other places" (Schneider and Crowe 1977). Twelve of these walleye were recaptured in Muskegon River spawning runs one to six years later.

The fact that twelve walleyes captured during the summer near Ludington were recaptured later during Muskegon spawning runs supports the contention that some walleyes were homing to the Muskegon River. However, the one of 48 walleyes tagged during a Big Sable spawning run that was recaptured during a spawning run in the Muskegon River supports Olson and Scidmore's finding that walleyes show different degrees of homing behavior. If this one Big Sable walleye was showing a consistent pattern of homing then the fish could have been captured only in spawning runs at either Big Sable River or the Muskegon River but not both places.

Neither Crowe (1955, 1962) nor Eschmeyer (1950) mention any sampling effort outside of the Muskegon River system during the spawning season except for the work done on the Sable River. Perhaps tagging efforts equal in proportion to those

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those on the Muskegon River, at the Sable River or other locations, would have provided more insight into the homing behavior of both Big Sable walleyes and Muskegon River walleyes. Although there was reason to believe that many walleyes moved from eastern Lake Michigan to Newaygo Dam to spawn, the Big Sable River and other areas may have been utilized by spawning walleyes from eastern Lake Michigan.

As previously noted, only 20.5% of the tags returned from walleyes caught in the Muskegon River system, in 1986 and 1987, were caught after spawning and before June first. This suggests that now many more walleyes are staying in the river system throughout the summer and fall than was previously observed by other investigators. Also, adult walleye are not using the Muskegon River system strictly for spawning as a much larger percentage of tag returns came from within the River system as opposed to Lake Michigan or other tributary systems.

Again, these studies rely on angler returns to "sample" tagged fish and differences in sampling methods may give the appearance of different results. No rewards were offered for tags returned from fish marked during the Newaygo transfer. However, Crowe (1955) felt that the Newaygo transfer created such local interest and had so much publicity that most anglers reported the recovery of tagged walleyes. In addition, "sampling" differences may have been caused by anglers targeting different species. A subs

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substantial number of tags returned from fish captured in Lake Michigan, in the 1940's and 1950's, were returned by commercial anglers while commercial and sport anglers fishing in Lake Michigan did not target walleyes in 1986 and 1987.

Although "sampling" differed, the large numbers of walleye observed and captured at Croton Dam during the spawning season indicate that many adult walleyes are homing to Croton Dam. However, if the same type of inferential data are used then it seems that most of the walleye are homing to Croton Dam from within the Muskegon River system and walleyes are leaving the system less frequently than walleyes tagged during the Newaygo transfer.

Rates of Exploitation, Survival and Mortality

As previously noted, walleyes tagged and released immediately were captured more frequently than walleyes kept for eggs. This could have been caused by differential mortality or different behavior of the fish kept for eggs. In order to distinguish between the effects of differential mortality or behavioral differences between sexes and sizes of walleyes, the population was divided into seven groups based on sex, size and treatment during the egg-take and tagging operations. The categories were immature fish and walleyes of undetermined sex, males less than the median size of all males captured that year, males greater than me

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median size, males kept for milt, females kept for eggs, females less than 4.5 pounds (2.0 kg) tagged and released immediately and females greater than 4.5 pounds (2.0 kg) tagged and released immediately.

The rate of exploitation (u) or the fraction of walleyes in the population captured by anglers was estimated by calculating the ratio of the number of tags returned by anglers to the number of fish marked and released in each category. Rates of exploitation were calculated for each category. The results of a Chi Squared analysis, using the rate of exploitation for the whole population as the expected value for each category, indicated that there was a significant difference between each of the ratios within each year (u86 Chi squared= 38.129, critical value= 11.070; u86-87 Chi squared= 39.435, critical value= 11.070; and u87 Chi squared= 38.872, critical value= 12.592). The rates of exploitation were influenced by the size of the fish and the treatment of the fish after capture. Therefore, the total annual mortality rate (A), survival rate (S), instantaneous rate of mortality (Z), instantaneous rate of fishing mortality (F), instantaneous rate of natural mortality (M), rate of exploitation (u), expectation of natural death (v) and the conditional rate of fishing mortality (n) were calculated for the various sub-populations so that comparisons could be made between subpopulations and with other walleye populations.

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The ratios of returns to fish tagged in 1986 indicate that anglers captured more of the smaller fish than larger fish (Table 2). The immature and undetermined sex category generally had the smallest fish and had the highest exploitation rate (u=0.194). The second and third highest exploitation rates were from males less than the median size of 19.1 inches (48.5 cm) (u=0.126) and females less than 4.5 pounds (2.0 Kg) (u=0.154). The smallest males and females tagged and released immediately had higher exploitation rates than their larger counterparts. The lowest rate of exploitation of 1986 walleyes was fish kept for eggs. This group should have been comparable to the females greater than 4.5 pounds (2.0 kg) that were tagged and released immediately. However, the rate of exploitation of the females kept for eggs was approximately one-sixth that of similar sized females tagged and released immediately.

The ratios of returns to fish tagged in 1987 indicate a similar trend. The smallest males and females tagged and released immediately had greater rates of exploitation than their larger counterparts. However, the immature and undetermined sex category had a lower rate of return than all females tagged and released immediately but the estimate was based on one return from eight tagged fish. Again, the fish kept for eggs had a substantially lower rate of exploitation than females greater than 4.5 pounds (2.0 kg) tagged and released immediately.

Table 2. Estimated rates of exploitation, survival and mortality of sub-populations for Muskegon River walleyes.

Table 2. Estimated rates of exploitation, survival and mortality of sub-populations for Muskegon River walleyes.

	Immature or undet. sex	Males < median length	Males > median length	Females < 4.5 pounds	Females > 4.5 pounds	Males Kept for Milt	Females Kept for Eggs	All Walleyes Combined	All minus Fish kept for Eggs
Rate of exploitation									
u c86/m86 *	0.194	0.126	0.094	0.154	0.095		0.016	0.071	0.112
u c86&87/m86	0.194	0.140	0.118	0.173	0.104		0.019	0.084	0.127
u c87/m87	0.125	0.102	0.049	0.167	0.146	0.018	0.008	0.052	0.860
Annual Survival (S)		0.14	0.47	0.12	0.062		0.28	0.20	0.18
standard deviation		+/-0.08	+/-0.25	+/-0.13	+/-0.049		+/-0.32	+/-0.06	+/-0.06
Annual Mortality (A)		0.86	0.53	0.88	0.94		0.72	0.80	0.82
Inst. Mortality (Z)		2.0	0.75	2.2	2.8		1.3	1.6	1.7
Inst. Fishing Mort. (F)		0.29	0.13	0.38	0.27		0.028	0.16	0.24
Inst. Natural Mort. (M)		1.7	0.61	1.2	2.5		1.2	1.5	1.5
Expect. of Nat. Mort. (v)		0.74	0.43	0.73	0.84		0.71	0.61	0.71
Cond. Fishing Mort. (m)		0.25	0.12	0.31	0.24		0.028	0.14	0.21
Cond. Natural Mort. (n)		0.82	0.46	0.83	0.92		0.71	0.77	0.78

* c = captured by anglers
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Rates of exploitation were calculated from all Muskegon walleyes tagged and released immediately and these rates were generally less than those reported by other investigators (Table 3). Angler effort and angler cooperation with each study will influence comparisons between rates of exploitation. If tags are taken but not reported the estimated rate of exploitation would be less than the true rate of exploitation. In addition, any factor that will decrease the proportion of marked to unmarked fish in the population will cause the rate of exploitation to be low. For example, a higher rate of emigration of marked fish, immigration of unmarked fish and differentially higher mortality of marked fish will decrease the proportion of marked fish to unmarked fish and cause the estimated rate of exploitation to be less than the true rate of exploitation. The reliability of conclusions about comparisons to other walleye populations will depend on the relative importance of these extraneous influences on estimated rates of exploitation.

After collecting eighteen years of angler returns from one year of tagging, Schneider et al. (1976) noted that the rate of exploitation for females was 12.6% while the rate of exploitation for males was 7.3%. They also found a significant difference in rates of exploitation among sexes when they considered all walleyes tagged, walleyes tagged and released which were 483 mm or less, and walleyes tagged

Table 3.

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Table 3. Estimated rates of exploitation, survival and mortality of Muskegon River walleyes tagged and released immediately and of walleye populations from other locations.

Investigator and Location	Parameters* u	S	A	Z	F	M	v	m	n
Muskegon (1986) m&f combined	0.112	0.18	0.82	1.7	0.24	1.5	0.71	0.21	0.77
males	0.110	0.25	0.75	1.4	0.20	1.2	0.64	0.18	0.70
females	0.106	0.079	0.92	2.5	0.29	2.2	0.82	0.25	0.89
Eschmeyer (1950)	.024-.147								
Inland Waterways, Mich	avg= .107								
Olson (1958)									
Many Points Lake, Minn.	0.18	0.62	0.38	0.48	0.23	0.25	0.20		0.47
Niemuth et al. (1962)									
Escanaba Lake, Wisc.	.23-.47		.10-.15						
Priegel (1967), Wisconsin									
Big Lake Butte des Morts 1962	0.122								
1962-1966	0.155								
Spoehr's Marsh 1962-1963	0.207								
Forney (1967)									
Oneida Lake, N.Y.	.10-.47		.11-.54				.01-.07		0.88
Kelso and Ward (1972)	(unexploited)								
West Blue Lake, Manitoba	0.0	.20-.37	.63-.80	1.61-1.4	0.0	1.61	1.61-1.4	0.0	.63-.80
Schneider et al. (1976)									
Lake Gogebic, Mich									
males	0.073	0.804	0.196	0.218	0.081	0.137	0.123	0.078	0.128
females	0.126	0.654	0.346	0.425	0.155	0.270	0.220	0.144	0.237
Spangler et al. (1977)									
Missagi River, Ontario	0.266	0.436	0.564	0.836	0.394	0.442	0.298	0.324	0.355
Nelson and Walburg (1977)									
Four Missouri River Res.		.44-.55							
Laarman (1981)									
Manistee Lk. 1973-1978	0.17	0.44	0.56	0.82	0.25	0.57	0.39	0.22	0.43
Craig and Smiley (1986)									
Alberta, Canada									
Ethel Lk males		0.65	0.35	0.43					
females		0.64	0.36	0.45					
Marie Lk.males		0.78	0.22	0.25					
females		0.78	0.22	0.25					
Wolf Lk. males		0.65	0.35	0.43					
females		0.67	0.33	0.39					

* u = rate of exploitation
S = annual survival
A = annual mortality
Z = instantaneous mortality
F = instantaneous fishing mortality
M = instantaneous natural mortality
v = expectation of natural mortality
m = conditional fishing mortality
n = conditional natural mortality

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and released which were greater than 483 mm. They attributed the difference to more aggressive feeding behavior among the females and consequently greater vulnerability to angling. Similarly, small female walleyes tagged and released immediately at Croton Dam in 1986 and 1987 had higher rates of exploitation than smaller males. Also, large females tagged and released immediately in 1987 had higher rates of exploitation than large males. However, large females tagged and released immediately in 1986 were captured at approximately the same rate as large males tagged in 1986.

The mark and recapture data were used to calculate annual survival and mortality rates. The survival rate (S) is the proportion of fish alive at the end of a year while the annual total mortality rate (A) is the proportion of fish that have died at the end of one year. Estimates of survival calculated with mark and recapture data will be underestimated if differential mortality of marked fish, differential emigration of marked fish or immigration of unmarked fish serve to decrease the proportion of marked to unmarked fish. The survival rate and standard error were calculated using formulae from Ricker (1975).

$S= R12*M2/M1*R22$
$\text{std. err.}=(S^2*(1/R12+1/R22-1/M1-1/M2))^{1/2}$

Where:

S= survival rate
M1= number of fish tagged and released in 1986
M2= number of fish tagged and released in 1987
R12= number of tags returned by anglers in 1987 from fish tagged in 1986
R22= number of tags returned by anglers in 1987 from fish tagged in 1987

The annual total mortality rate is calculated by subtracting S from one. Annual survival rates and mortality rates calculated for the six different categories and for the total population are presented in Table 2. The highest survival rate was 0.47 +/- 0.25 calculated for males greater than the median size. The next highest survival rate was for the females kept for eggs (0.28 +/- .32) and the lowest survival rate was for females greater than 4.5 pounds (2.0 kg), tagged and released immediately (0.062 +/- 0.049).

The larger females released immediately had a higher estimated mortality rate than the smaller females. If larger females were leaving the system more often and were not exposed to the same fishing pressure then angler tag returns would decrease over time as more fish left the system. This decrease in the rate of return combined with the expected decrease in the rate of return due to mortality would inflate the estimated annual mortality rate of the larger females.

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The large females tagged and released immediately can be used as a natural control group to compare fish kept for eggs. The survival rate of females kept for eggs was not statistically different than the survival rate of females tagged and released immediately. However, the relatively high survival rate calculated for females kept for eggs compared to the survival rate of females tagged and released immediately seems to contradict the notion of increased mortality among the former due to egg-take operations. The estimated survival of fish kept for eggs was not precise due to the relatively low number of angler returns (one tag returned in 1987 from a fish tagged in 1986 and three tags returned in 1987 from fish tagged in 1987) and the true survival rate may be lower.

Another possible explanation for the apparent contradiction could be that the estimated survival rate only applies to fish that survive the initial shock of egg-take operations. Estimated survival rates were calculated using tags returned by anglers and the walleye season did not open until May 15th in 1986 and April 30 in 1987. If mortality caused by the egg-take operation occurred before the start of the season then R12 and R22 from the equation above would reflect the rates of recapture of the surviving group. Therefore survival estimates would only be applicable to the group of walleyes that survive the initial shock. It is possible that high mortality immediately following egg-take

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causes the rate of exploitation to be low while the estimated rate of survival applies to the cohort that survives the egg-take.

In order to compare survival and mortality estimates from Muskegon walleyes to estimates from other walleye populations survival and mortality estimates were calculated for all walleyes tagged and released immediately. The estimate of the annual survival rate of Muskegon walleyes was 18% and was lower than those from populations in other bodies of water (Table 3). Estimates of annual survival rates ranged from 80.4% for male walleyes from Lake Gogebic in Michigan's Upper Peninsula to 20% for an unexploited walleye population in West Blue Lake, Manitoba and the average annual survival rate was 55.0% for all populations and sexes of walleyes presented in Table 3. It is likely that the estimated survival of Muskegon River walleyes was an underestimate of the actual rate caused by factors previously discussed. Also, the studies conducted on other walleye populations were conducted on closed systems or used different methods. Therefore, estimates of survival would not be effected in the same manner as estimates for Muskegon River walleyes.

Schneider et al. (1976) found that the annual survival rate of male walleyes from Lake Gogebic (80.4%) was higher than the survival rate of females (65.4%). However, Nelson and Walburg (1977) found that females exhibited higher sur

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survival rates in Main Stem Missouri River reservoirs. Craig and Smiley (1986) studied walleye populations in three Alberta, Canada lakes and found that the annual survival rates of males and females were similar. Survival rates were estimated for Muskegon males and females using only walleyes tagged and released immediately and the estimated survival rates were higher for males. If the female walleyes are leaving the system more often than the males then the survival rates calculated for females will be lower and more biased than those calculated for males.

The expectation of natural death (v) is the difference between annual mortality rate and the rate of exploitation and it is simply the proportion of annual mortality that was not caused by anglers. Again, the proportion of natural mortality to total mortality was the lowest for large males and highest for large females tagged and released immediately. In all cases the expectation of natural death is a larger part of the total mortality that the rate of exploitation. These estimates suggest that a Muskegon walleye is much more likely to die of natural causes than be captured by anglers. However, as previously noted, immigration and differential emigration of marked fish will lower the estimated rate of exploitation and increase the estimated mortality. Most of the estimates of the expectation of natural death from other walleye populations were larger than the corresponding rate of exploitation.

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The difference was usually not as large as that evidenced by Muskegon walleyes. Incomplete reporting of tags collected by anglers will lower the estimated rate of exploitation. Therefore, conclusions about differences between walleye populations will be partially dependent on angler cooperation with each study.

Instantaneous mortality rates are often calculated for use in modeling and the total instantaneous mortality rate (Z) can be calculated using the following formula: $(1-A)^{-Z}=e)$. The instantaneous mortality rates show the same relative pattern with the highest rates for large females, small females and small males and the lowest rates were estimated for large males and females kept for eggs.

Total instantaneous mortality rates can be broken down into instantaneous mortality rates from fishing (F=u*Z/A) and instantaneous mortality rates from natural causes (M=Z-F). In all cases the instantaneous natural mortality rate is higher than the instantaneous fishing mortality rate. The proportion of instantaneous fishing mortality rate to total mortality rate was highest for large males (18%) followed by small females (17%) and small males (15%). Instantaneous fishing mortality accounted for only 2.2% of the total instantaneous mortality rate for females kept for eggs while instantaneous fishing mortality accounted for 11% of total instantaneous mortality for large females tagged and released immediately.

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Instantaneous mortality from natural causes and from fishing will be inflated by differential mortality of marked fish, differential emigration of marked fish or immigration of unmarked fish. In addition, incomplete reporting of angler returns will decrease the estimate of instantaneous fishing mortality rate and increase the estimate of instantaneous natural mortality rates.

Conditional natural mortality rate (n) is the fraction of the initial stock that would die from causes other than fishing during a year if there were no fishing mortality. The conditional fishing mortality rate (m) is the fraction of the initial stock that would be caught during the year if no other causes of mortality operated. Conditional fishing mortality rates were higher for small males and females than for large males and females and higher for females kept for eggs than for large females tagged and released immediately. Conditional natural mortality rates were highest for all females tagged and released immediately and small males and lowest for larger males and females kept for eggs.

Conditional fishing mortality for the whole population tagged and released immediately was nearly double the rate of exploitation while the conditional natural mortality was not substantially larger than the natural mortality rate. Therefore, decreases in natural mortality rates should have a relatively large impact on the rate of exploitation while a decrease in the rate of exploitation will have a relat

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relatively minor impact on natural mortality rates. Incomplete angler returns will cause conditional fishing mortality to be underestimated while conditional natural mortality is overestimated. Conditional natural mortality calculated for Muskegon River walleyes was higher than most of the estimates from other walleye populations but conditional fishing mortality was similar to other populations (Table 3). This conclusion will be effected by differences in angler cooperation between the various studies.

Again, ratios of conditional fishing mortality to conditional natural mortality and instantaneous fishing mortality to instantaneous natural mortality indicate that natural mortality is much higher than fishing mortality. Literature values indicate that mortality accounted for by angler tag returns ranged from 30% to 88% of the total annual mortality with the average being 46%. Mortality accounted for by Muskegon River angler returns ranged from 3.1% for females kept for eggs to 17.9% for large males tagged and released immediately. Comparisons to other systems will be partially influenced by angler cooperation but it seems that natural mortality is a much higher percentage of total mortality than in most other systems examined.

These conclusions may also be biased since natural mortality estimates are based partly on the annual mortality rates w

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rates which will be overestimated by immigration and emigration. As previously noted, when tagged fish leave the system the proportion of tagged fish will be diluted and anglers will catch fewer tagged fish. The lower proportion of recaptures will inflate the annual mortality rates and increase estimates of natural mortality while the rate of exploitation and conditional fishing mortality estimates decrease. This seems likely since emigration was documented. Immigration of untagged walleyes to the system will further dilute the proportion of tagged fish to untagged fish and distort estimates. Again, Incomplete reporting of angler returns will decrease estimates of the rate of exploitation, instantaneous fishing mortality and conditional fishing mortality while causing instantaneous natural mortality rates and conditional natural mortality rates to be inflated.

Growth

Body Length-Scale Radius Relationship

To estimate the length of walleyes at a previous age, a relationship between body length and scale radius was developed. The relationship between scale radius (mm at 22X magnification) and total length (inches) of walleyes captured in 1986 and 1987 is presented in Figures 4 and 5. Data from the seventeen juvenile walleyes captured during

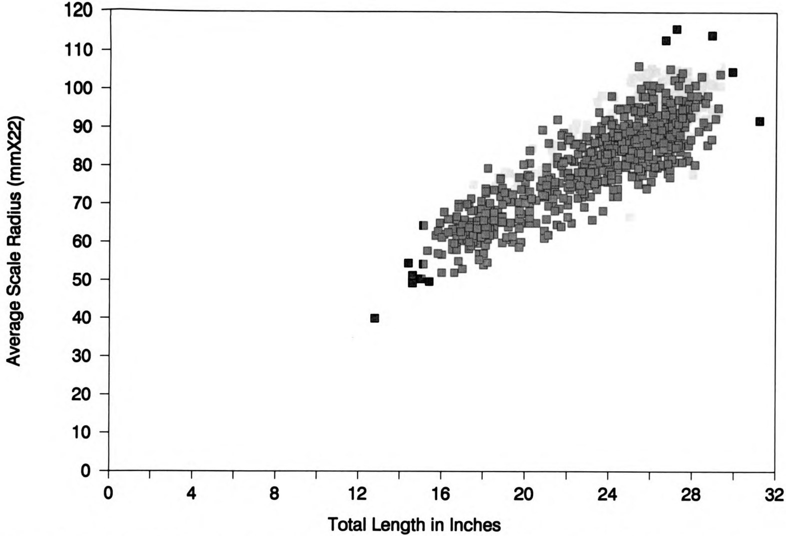


Figure 4. The relationship between total length (inches) and scale radius (millimeters at 22X magnification) of adult walleyes captured in 1986.

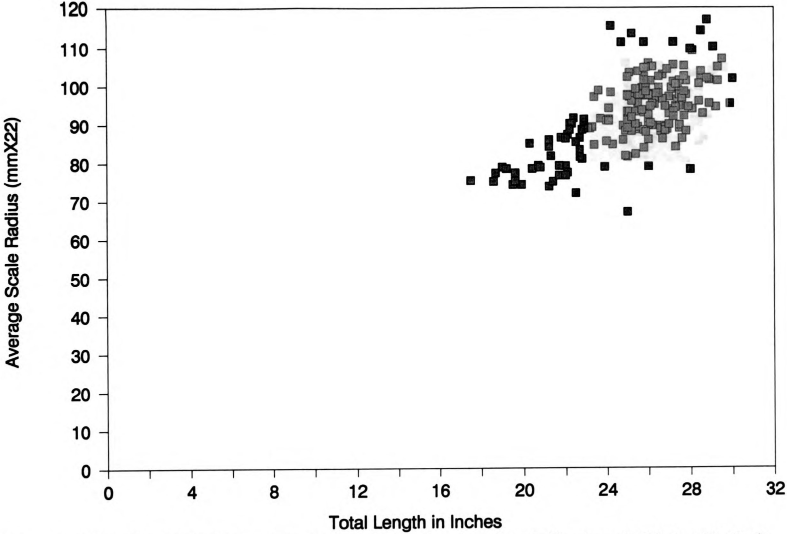


Figure 5. The relationship between total length (inches) and scale radius (millimeters at 22X magnification) of adult walleyes captured in 1987.

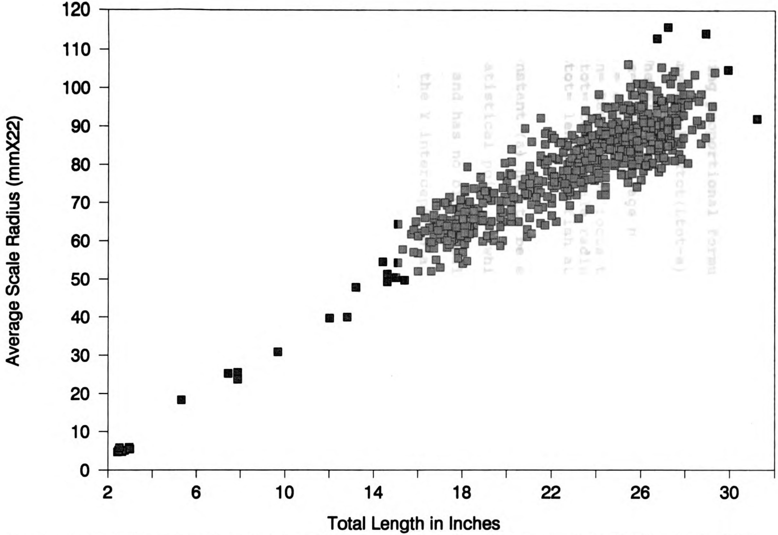


Figure 6. The relationship between total length (inches) and scale radius (millimeters at 22X magnification) of adults and juveniles captured in 1986.

the 1986 season were combined with the data from the adults captured in 1986 and are presented in Figure 6.

Length at each age was back calculated using the following proportional formula:

Ln= a + Rn/Rtot(Ltot-a)

Where:
Ln= length at age n
a = constant
Rn= Radius from focus to annuli n
Rtot= total scale radius
Ltot= length of fish at capture

The constant (a) had to be estimated. The (a) constant is the statistical point at which the linear relationship starts and has no biological meaning. Typically the constant (a) is the Y intercept in a length-versus-scale-radius least square linear regression equation but because of non-homogenous variance the data needed to be transformed.

According to Smale and Taylor (1987), averaging scale radius at fixed length intervals is an unbiased method for correcting heterogenous variance. To determine the fixed length interval, Steins' two stage sampling formula (Steel and Torrie 1980) was used along with a mean scale radius precision arbitrarily selected to be +/- 3mm (22X) and an alpha=0.05 to estimate a sample size. Then length intervals were set so that they had the necessary sample size to ensure the mean scale radius, within each length interval, had a precision of +/- 3mm (22X)

Another assumption of regression analysis is that the distribution of the dependent variable is normal. According to Smale and Taylor (1987) the constant (a) should not be estimated using a scale-radius-versus-length regression because the distribution of the dependent variable may not be normal. Since many sampling methods bias towards lengths of fish, length at scale size may not be normally distributed while scale size at length will tend to be normal because fish are not being selected based on scale size. Therefore, the independent variable and dependent variables were reversed and scale radius became the dependent variable while total length became the independent variable. According to Smale and Taylor (1987) no distinction can be made between regression relationships of scale size on length or length on scale size. Regressions of mean scale radii on length estimate the relationship between scale size and length for the average or typical fish. The "a" constant then becomes the X-intercept in the scale radius versus length regression equation.

According to Whitney and Carlander (1956) it is incorrect to use a regression equation of mean scale measurement versus fixed body lengths but they also acknowledge that error will be small and decrease toward zero as the correlation coefficient (r^2) approaches unity.

Four separate regression equations of scale-radius-versus-length were calculated for adult males and females in

1986 and 1987. There was no significant difference between slopes or intercepts calculated for males and females within each year (calculated Student's t test value for slopes: 1986 t=0.627, 1987 t=0.805 , for Y intercept 1986 t=0.48, 1987 t=2.81). Data for males and females were combined and two new scale-radius-versus-length regression equations were calculated, one for 1986 fish and one for 1987 fish. However, there was a significant difference (alpha =0.05) between both the slope (t= 4.36) and the intercept (t= 8.054) of the 1986 regression equation and the 1987 regression equation. Therefore the data from the two years could not be combined.

Next, the scale measurements and lengths from the seventeen juvenile walleyes captured in 1986 were added to the length and scale measurement data from the 1986 egg-take (Figure 7). The estimated scale-radius-versus-length regression equation was: Scale radius=-0.03870+ 3.448(Length) with an r^2 of 0.99 and the X-intercept was estimated to be 0.01122 inches. The estimated scale radius versus length regression equation from 364 scales taken from walleye captured during 1987 was: Scale radius= 25.789+ 2.636(Length) (r^2 = 0.98) and the X-intercept was estimated to be -9.784 (Figure 8).

Again the constant (a) has no biological meaning and is simply the mathematical point at which the relationship starts. The X-intercept or constant (a) estimated from the

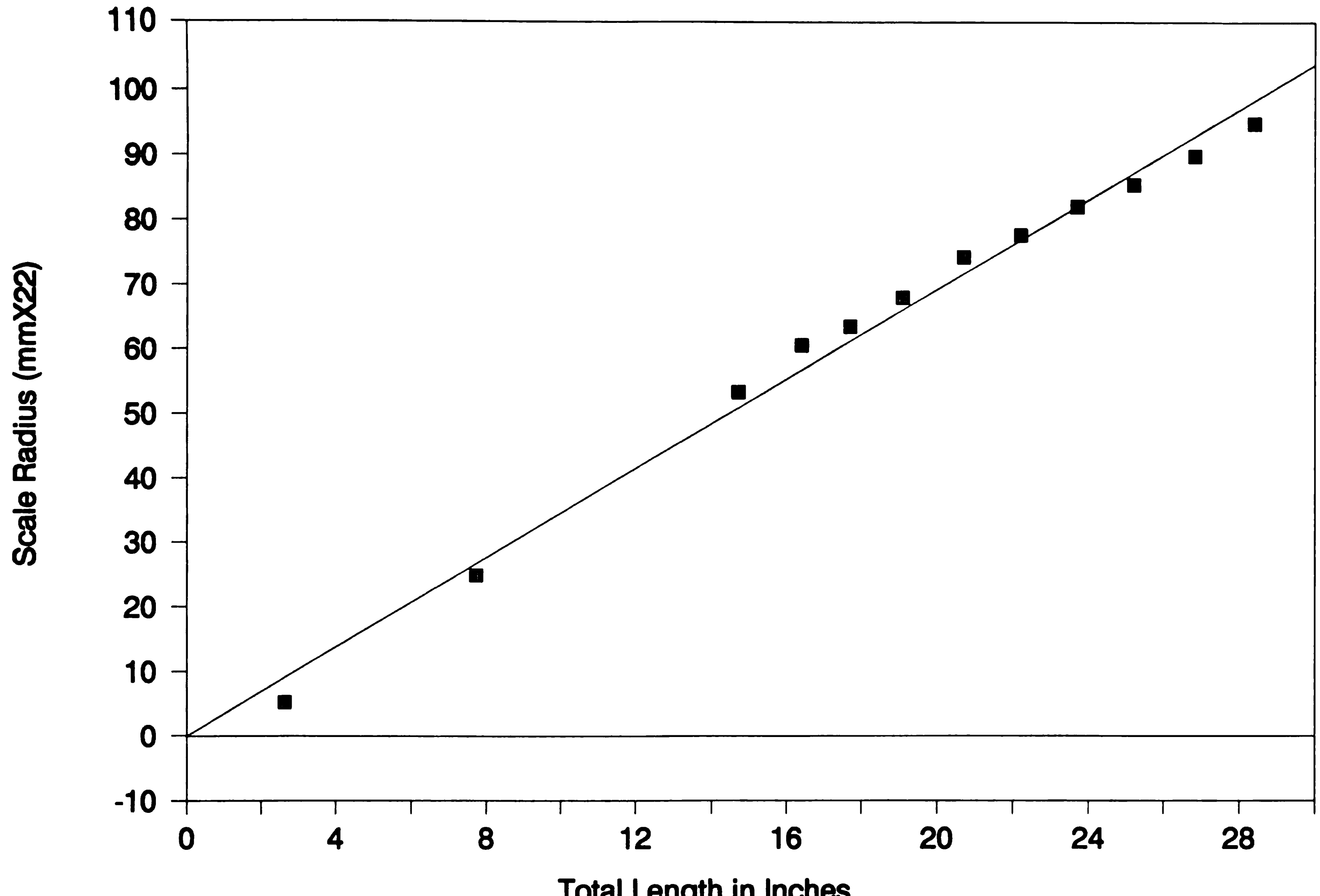


Figure 7. The transformed relationship between scale radius (millimeters at 22X magnification) and total length (inches) of adult and juvenile walleyes captured in 1986.

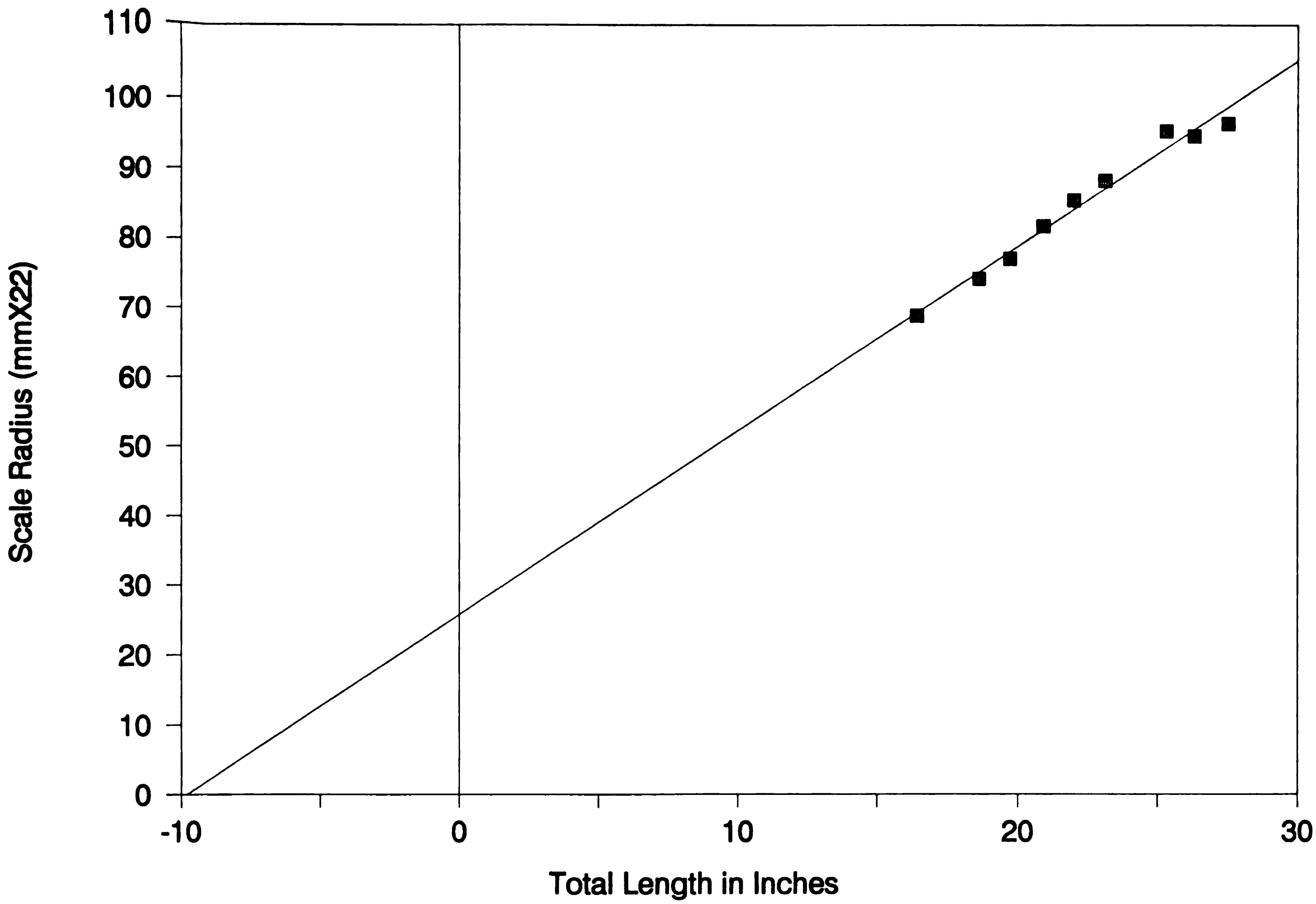


Figure 8. The transformed relationship between scale radius (millimeters at 22X magnification) and total length (inches) of adult walleyes captured in 1987.

1986 data is probably better than that calculated from the 1987 data partly because the sample size was larger (1,139 in 1986 and 349 in 1987) but mostly because the scale and length data from the seventeen juveniles allows the relationship to be extended to younger fish. Therefore the constant (a) calculated from 1986 data was used in the back calculation formula.

Lengths at each age were back calculated and averaged for males in 1986 and 1987 and for females in 1986 in 1987 (Table 4). A grand average length at each age was calculated for all males and for all females. In order to test for Lee's phenomenon back calculated lengths at each age were regressed against age and the slopes were tested to determine if they were statistically different than zero. Lee's phenomenon is the appearance of a decrease in the length at each annulus of older fish. Causes of Lee's phenomenon may include failure to correctly identify all of the annuli (Olson 1980), selective mortality of more rapidly growing individuals and failure to use a correct body scale relationship in computing lengths, or biased sampling of the stock (Duncan 1979).

Average back calculated length at age versus age regression slopes for 1986 males and females were all negative. The first three regression equations produced slopes that were statistically different than zero indicating the presence of Lee's phenomenon (Table 5).

Table 4. Back calculated lengths of Muskegon River walleyes

Age	Number of Fish Aged	Total Length at Each Annulus Formation (inches)									
		I	II	III	IV	V	VI	VII	VIII	IX	X
Males 1986											
I											
II											
III	7	6.8	12.1	14.6							
IV	70	6.5	11.4	14.6	17.1						
V	127	6.1	10.0	13.8	16.3	18.1					
VI	63	6.1	10.6	14.4	17.0	18.7	20.1				
VII	83	6.2	10.9	14.9	17.6	19.3	20.5	21.5			
VIII	61	6.1	10.2	14.0	17.1	19.1	20.5	21.6	22.5		
IX	15	5.8	9.5	13.2	17.0	18.8	20.4	21.5	22.4	23.2	
X	1	5.2	8.2	12.3	15.3	17.2	18.7	19.6	20.8	21.7	22.5
Average	427	6.2	10.5	14.3	16.9	18.7	20.4	21.5	22.5	23.1	22.5
1987 Males											
I											
II											
III	1	7.9	13.6	16.3							
IV	10	6.4	11.3	14.5	16.4						
V	37	6.5	11.1	14.6	16.8	18.5					
VI	29	6.2	10.4	14.0	16.6	18.4	19.7				
VII	46	6.5	12.0	16.1	18.6	20.0	21.2	22.0			
VIII	26	6.3	11.3	15.4	18.0	19.6	20.7	21.6	22.3		
IX	14	6.1	10.8	15.2	17.4	19.3	20.7	21.8	22.8	23.6	
X	4	6.3	10.8	14.5	17.0	18.8	20.2	21.6	22.6	23.2	23.9
Average	167	6.4	11.3	15.1	17.5	19.2	20.6	21.8	22.5	23.5	23.9
Males 1986 and 1987											
I											
II											
III	8	7.0	12.3	14.8							
IV	80	6.5	11.4	14.6	17.0						
V	164	6.2	10.2	14.0	16.4	18.2					
VI	92	6.1	10.5	14.3	16.9	18.6	20.0				
VII	129	6.3	11.3	15.3	18.0	19.5	20.8	21.7			
VIII	87	6.2	10.5	14.4	17.4	19.3	20.6	21.6	22.4		
IX	29	5.9	10.1	14.2	17.2	19.0	20.5	21.6	22.6	23.4	
X	5	6.1	10.3	14.1	16.7	18.5	19.9	21.2	22.2	22.9	23.6
Grand Average	594	6.2	10.7	14.5	17.1	18.8	20.5	21.6	22.5	23.3	23.6

Table 4 (cont'd).

Age	Number of Fish Aged	Total Length at Each Annulus Formation (inches) I	II	III	IV	V	VI	VII	VIII	IX	X
Females 1986											
I											
II											
III											
IV	7	7.4	12.5	17.2	20.2						
V	41	6.8	11.8	16.1	18.9	21.0					
VI	90	6.5	11.6	16.1	19.4	21.8	23.5				
VII	213	6.9	12.2	16.8	20.0	22.2	23.7	25.0			
VIII	245	6.6	11.7	16.2	20.0	22.2	23.8	25.1	26.1		
IX	92	6.7	10.9	15.2	18.8	21.5	23.3	24.6	25.7	26.6	
X	19	6.5	10.9	15.2	18.9	21.4	23.1	24.5	25.6	26.1	26.8
XI	3	6.3	9.7	11.6	14.9	17.6	20.8	22.9	24.5	25.5	26.3
Average	710	6.7	11.8	16.2	19.7	21.9	23.6	25.0	26.0	26.5	26.7
Females 1987											
I											
II											
III											
IV	3	8.0	13.8	18.4	20.9						
V	9	7.5	13.6	17.7	20.4	22.1					
VI	12	6.6	11.6	15.7	18.8	21.0	22.6				
VII	24	7.0	12.9	17.0	20.0	22.3	23.8	24.9			
VIII	61	7.0	12.7	16.9	20.0	22.1	23.7	25.1	26.1		
IX	57	6.8	12.3	16.4	19.5	21.9	23.6	25.1	26.1	26.9	
X	16	6.9	11.9	15.8	18.7	21.0	22.9	24.3	25.6	26.6	27.5
Average	182	6.9	12.5	16.6	19.7	21.9	23.5	25.0	26.0	26.8	27.5
Females 1986 and 1987											
I											
II											
III											
IV	10	7.6	12.9	17.6	20.4						
V	50	7.0	12.1	16.4	19.2	21.2					
VI	102	6.5	11.6	16.1	19.3	21.7	23.4				
VII	237	6.9	12.3	16.8	20.0	22.2	23.7	25.0			
VIII	306	6.7	11.9	16.3	20.0	22.1	23.8	25.1	26.1		
IX	149	6.7	11.4	15.7	19.1	21.7	23.4	24.8	25.9	26.7	
X	35	6.7	11.4	15.5	18.8	21.2	23.0	24.4	25.6	26.3	27.1
XI	3	6.3	9.7	11.6	14.9	17.6	20.6	22.9	24.5	25.5	26.3
Grand average	892	6.8	11.9	16.3	19.7	21.9	23.6	25.0	26.0	26.6	27.1

Table 5. Slopes of age versus length at each age calculated and tested for significant deviations from zero to indicate the presence of Lee's Phenomenon. An asterisk (*) indicates that the slope is significantly different than zero (Alpha 0.05) and Lees's phenomenon was detected.

	Age Class Age I	Age II	Age III	Age IV	Age V	Age VI	Age VII	Age VIII	Age IX
Males 1986									
slope	-0.175	-0.422	-0.262	-0.139	-0.125	-0.290	-0.580	-0.850	
students-t	5.152*	4.490*	2.698*	0.976	0.641	1.292	1.727	1.963	
deg. free.	6	6	6	5	4	3	2	1	
crit. val.	2.447	2.447	2.447	2.571	2.776	3.182	4.303	12.706	
Males 1987									
slope	-0.155	-0.237	-0.055	0.157	0.109	0.050	-0.100	0.150	
students-t	2.115	1.754	0.406	1.052	0.671	0.243	1.291	0.754	
deg. free.	6	6	6	5	4	3	2	1	
crit. val.	2.447	2.447	2.447	2.571	2.776	3.182	4.303	12.706	
All Males									
slope	-0.104	-0.223	-0.060	0.036	0.070	-0.035	-0.139	-0.100	
students-t	3.250*	2.579*	0.844	0.345	0.529	0.255	1.921	0.685	
deg. free.	6	6	6	5	4	3	2	1	
crit. val.	2.447	2.447	2.447	2.571	2.776	3.182	4.303	12.706	
Females 1986									
slope	-0.112	-0.321	-0.560	-0.463	-0.418	-0.480	-0.480	-0.490	-0.550
students-t	3.165*	4.414*	3.138*	2.180	1.524	2.242	2.862	3.406	19.053*
deg. free.	6	6	6	6	5	4	3	2	1
crit. val.	2.447	2.447	2.447	2.447	2.571	2.776	3.182	4.303	12.706
Females 1987									
slope	-0.169	-0.257	-0.329	-0.257	-0.086	0.040	-0.180	-0.250	
students-t	2.469	2.043	2.343	2.107	0.573	0.206	1.099	1.732	
deg. free.	5	5	5	5	4	3	2	1	
crit. val.	2.571	2.571	2.571	2.571	2.776	3.182	4.303	12.706	
Females 1986									
slope	-0.125	-0.325	-0.571	-0.490	-0.440	-0.470	-0.487	-0.505	-0.607
students-t	3.005*	3.779*	3.040*	2.356	1.654	2.129	2.875	3.428	4.756
deg. free.	6	6	6	6	5	4	3	2	1
crit. val.	2.447	2.447	2.447	2.447	2.571	2.776	3.182	4.303	12.706

Average back calculated lengths at age I, II and III were larger for younger fish than for older fish and as previously mentioned there are several possible explanations. Considering the sampling methods the most likely explanation for this trend is that fish that grow faster and mature faster become part of the spawning run before the slower growing members of their year class. Therefore, younger age classes in the spawning run would bias average back calculated length estimates toward a higher average length than is actually representative of the population. Conversely, it is possible that since a proportionally larger number of older fish were sampled, differentially higher mortality of faster growing fish could have biased the estimated average length at ages I, II and III of older fish.

None of the average back calculated length at age versus age regression slopes calculated for 1987 males and females were statistically different than zero (Table 5). Fewer scales were collected in 1987 and a higher proportion of scales were taken from fish kept for eggs. Again, fish kept for eggs were primarily selected on the basis of size and therefore tended to be larger and older than the average spawning adult. The contribution to the data set of smaller but faster growing fish from the younger age classes was proportionally less in 1987. If the 1986 and 1987 populations of spawning adults were similar then faster growing young fish are contributing more to Lee's phenomenon than differentially higher mortality of faster growing older fish. Since the proportional contribution of older fish was higher in 1987 the effects of differentially higher mortality should have been more pronounced on the 1987 data. However, Lee's phenomenon was not detected.

As previously noted, mature female walleyes collected at Croton Dam were substantially larger than mature males of the same age. Comparison of length at age I between males and females indicates that differential growth between males and females may start before the first complete year of growth. Back calculated lengths from both 1986 and 1987 scales show small differences in length at age I but the length gap between the sexes increases each year. However, the apparent difference in lengths at age I may be due to bias in back calculated lengths at age I caused by the relatively small number of YOY fish used to develop the scale-radius-versus-length relationship. Other investigators have found that male and female walleyes were the same length at age for the first three years before females began to grow larger (Carlander and Whitney 1961, Forney 1965, Nelson and Walburg 1977, Smith 1977 and Craig and Smiley 1986).

Grand average back calculated lengths were compared to the actual size of the fish collected. Although there are only eight age III males (seven age III fish from 1986 and one age III fish from 1987) the actual measured length of the males appears to be longer than the average back calculated length (Table 6). Since age III fish made up a small portion of the run, these fish may be the faster maturing members of the age three cohort. Back calculated lengths from age IV and up were similar between 1986 and 1987. Average lengths back calculated from scales collected in 1986 and 1987 were also similar to the actual measured lengths. Again, this seems to support the contention that faster growing younger adults are causing Lee's phenomenon observed in the 1986 back calculated lengths.

An unweighted mean of average back calculated lengths from 1986 and 1987 was estimated for each sex and compared to average length at age of walleyes from other systems. The unweighted mean of all the literature values was calculated and is lower at all ages than the mean length for both male and female Muskegon Lake walleyes (Table 7).

Walleyes captured in the Muskegon River system are larger at each age than walleyes from most other systems. However, female walleyes age I through III from Lake Puckaway, Wisconsin were larger than females captured in the Muskegon River and female walleyes age III to VIII from Southern Green Bay and age VIII and IX from Northern Green Bay were larger than their counterparts captured at Croton Dam (Niemuth et al. 1962). Also, male walleyes age I to III from Lake Puckaway, Wisconsin and Lake Ripley, Wisconsin

Table 6. Actual lengths of walleye captured at Croton Dam along with back calculated lengths.

		1986				1987			
Age	Sex*	Number	Actual Length	Number	B-Calc. Length	Number	Actual Length	Number	B-Calc. Length
1	U								
	M			427	6.2			167	6.4
	F			712	6.7			182	6.9
2	U								
	M			427	10.5			167	11.2
	F			712	11.7			182	12.5
3	U					1	14.0		
	M	7	15.6	427	14.2	1	16.3	167	15.0
	F			712	16.1			182	16.6
4	U		16.4						
	M	70	17.1	420	16.9	10	16.5	166	17.4
	F	7	20.2	712	19.6	3	20.9	182	19.6
5	U	13	17.5			1	22.1		
	M	127	18.1	350	18.6	37	18.5	156	19.1
	F	41	21.0	705	21.9	9	22.1	179	21.8
6	U	3	20.8			2	17.3		
	M	63	20.1	223	20.3	29	19.8	119	20.6
	F	90	23.5	664	23.6	12	22.6	170	23.5
7	U	5	22.0						
	M	83	21.5	160	21.5	46	22.1	90	21.8
	F	213	25.0	451	24.9	24	25.0	158	24.9
8	U	3	23.0						
	M	61	22.5	77	22.4	26	22.4	44	22.4
	F	245	25.2	206	25.9	61	26.1	134	26.0
9	U								
	M	15	23.2	16	23.1	14	23.6	18	23.5
	F	92	26.7	114	26.4	57	27.0	73	26.8
10	U								
	M	1	25.0			4	24.0		
	F	19	27.1	22	26.7	17	27.6		
11	U								
	M								
	F	3	27.2						

* U indicates Undetermined sex
M indicates Males
F indicates Females

Table 7. Comparison between back calculated lengths of Muskegon River walleyes and walleyes from other areas.

Location and Date	Total Length at Annulus Formation									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Males										
Red Lakes, Minn. 1940-56	5.4	8.2	10.4	12.0	13.3	14.3	15.0	15.7	16.3	
(Smith 1977)										
Oneida Lk., N.Y. 1939-62	6.1	9.2	11.6	13.4	14.4	15.3	15.9			
(Forney 1965)										
Escanaba Lk., Wis. 1965-1969				13.6	15.3	16.6	17.6	18.9	19.9	
(Kempinger and Carline 1977)										
Lake Puckaway, Wis.	7.5	12.7	15.5	17.0	18.1	18.9	19.6	20.3	21.3	
(Priegel 1966)										
Ethel Lk., Alberta	4.7	8.3	11.4	14.2	16.1	16.9	18.5			
Marie Lk., Alberta	6.3	9.4	13.0	15.0	16.1	17.7	18.5			
Wolf Lk., Alberta	5.9	8.7	10.6	12.6	14.6	15.7	17.3			
(Craig and Smiley 1986)										
Clear Lk., Iowa	7.4	11.8	15.5	17.7	19.1	20.1	22.5			
(Carlander and Whitney 1961)										
Lake Ripley, Wis	6.7	12.9	15.7	16.8	17.2					
Lake Winnebago, Wis.	6.1	10.7	13.0	14.7						
Escanaba Lk., Wis.		10.5	12.5	14.1	15.2	16.2	17.1			
N. Green Bay, Wis.	6.6	10.1	12.8	15.1	17.2	18.6	19.7	24.8	25.8	26.8
S. Green Bay, Wis.	6.6	10.1	15.7	18.5	19.4					
(Niemuth et al. 1962)										
Lower Red Lake, Minn.	5.5	8.4	10.5	12.2	13.5	14.3	15.1	15.6	16.1	
(Smith and Pycha 1961)										
Lake Oahe, S.D.	6.4	11.2	13.7	15.5	16.8	17.9	19.7	21.9	22.6	
(Nelson and Walburg 1977)										
Lake Gogebic, Mich.	4.4	9.3	11.8	13.9	15.2	16.3	16.9	17.3	17.7	18.1
(Eschmeyer 1950)										
Grand Unweighted Average	6.1	10.1	12.9	14.7	16.0	16.8	17.9	19.2	20.0	22.5
Muskegon River 1986-1987	6.2	10.7	14.5	17.1	18.8	20.5	21.6	22.5	23.3	23.6

Table 7 (cont'd).

Location and Date	Total Length at Annulus Formation										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Females											
Red Lakes, Minn. 1940-56 (Smith 1977)	5.5	8.2	10.4	12.1	13.5	14.8	15.9	16.9	18.0		
Oneida Lk., N.Y. 1939-62 (Forney 1965)	6.3	9.5	12.1	14.1	15.5	16.7	17.6				
Escanaba Lk., Wis. 1965-1969 (Kempinger and Carline 1977)				15.5	16.7	18.2	19.9	21.7	22.4		
Lake Puckaway, Wis. (Priegel 1966)	7.8	13.6	17.3	19.6	21.1	22.4	23.6	24.7	25.5		
Ethel Lk., Alberta	4.7	7.9	11.4	14.2	16.1	17.7	19.7				
Marie Lk., Alberta	5.9	9.1	12.2	13.8	15.7	16.9	19.7				
Wolf Lk., Alberta (Craig and Smiley 1986)	5.9	8.7	10.6	13.0	14.6	16.5	18.5				
Clear Lk., Iowa (Carlander and Whitney 1961)	7.4	11.9	15.9	19.0	21.4	22.5	23.5				
Lake Ripley, Wis	6.7	12.0	16.4	18.1	19.5						
Lake Winnebago, Wis.	6.1	10.7	13.2	17.2							
Escanaba Lk., Wis.			15.9	17.0	18.4	19.2					
N. Green Bay, Wis.	6.7	10.2	12.9	15.7	18.1	19.8	21.1	26.8	27.9		
S. Green Bay, Wis. (Niemuth et al. 1962)	6.7	10.2	16.6	19.7	22.0	24.3	27.2	28.0			
Lower Red Lake, Minn. (Smith and Pycha 1961)	5.6	8.3	10.5	12.2	13.6	14.9	15.8	16.7	17.8		
Lake Oahe, S.D. (Nelson and Walburg 1977)	6.4	11.2	13.7	15.9	17.9	18.8	20.4	22.7	24.7		
Lake Gogebic, Mich. (Eschmeyer 1950)	4.9	9.4	12.4	14.5	16.3	17.9	18.9	19.4	20.4	21.0	
Grand Unweighted Average	6.2	10.0	13.4	15.7	17.3	18.5	20.0	22.1	22.3	21.0	
Muskegon River 1986-1987	6.8	11.9	16.3	19.7	21.9	23.6	25.0	26.0	26.6	27.1	27.2

were larger than the estimated length of male walleyes from the Muskegon River system. Back calculated lengths of walleye captured at Croton Dam were less than lengths of male walleyes age I-V and VII captured in Clear Lake Iowa, walleyes age I, III-IV captured in Southern Green Bay and walleyes age I, VIII and IX from Northern Green Bay.

Grand average incremental growth is presented in Figures 9 and 10. Maximum growth in length occurred in the first year of life for both males and females and declined in the following years. The greatest average length increase per year was 6.3 inches (16.0 cm) for males and 6.8 inches (17.3 cm) for females and declined to 0.3 inches (0.8 cm) for males and 0.1 inches (.3 cm) for females. The absolute growth rate in terms of inches per year was usually higher for females than for males but the proportional increase in length at each age was similar.

Walford Plots

Walford (1946) proposed a method of transforming growth increment plots into a straight line by plotting length at age n+1 versus length at age n. The slope of this line (k) is positive and less than one and the higher the k value the more slowly growth approaches a limiting length. The absolute value of the natural logarithm of k provides an estimate of the growth coefficient (K) (Everhart and Youngs 1981). The Walford plot can also be used to determine the

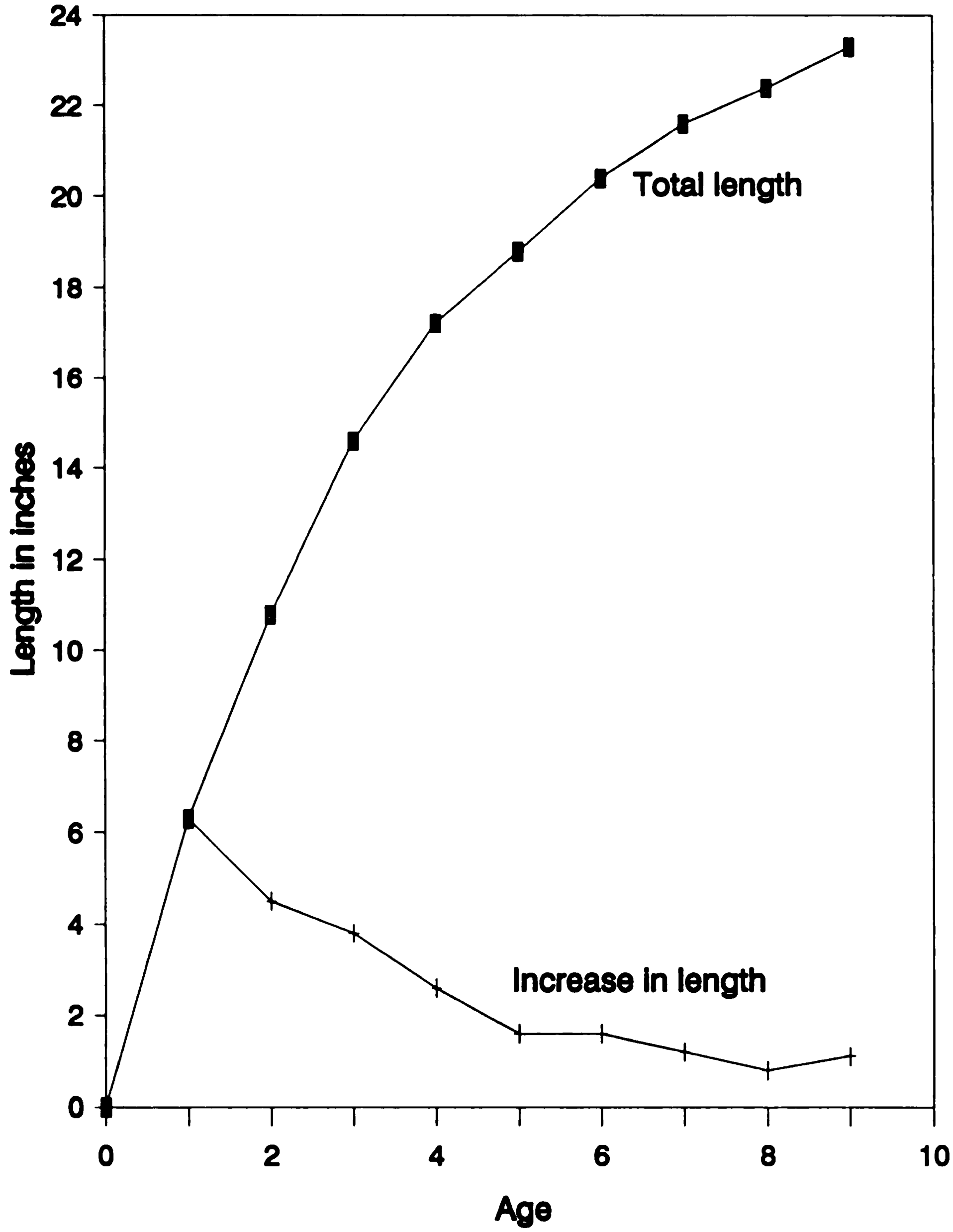


Figure 9. Grand average incremental growth of male walleyes captured at Croton Dam.

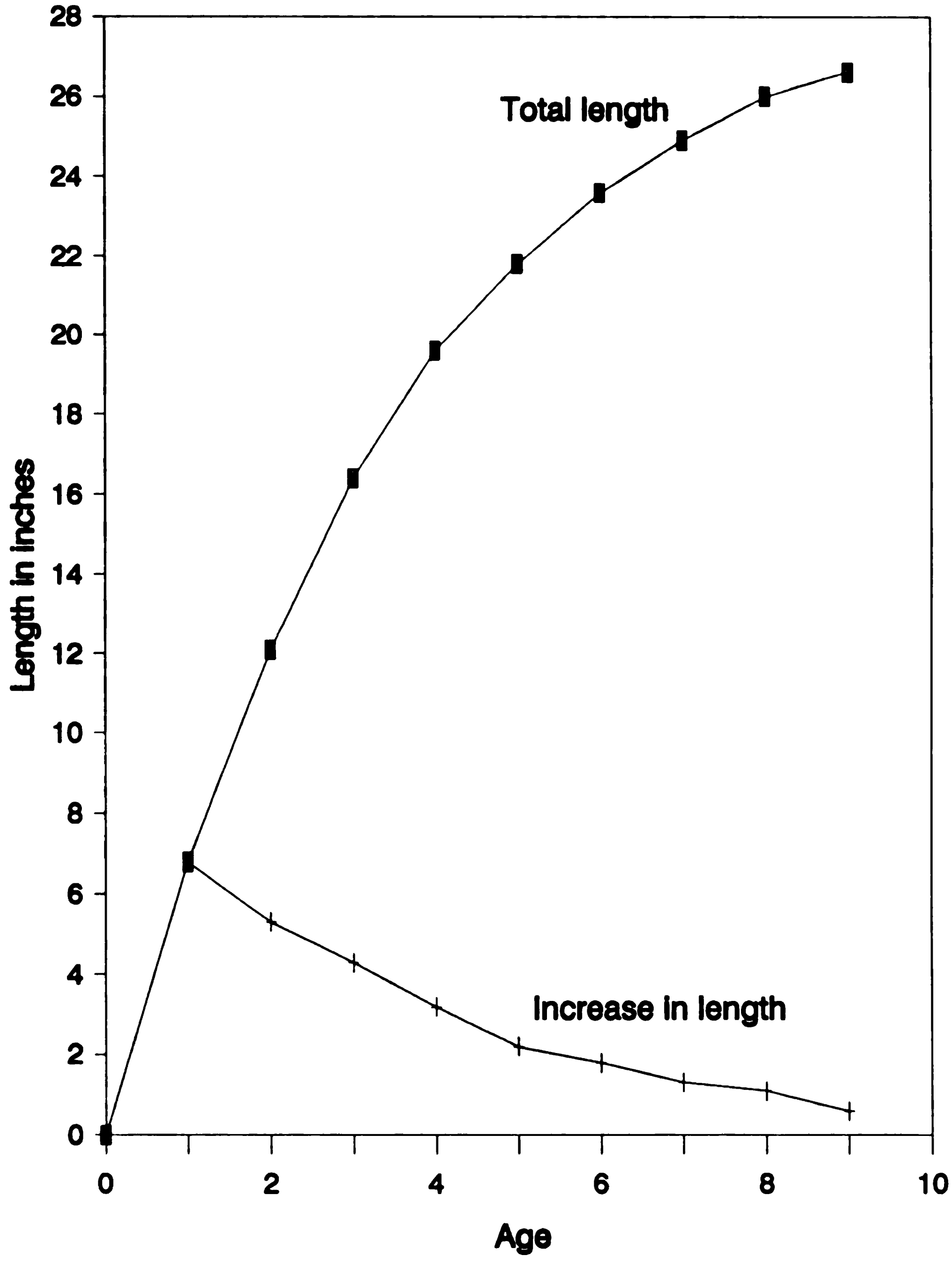


Figure 10. Grand average incremental growth of female walleyes captured at Croton Dam.

limiting length (length at infinity, L_∞) or the theoretical maximum size which is approached but never attained.

In order to compare the growth of Muskegon River system walleyes with other walleye populations a Walford line was plotted. Least-squares linear regression equations of length at age n+1 versus length at age n were calculated for males captured in 1986 and 1987 and females captured in 1986 and 1987. A t-test indicated that there was a significant difference between the y-intercept calculated for 1986 males and 1986 females (t=3.78). However, there was not a significant difference (a=0.05) between slopes and intercepts calculated for males in 1986 and males in 1987 (intercept t=1.896, slope t=1.383) nor was there a significant difference between slopes and intercepts calculated for females in 1986 and females in 1987 (intercept t=0.447, slope t=0.0224). Therefore, two new least squares linear regression equations were calculated, one for all males and one for all females. Walford plots were made for all males and for all females. Since there were only three age XI females and they did not line up well on the plot, a third regression equation was calculated excluding these three fish (Figures 11, 12 and 13). The regression equation for males was: Total Length at Age n+1=6.09+0.7585(Total Length at age n) with an r^2=0.996. The regression equation for all females was: Total length at Age n+1=7.11 +.7522(Total Length at Age n) with an

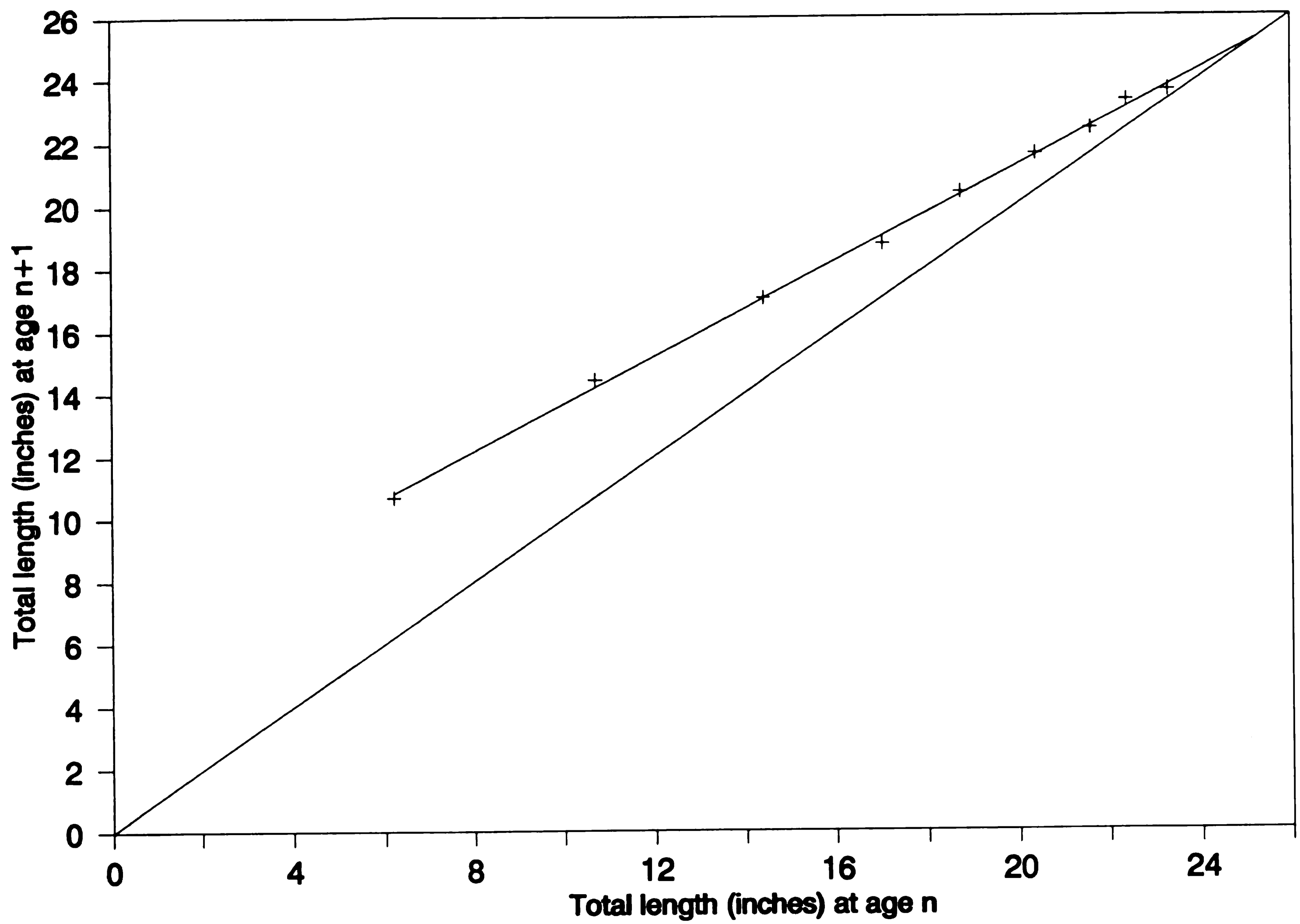


Figure 11. Walford line calculated for males captured at Croton Dam in 1986 and 1987.

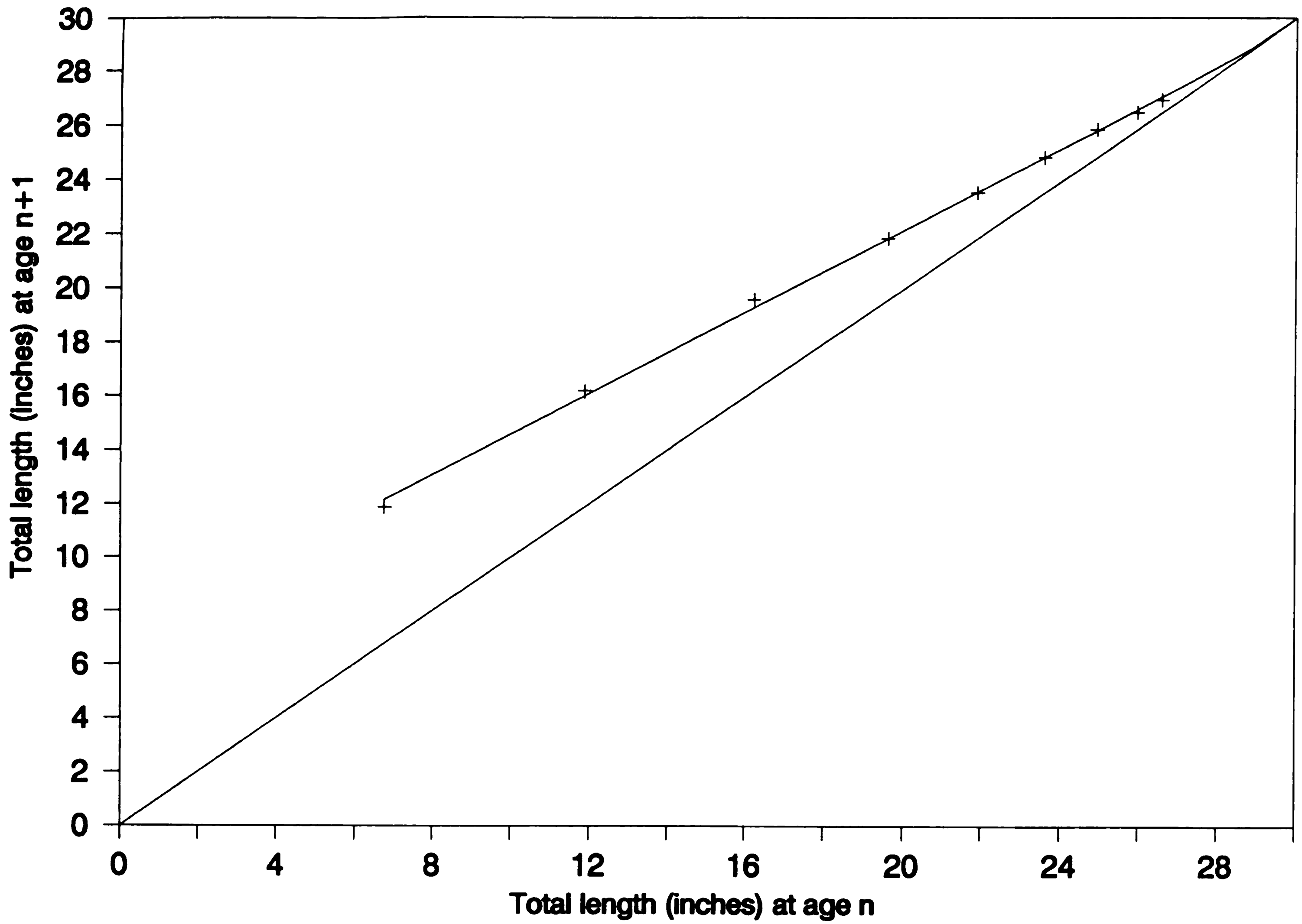


Figure 12. Walford line calculated for females age X and under captured at Croton Dam in 1986 and 1987.

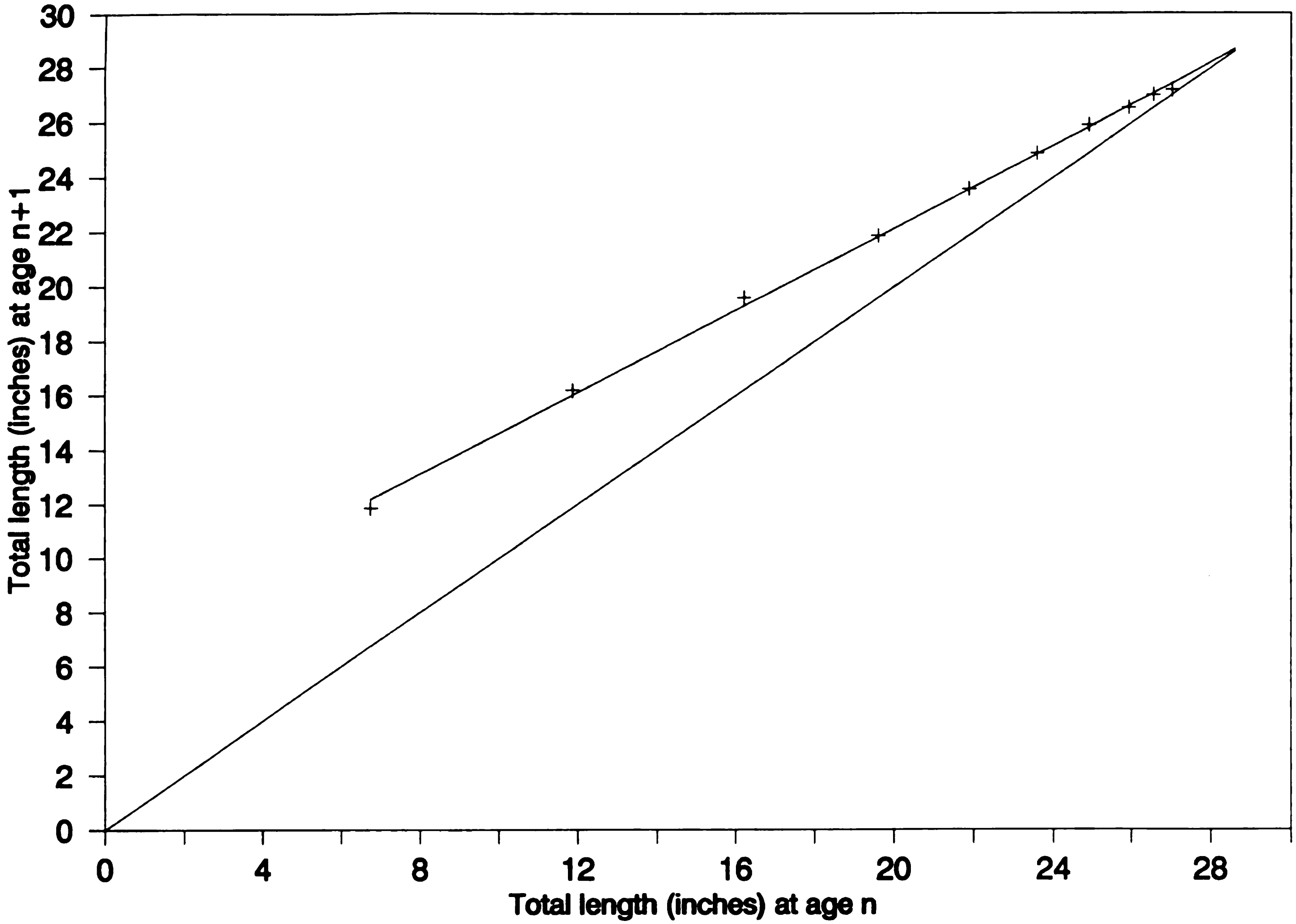


Figure 13. Walford line calculated for females age XI and under captured at Croton Dam in 1986 and 1987.

r^2=0.999. The regression equation for females age X and under was: Total Length at Age n+1=7.04+.7568(Total Length at age n) with an r^2=0.999.

The growth coefficient and the theoretical maximum size were estimated using the following formulae.

$K=e^{-k}$

where:
K= growth coefficient
k= the slope of the Walford line

$L_\infty=a/(1-k)$

where:
L_∞= theoretical maximum size
k= slope of the Walford line
a= intercept from the Walford line

The growth coefficient and the ultimate length can then be used in the von Bertalanffy growth equation to estimate $A_{(0.95)}$ or the age at which 95% of the growth is complete. The von Bertalanffy growth equation is :

$l_t= L_\infty*(1-e^{(-K(t-t0))})$

where:
l_t= length at age t
L_∞= ultimate length or theoretical maximum length
K= growth coefficient
t= age
t_0= theoretical age at length 0.0

In order to calculate $A_{(0.95)}$, an estimate of (t_0) is necessary and can be obtained from the von Bertalanffy equation. According to Everhart and Youngs (1981) "plotting the natural logarithm of $L_\infty-l_t$ against age t should result in a straight line if the data conform to von Bertalanffy's equation and if [the] preliminary estimate of L_∞ is accurate." The least squares linear regressions calculated for males was $Y=3.2273-0.27896(X)$ ($r^2=.996$) and for females less than 11 years old was $Y=3.3631-.2771(X)$ ($r^2=0.998$). The theoretical age at length 0.0 can be calculated from the following formula:

$$t_0=(\text{intercept}-\ln L_\infty)/K$$

where:
t_0= theoretical age at length 0
intercept= Y intercept of plot of $\ln(L_\infty-l_t)$ vs age (t)
K= growth coefficient

The age at which the average walleye reaches a length of 95% of the ultimate length can be calculated from the following derivation of the von Bertalanffy equation:

$$\ln(L_\infty-l_{t0.95})=\ln L_\infty + Kt_0-Kt_{0.95}$$

where:
L_∞=ultimate length
$l_{t0.95}$= 95% of the ultimate length (L_∞*0.95)
K= growth coefficient
t_0= theoretical age at length 0
$t_{0.95}$= age at which 95% of the growth is complete

The ultimate length, growth coefficient, theoretical length at age 0, and age at which 95% of the growth is completed are presented in Table 8. The ultimate length of female walleyes captured at Croton was less than the ultimate length of Ethel and Marie lake females but greater than Wolf Lake females (Craig and Smiley 1986).

Carlander and Whitney (1961) combined males and females to develop a Walford slope. They found that their Walford plot lined up well for ages II through VII but did not give

Table 8. The ultimate length (L inf), growth coefficient (K), theoretical age at length 0.0 (t0), and age (years) at which 95% of the ultimate length has been attained (A0.95).

Location and Date	Sex	L(inf)	K	t0	A0.95
Muskegon River	Males	25.2"	0.2790	0.0016	10.7
1986-1987	Females	28.7"	0.2811	-.0433	10.6
	Females				
	< 11yrs	29.0"	0.2711	-0.0090	10.8
Alberta, Canada					
(Craig and Smiley)					
1985					
Ethel Lk.	Males	59.0 cm	0.2252	-0.0034	13
	Females	76.6 cm	0.1468	-0.1754	20
Marie Lk.	Males	56.4 cm	0.2644	-0.1052	11
	Females	81.2 cm	0.1201	-0.7284	24
Wolf Lake	Males	61.0 cm	0.1628	-0.6758	18
	Females	71.6 cm	0.1305	-0.7618	22
Clear Lake, Iowa					
(Carlander and Whitney)					
1961	Both Sexes				
	Age 1-12	31.1"	0.1791		
	Age 2-7	26.3"	0.2485		
	n,n+1 from				
	individual fish				
	Age 1-12	28.8	0.1887		
	Age 2-7	24.4	0.2783		

a satisfactory fit for ages V through X where the Walford line was approximately parallel to a 45 degree line. They also point out that females appear to grow faster than males from the III through the VI year and that females generally grow faster and live longer. In this case Carlander and Whitney's combined-sexes Walford plot may actually be a combination of two separate lines, one representing males and one representing females. since the Walford plots were calculated using different methods, direct comparisons between Clear lake walleyes and Muskegon walleyes may not be meaningful.

The growth coefficient (K) can be defined as the rate at which length tends toward the asymptote or ultimate length L_∞ (Cushing 1981). Muskegon walleyes had higher growth coefficients than walleye populations in all three Alberta Lakes (Table 8). Male and female walleyes captured in Muskegon Lake had similar growth coefficients and therefore reached 95% of the ultimate length at approximately the same time. On the other hand, males from the three Alberta Lakes had higher growth coefficients than did the females and consequently reached 95% of their ultimate length much sooner. The difference was most dramatic in Marie Lake where the $A_{0.95}$ for females was more than twice the $A_{0.95}$ of males.

Ninety-five percent confidence intervals were calculated for the ultimate length using procedures outlined by Sokal and Rolf (1973) for estimates derived from least-squares linear regression. The 95% confidence interval on the ultimate length of female walleyes (Age X and under) was +/- 0.23 inches (0.58 cm) and for males it was +/- 0.25 inches (0.64 cm). However there were fourteen females and nine males captured at Croton Dam that exceeded their respective ultimate lengths +95% confidence interval. This phenomenon may be due to random variability. Carlander and Whitney (1961) also captured several fish larger than the ultimate length calculated with fish aged II through IV. Although this may be attributed to problems with a plot that includes both sexes, they felt that the phenomenon could be caused by differences in growth patterns for larger fish or a difference in the ability to read the scales (and therefore estimate ages) of larger fish.

Explanations presented by Carlander and Whitney (1961) may also apply to the Muskegon River spawning population. However, because the Muskegon River system is not a closed system immigrants from a faster growing population could move in with the spawning run or slower growing, older individuals sampled at a higher rate could be biasing the estimated ultimate length below the actual ultimate length.

Weight-Length Relationship

The relationship between weight and length can be described mathematically by $W=aL^b$ and is used primarily to estimate either weight or length from the other. Six different weight-versus-length relationships were calculated for Muskegon Lake walleyes since the relationship may be affected by the sex and spawning condition of the fish. Weight-versus-length relationships were calculated for males captured in 1983 and 1987, ripe and green females in 1986 and 1987 and spent females in 1986 and 1987. A t-test was used to determine differences between slopes and intercepts calculated for each year, in each of the three categories, and a significant difference was found between both the slopes and intercepts of the lines calculated for spent females in 1986 and spent females in 1987 (calculated t slopes=2.165, t intercept= 6.967). There was not a statistically significant difference between the slopes and intercepts for the other two groups (ripe and green females 1986 vs ripe and green females 1987 and males 1986 vs males 1987). therefore, two new weight-versus-length relationships were quantified; one for all males and one for all ripe and green females. The slopes and intercepts were tested and no significant difference between slopes or intercepts was detected (Student's t value for the intercepts= 1.157, Student's t value for the slopes= 0.348). One equation was used to quantify the weight-versus-length relationship for all gravid males and females ($\log W = -4.1739 + 3.5598(\log L)$), one equation for spent females measured in

1986 ($\log W = -2.776 + 2.5238(\log L)$) and one equation for spent females captured in 1987 ($\log W = -3.203 + 2.830(\log L)$).

The value of "b" from the log weight versus log length equation can be used as an indicator of fish growth form. A "b" value equal to 3 indicates symmetrical or isometrical growth while a "b" value greater than 3 indicates allometric growth which means the fish are heavier at each length as they grow larger. The value "b" is influenced by spawning conditions and was above three for gravid Muskegon walleyes but below 3 for the spent females.

It is difficult to make generalizations about the growth form for the entire year since growth form estimates are partially dependent on spawning condition and it is also difficult to compare to other studies unless similar methods were used. Spangler et al. (1977) calculated a weight-length relationship of $\log(W) = -5.683 + 3.456 \log(L)$ for gravid walleyes collected in the Moon River, a tributary of Lake Huron, Kempinger and Carline (1977) calculated a relationship of $\log(W) = -5.14 + 3.10 \log(L)$ for walleyes captured while spawning in Escanaba Lake, Wisconsin and Craig and Smiley (1986) calculated a relationship of $\log(W) = -1.69 + 3.044 \log(L)$ for gravid females from Wolf Lake, Alberta. The "b" value for gravid Muskegon River walleyes was greater than "b" values from the other gravid populations indicating that adult Muskegon walleyes were heavier at a given length (Table 9).

Table 9. Constants a and b estimated from length versus weight relationships presented by other investigators. The constant a is dependent on the units of length and and weight but the b value is independent of units. All units are inches and pounds unless otherwise noted.

Location and Date	Log a	b
Muskegon River		
1986-1987		
males and females	-4.17	3.560 (gravid)
Smith and Pycha (1961)		
Red Lks. Minn.	-3.55	3.049
Muth and Wolfert (1986)		
W. Lake Erie 1964-67		
m	-5.69	3.270
f	-5.73	3.292
1974-1977		
m	-5.71	3.280
f	-5.88	3.344
1981-83		
m	-6.03	3.386
f	-6.12	3.422
Kempinger and Carline (1977)		
Escanaba Lake, Wis. 1965-69	-5.14	3.10 (gravid)
Carlander and Payne (1977)		
Clear Lk., Iowa	-5.41	3.141
Spangler et al. (1977)	(units are cms and kgs)	
Lk Huron		
Mississagi River	-4.77	2.907
Moon River	-5.68	3.456 (gravid)

Although the "b" value yields information about growth forms, variations in weight at age between populations can be seen more clearly by back calculating weight at each year of life using estimated lengths and a weight-versus-length relationship. The lengths and weights of the seventeen juveniles captured in 1986 were combined with all gravid adults and a new regression equation was calculated: LogW=3.7667+3.2578(LogL). this relationship was used to estimate weights at each age. Average back calculated weights at each age and average actual weights measured from gravid walleyes captured at Croton Dam are presented in Table 10. The actual weights and the back calculated weights are generally similar for walleyes aged V through VII. Since back calculated lengths were used to estimate weights it is not surprising that the average measured weights of age III male walleyes and age IV female walleyes were higher than estimated weights. The same phenomenon was noted for back calculated lengths and attributed to the capture of faster growing members of the younger year classes.

Muskegon River system walleyes were heavier at each age than walleyes captured by Kempinger and Carlander (1977) in Escanaba Lake, Wisconsin and by Smith (1977) in Red Lakes Minnesota (Table 11). However, walleyes (males and females combined) from Western Lake Erie were heavier than walleyes captured in the Muskegon River (Regier et al. 1969). This

Table 10. Actual weights (pounds) of gravid walleyes captured at Croton Dam compared to back calculated weights of gravid walleyes.

		1986				1987			
Age	Sex*	Number	Actual Weight	Number	B-Calc. Weight	Number	Actual Weight	Number	B-Calc. Weight
1	U								
	M			427	0.07			167	0.07
	F			550	0.09			46	0.09
2	U								
	M			427	0.41			167	0.48
	F			550	0.56			46	0.76
3	U					1	0.70		
	M	7	1.31	427	1.07	1	1.30	167	1.23
	F			550	1.59			46	1.91
4	U		1.64						
	M	70	1.84	420	1.82	10	1.18	166	1.96
	F	7	3.00	550	2.91	1	4.50	46	3.07
5	U	13	1.96			1	3.50		
	M	127	2.17	350	2.47	37	1.77	156	2.61
	F	38	3.86	543	4.10	6	4.77	45	4.18
6	U	3	3.32			2	1.25		
	M	63	3.16	223	3.24	29	2.45	119	3.31
	F	75	5.49	505	5.19	7	4.93	39	5.15
7	U	5	4.22						
	M	83	3.82	160	3.86	46	3.58	90	3.96
	F	153	6.83	430	6.18	3	6.67	32	6.27
8	U	3	4.46						
	M	61	4.47	77	4.40	26	3.67	44	4.43
	F	192	7.87	277	7.03	17	7.92	29	7.01
9	U								
	M	15	4.84	16	4.82	14	4.73	18	5.05
	F	69	8.50	85	7.51	8	8.64	12	7.73
10	U								
	M	1	7.10		4.34	4	5.05	4	5.53
	F	13	8.96	16	7.79	4	9.78	4	8.85
11	U								
	M								
	F	3	8.60	3	8.07				

* U indicates undetermined sex
M indicates Males
F indicates Females

Table 11. Back calculated weights (pounds) of Muskegon River walleyes compared to average weights of walleyes from other areas.

Location and Date	Sex	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
		Average Weight at each Age										
Red Lakes, Minn.	m	0.05	0.18	0.36	0.58	0.79	0.95	1.12	1.29	1.44		
Smith and Pycha (1961)	f	0.05	0.18	0.36	0.59	0.82	1.08	1.34	1.62	1.98		
Western Basin, Lk. Erie Regier et al. (1969)	comb.		1.19	2.11	3.09	3.80	4.96	6.87	8.54			
Escanaba Lake, Wis. Kempinger and Carline (1977)	comb.		0.31	0.56	0.85	1.28	1.75	2.32	3.05	3.71		
Muskegon River (1986-1987)	m	0.07	0.43	1.11	1.86	2.52	3.27	3.89	4.41	4.94	5.29	
	f	0.09	0.57	1.60	2.91	4.10	5.18	6.17	7.00	7.55	8.06	8.07

is especially noteworthy since the weights of females alone may have been substantially higher if they were not averaged together with the males.

The larger, spent females captured in 1987 were heavier than spent walleyes of the same length captured in 1986. It was surprising that only spent females showed a difference in length-weight relationships between years. The difference may be attributable to a difference in sampling techniques between the two years. In 1986, most of the spent female walleyes were spent when they were captured and weighed as such. However, in 1987, most of the spent walleyes were fish that had been kept for eggs and were weighed after fisheries personnel removed the eggs. Eschmeyer (1950) estimated that up to 2.8% of the eggs were left in the ovaries of females that spawned naturally. Field personnel may have removed a lower percentage of eggs than would have been spawned out naturally.

If the assumption is made that all of the fish are from the same population (not sub-populations arriving from different areas and ripening at different times) then the difference in weights between gravid fish and spent fish could be attributed entirely to the loss of eggs. The difference in weight at each length is plotted in Figure 14 and females 28 inches (71 cm) would yield roughly 1.0 to 1.3 pounds (0.45 to .60 kg) of eggs. It may be useful in some modeling exercises to calculate the change in biomass from

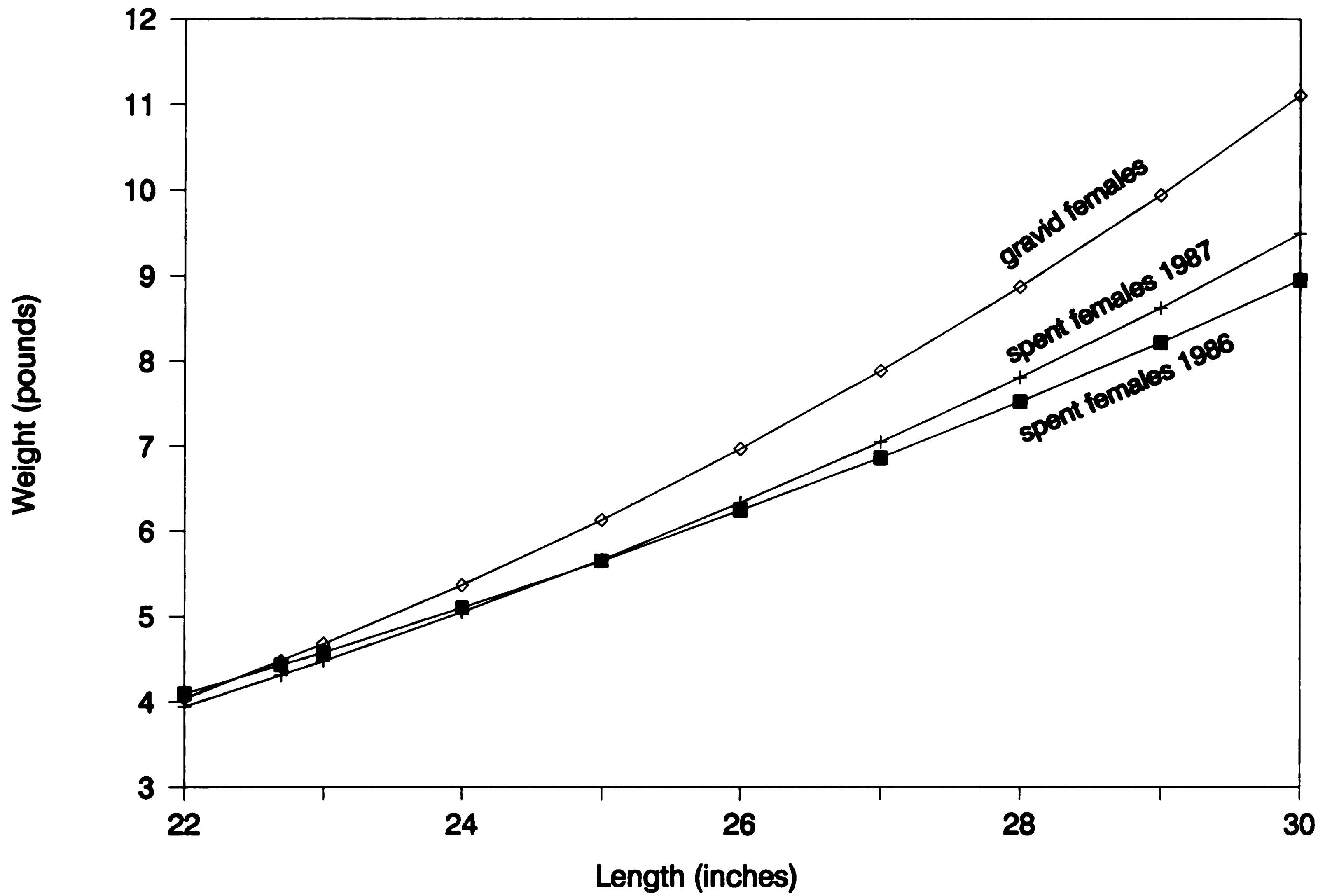


Figure 14. A comparison between estimated weights of gravid females and spent females captured in 1986 and 1987.

pre-spawning to post spawning populations and to calculate the biomass devoted to egg production. However, no attempt was made to calculate these estimates.

Instantaneous Growth Rates

Instantaneous growth rates were computed using back calculated weights and the following formula:

$$G = \ln(W_{n+1}) - \ln(W_n)$$

where:

G= instantaneous growth rate
W= weight
n= age
ln= natural logarithm

It was noted earlier that female walleyes from the Muskegon River system usually had a slightly higher absolute growth rate at all ages than their male counterparts and instantaneous growth rates followed the same trend (Figure 15). Instantaneous growth rates are often used in modeling and Kempinger and Carline (1977) used instantaneous growth rates with mean biomass to calculate production and equilibrium yields. Thus they were able to calculated peak yields using different size limits and predict the consequences of different size limits. Also, Carlander and Payne (1977) correlated instantaneous growth rates with stocking density, water temperature and water levels in order to determine how density dependent and density independent factors influenced walleye growth.

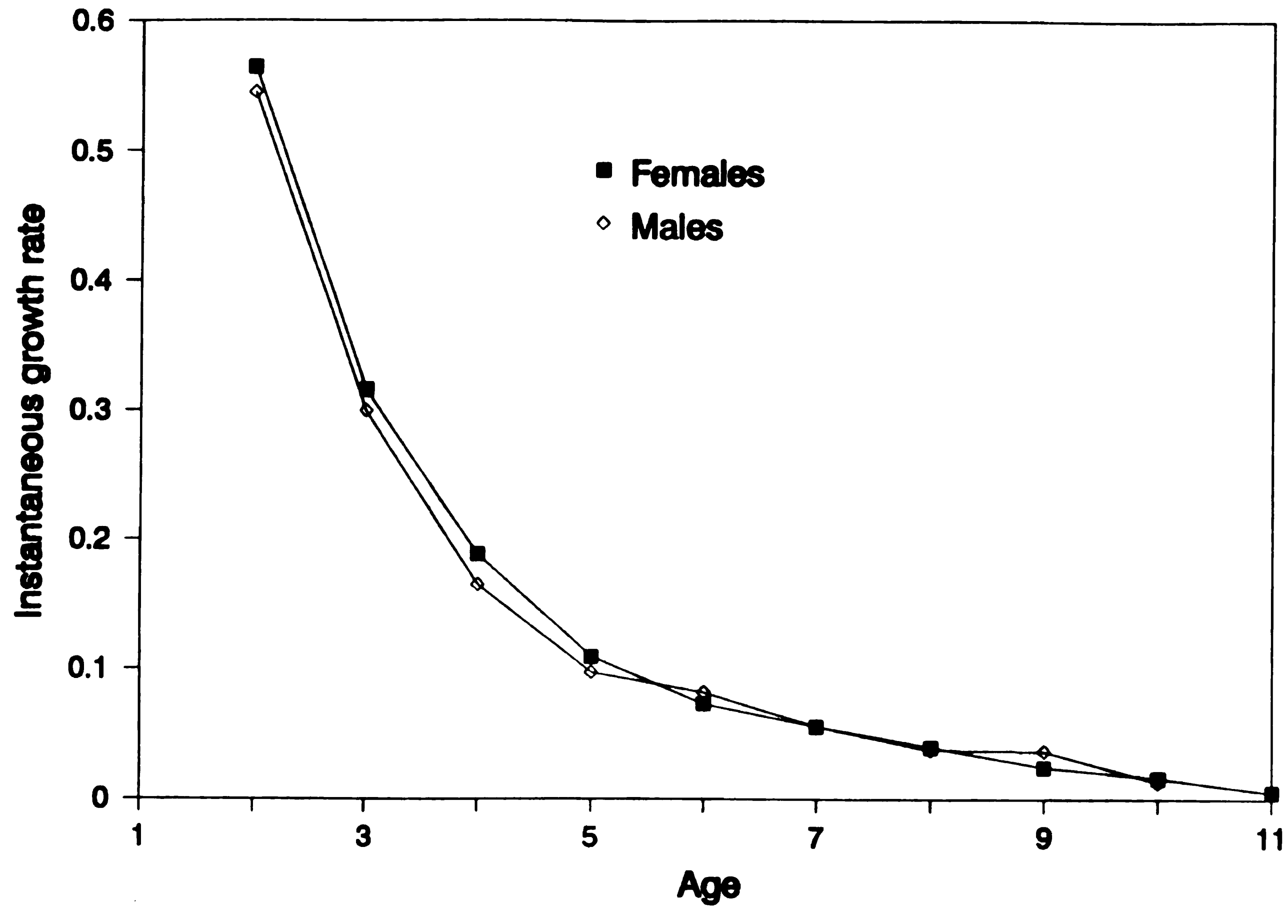


Figure 15. Instantaneous growth rates at each age for male and female walleyes captured at Croton Dam.

Fecundity

The fecundity estimates with 95% confidence intervals for Muskegon walleyes ranged from 65,723 +/- 1993 eggs in a 19.6 inch (49.8 cm), 4.1 pound (1.9 kg) walleye to 377,687 +/- 10,640 eggs in a 25.5 inch (64.8 cm), 7.8 pound (3.5 kg) walleye. Fecundity versus total length and weight are plotted and in Figures 16 and 17. Linear regression equations were calculated for fecundity versus total length and total weight relationships and for Log fecundity versus Log total length and versus Log weight. The r^2 values were closer to unity using the log-log transforms. Therefore the log-log transformation was used. A Student's t-test was used to compare slopes and intercepts from 1986 and 1987 regression equations and fecundity data were combined after no significant difference between slopes and intercepts was detected (alpha=0.05). The fecundity versus length equation is: log fecundity (eggs per female)= -0.8698 + 4.455(log total length in inches) with an r^2 = 0.860 while the fecundity versus weight equation is: log fecundity (eggs per female)= 4.1865 + 1.355(log weight in pounds) with an r^2 = 0.811.

In order to determine the reproductive potential of a spawning population it is helpful to know which variables will provide the best estimate of fecundity. Wolfert (1969)

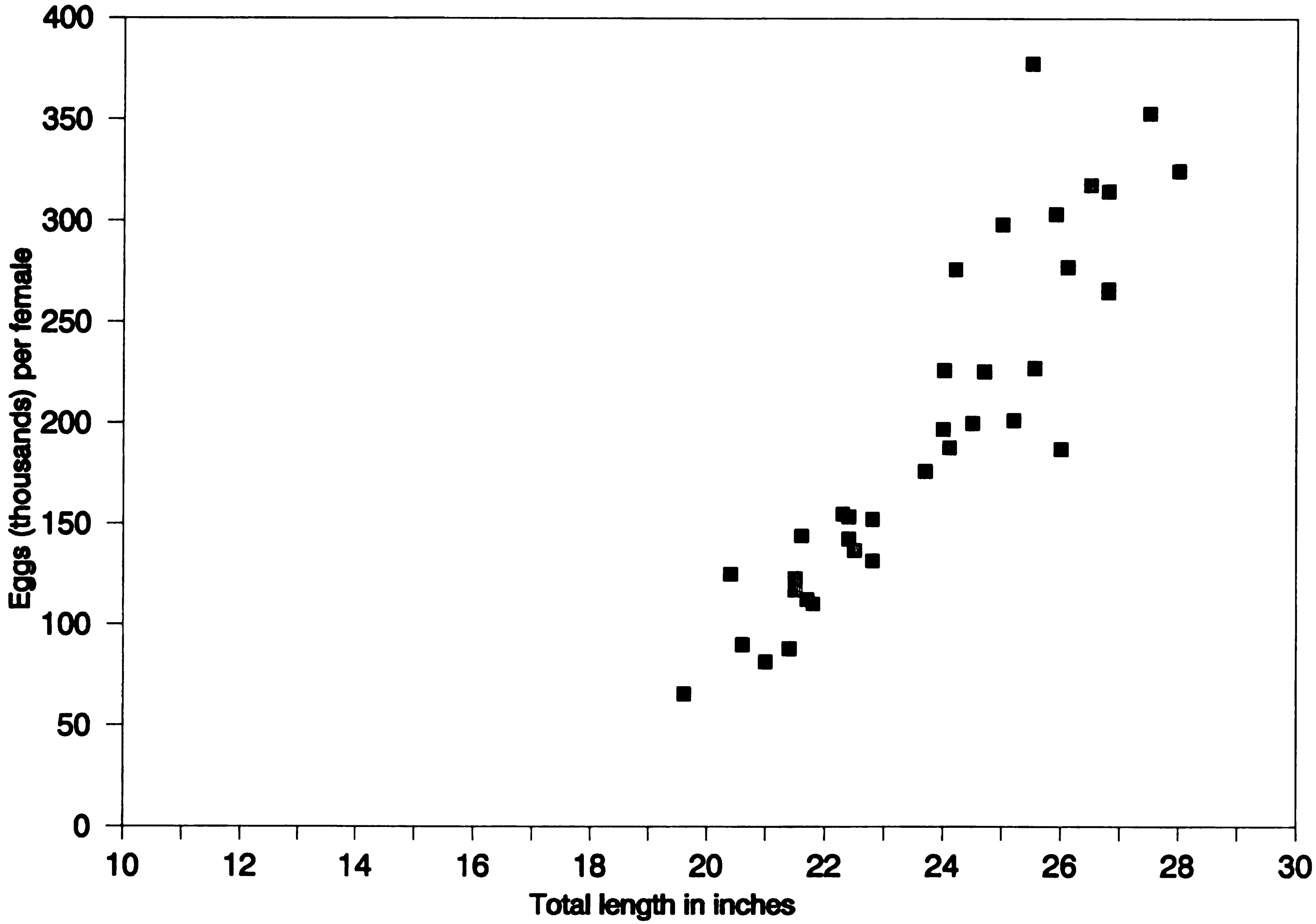


Figure 16. Fecundity of Muskegon River walleyes versus total lenght in inches.

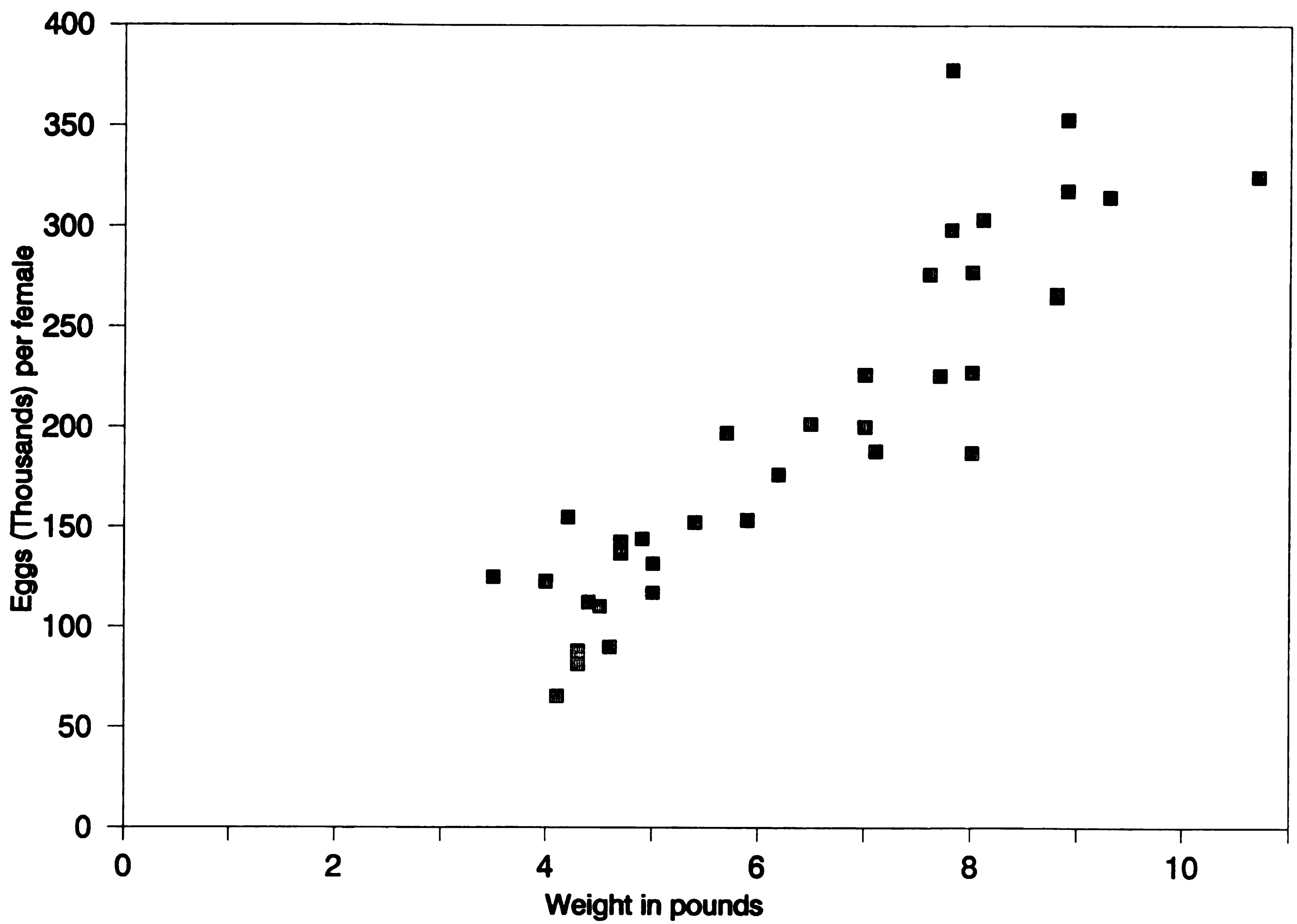


Figure 17. Fecundity of Muskegon River walleyes versus weight in pounds

calculated a multiple regression equation using Lake Erie walleyes then calculated standard partial regression coefficients (SPRC) of each variable on fecundity. The relative importance of each variable was then ranked according to the magnitude of the standard partial regression coefficient (Snedecor and Cochran 1967).

Wolfert used a log-log transformation and found that weight was a better predictor of fecundity than was length. However, the SPRC calculated for Muskegon walleye indicate that (log)length (SPRC=0.7673) was a better indicator of fecundity that (log) weight (SPRC=0.1678). Serns (1982) found that both length and weight were linearly related to fecundity and that fecundity was most highly correlated with length from walleye captured in Escanaba Lake, Wisconsin, in 1980. Craig and Smiley (1986) used length as a predictor of fecundity and found that the relationship was curvilinear.

In order to compare present fecundity estimates to past estimates the fecundity of 10 walleyes captured at Newaygo Dam in 1947 were plotted against total length (log fecundity vs log length) and a least squares linear regression equation was calculated. The fecundity predictor equations calculated from 1986-1987 data and 1947 data were plotted along with 95% confidence intervals of each line (Figure 18). The fecundity of walleyes captured in 1986-1987 was similar to 1947 predicted fecundities for the smallest fish but lower for the medium and large sized fish. However, at

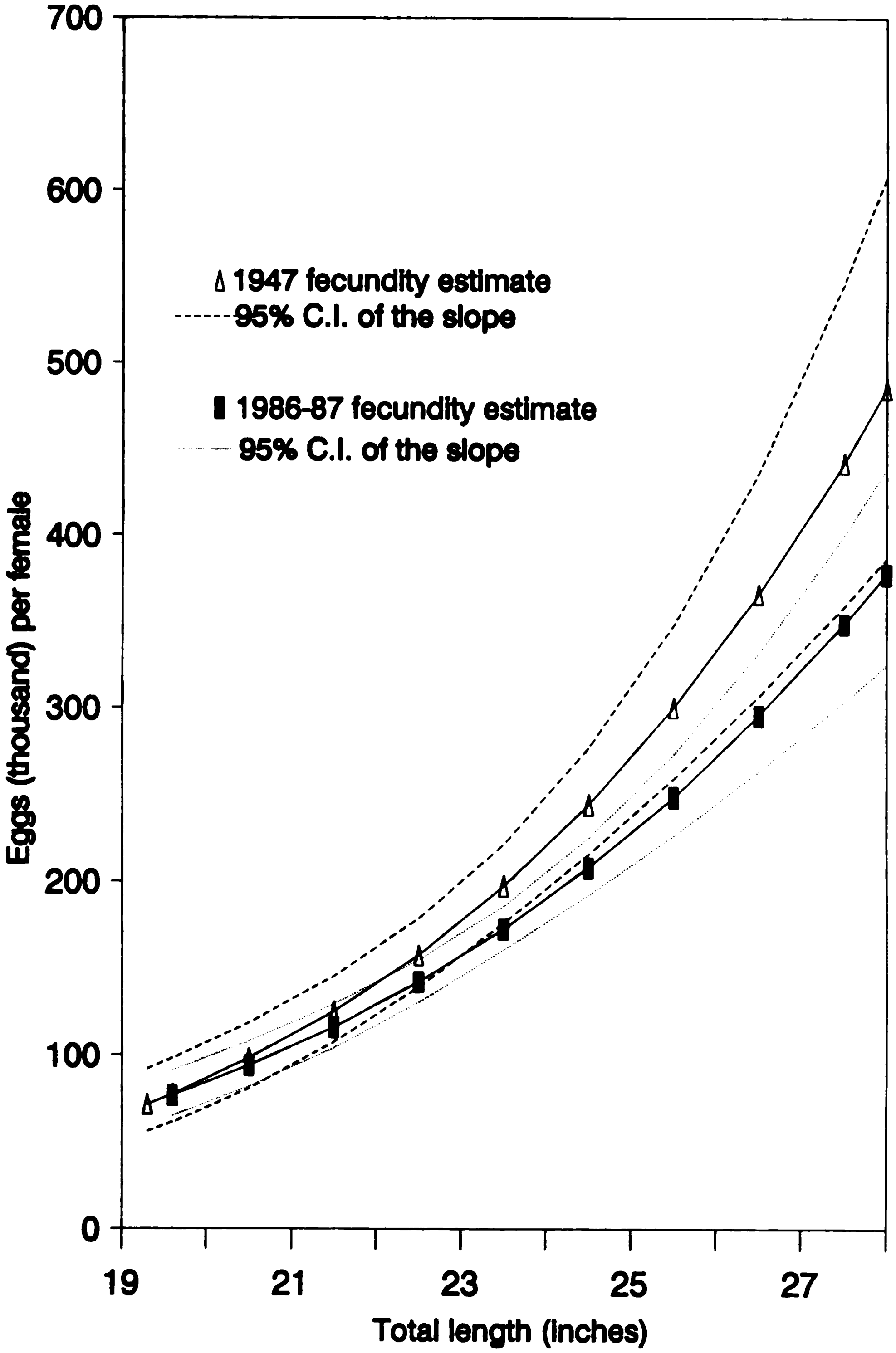


Figure 18. A comparison between fecundities estimated in 1947 and fecundities estimated in 1986-87.

no point were fecundity estimates statistically significantly different.

Although the difference between estimated fecundities was not significant, it is possible that fecundity may vary over time. One reason for the apparent decline in fecundity from 1947 to 1986-1987 could be a change in the level of intraspecific competition for food. Scott (1962) conducted laboratory experiments and made field observations of rainbow trout (Oncorhynchus mykiss) and noted that a lack of food caused the fish to absorb eggs and that increased intraspecific competition for food decreased fecundity. If the same phenomenon occurs in walleyes then an increase in intraspecific competition for food would decrease the number of eggs per female. Walleye populations were estimated to be more than twice as large in the late 1940's to early 1950's. However, present populations may be staying in the River system and although spawning populations are smaller, the number of fish remaining in the Muskegon River System all year may have increased and therefore intraspecific competition in the Muskegon River system may have increased. Data are not available to document changes in intraspecific competition for food.

The apparent decline in fecundity could also be due to a genetic shift in the population. Wolfert (1969) felt that fecundity differences between walleye populations in the East and West basins of Lake Erie could be due to racial differences between two discrete populations. It is possible that the Muskegon River population has genetically shifted over the past forty years.

Fecundity estimates reported by other investigators are presented in Table 12. In most cases the largest Muskegon River walleye had higher fecundities than comparably sized walleyes from other systems. Walleyes from both basins of Lake Erie had higher fecundities than Muskegon walleyes. Again, higher estimates of fecundity of Muskegon River walleyes could indicate genetic differences between Muskegon walleyes and other walleye populations or the relative level of intraspecific competition for food could be less in the Muskegon River.

Larval Walleyes

A total of 460 yolk-sac larval walleyes and 45 eyed-up walleye eggs were taken from 72 drift net samples during the spring of 1986. Of the 72 samples collected over three sampling dates, 56 samples contained yolk-sac walleyes or eyed-up walleye eggs. The maximum number of larval walleyes collected in one sample was 42 taken from each of two bottom drift net samples on May 3 at the Maple Island Station (Table 13). Total densities ($\#/m^2$) were calculated for each station at each depth and plotted against river miles downstream of Croton Dam (Figure 19). Densities in samples containing larval walleyes or eyed-up eggs ranged from 0.005

Table 12. Fecundity estimates of walleyes from the Muskegon River system compared to estimates reported by other investigators. All units are English unless otherwise noted.

Investigator, Date and Location	Sample Size	Length Range	Average Length	Average Weight	Average Fecundity	predictor equation
Eschmeyer (1950)	6	16-16.9	16.6	1.7	44,854	
Lake Gogebic,	7	17-17.9	17.5	2.0	52,020	
Michigan, 1947	6	18-18.9	18.6	2.6	79,020	
	6	19-19.9	19.4	2.8	74,392	
	5	20-20.9	20.5	3.4	103,574	
	1	21-21.9	21.1	4.0	110,571	
	3	22-22.9	22.3	4.1	115,888	
Wolfert (1969)	60			4.0	114,187 @	Log(F)=0.906+1.274Log(W gm)
				8.0	276,140 @	
W. Basin Lk. Erie	78			4.0	145,025 @	Log(F)=1.541+1.111Log(W gm)
				8.0	313,980 @	
Johnson (1971)	1	16-16.9	16.6	1.6	52,900	
Little Cut Foot	5	17-17.9	17.4	1.9	47,840	
Sioux Lake,	6	18-18.9	18.5	2.3	66,050	
Minn., 1942-1969	5	19-19.9	19.3	2.7	78,360	
	4	20-22.9	20.1	2.8	84,925	
	1	21-21.9	21.6	3.8	84,500	
	2	22-22.9	22.6	4.1	123,150	
	6	23-23.9	23.4	4.8	160,117	
	2	24-24.9	24.1	5.2	162,500	
Serns (1982)						
Escanaba Lake, Wis.						
1979	48			2.0	70,700 @	F=14,300+28,200(W)
				6.0	183,500 @	
1980	46			2.0	53,500 @	F=3,100+25,200(W)
				6.0	154,300 @	
1981	57		20.0		177,899 *	F=-101+8900(L)
			22.5		200,149 *	
			25.0		222,399 *	
Craig and Smiley (1985)	42		14.6		48,000 *	Log(F)=0.856+2.441Log(L cm)
Wolf Lake, Alberta			18.5		87,000 *	
Muskegon River, Mich.	37		20.0		84,390 *	Log(fec)=-0.8698+4.455Log(L)
1986-1987				4.0	100,529 @	Log(Fec)=4.1865+1.355Log(W)
			22.5		142,618 *	
				6.0	174,138 @	
			25.0		228,046 *	
				8.0	257,150 @	
			27.5		348,680 *	

* Calculated with the corresponding fecundity versus length relationship
@ Calculated with the corresponding fecundity versus weight relationship

Table 13. Current velocity, water volume filtered, duration of sampling, number and density of walleyes captured at six locations in the Muskegon River, on April 26-27, May 3, and May 9, 1986.

Date, Location and replicate

April 26-27, 1986

		Pine Sreet public access		High Rollaway public access		Newaygo City Park		Anderson Flats public access		Bridgeton public access		Maple Island public access	
	Replicate	surface	bottom	surface	bottom	surface	bottom	surface	bottom	surface	bottom	surface	bottom
Current Velocity (m/sec)	a	0.172	0.616	0.434	0.620	0.393	0.313	0.855	0.889	0.857	0.658	0.705	0.522
	b	0.644	0.730	0.456	0.606	-	0.355	1.037	0.948	0.766	0.637	0.601	0.499
Water Volume Through Net (cu.m)	a	16.55	59.13	50.01	59.55	30.01	26.44	155.98	110.94	86.34	65.86	67.66	54.73
	b	86.55	77.11	53.60	79.15	34.08	8.02	106.15	79.64	73.49	63.68	59.57	49.94
Depth of Bottom Net (m)	a		0.52		0.55		1.12		1.74		1.39		1.04
	b		0.78		0.52		0.69		1.25		-		1.35
Duration of Sampling (min.)	a	10:00	10:00	12:00	10:00	7:00	10:00	19:00	13:00	10:30	10:25	10:00	10:20
	b	14:00	11:00	12:15	12:30	-	10:00	8:45	10:40	10:00	10:25	10:20	10:25
Number of Larvae	a	8	9	6	2	3	2	28	14	2	1	3	14
	b	4	8	3	2	0	1	7	18	6	5	4	8
Number of Eggs	a	25	1	1	1	0	0	1	5	0	0	0	1
	b	2	4	0	0	0	0	0	0	0	1	0	2
Total Number of Eggs and Larvae		61		15		6		73		15		32	
Total Volume (cu. m)		239.34		242.31		98.55		452.71		288.36		231.91	
Density (#/cu. m)		0.255		0.062		0.061		0.161		0.052		0.138	

Table 13 (cont'd.)

May 3, 1986

		Pine Sreet public access		High Rollaway public access		Newaygo City Park		Anderson Flats public access		Bridgeton public access		Maple Island public access	
	Replicate	surface	bottom	surface	bottom	surface	bottom	surface	bottom	surface	bottom	surface	bottom
Current Velocity (m/sec)	a	0.641	0.500	0.855	0.868	1.220	0.216	1.105	0.812	0.801	0.599	0.772	0.642
	b	0.628	0.576	0.909	0.698	1.204	0.761	0.948	0.794	0.806	0.691	0.771	0.619
Water Volume Through Net (cu.m)	a	61.54	47.99	80.28	86.51	114.38	21.26	96.60	79.85	76.91	58.56	73.35	62.16
	b	61.63	55.77	87.70	69.91	111.74	88.14	91.30	80.60	77.40	65.56	74.29	58.59
Depth of Bottom Net (m)	a		0.75		0.87		1.21		0.868		1.20		1.17
	b		0.75		2.54		1.21		1.35		1.50		1.36
Duration of Sampling (min.)	a	10:00	10:00	9:47	10:23	9:45	10:15	9:55	10:15	10:00	10:11	9:54	10:05
	b	10:13	10:05	10:03	10:20	9:40	12:05	10:00	10:33	10:00	9:53	10:00	9:52
Number of Larvae	a	7	4	2	34	12	1	7	15	8	17	3	42
	b	5	12	5	10	13	3	9	9	4	18	5	42
Number of Eggs	a	0	2	0	0	0	0	0	0	0	0	0	0
	b	0	0	0	0	0	0	0	0	0	0	0	0
Total Number of Eggs and Larvae		30		51		29		40		47		92	
Total Volume (cu. m)		226.93		324.40		335.52		340.08		278.43		268.39	
Density (#/cu. m)		0.132		0.157		0.086		0.118		0.168		0.343	

Table 13 (cont'd.)

May 9, 1986

	Replicate	Pine Sreet public access surface	Pine Sreet public access bottom	High Rollaway public access surface	High Rollaway public access bottom	Newaygo City Park surface	Newaygo City Park bottom	Anderson Flats public access surface	Anderson Flats public access bottom	Bridgeton public access surface	Bridgeton public access bottom	Maple Island public access surface	Maple Island public access bottom
Current Velocity (m/sec)	a	0.699	0.557	0.581	0.444	0.964	0.514	0.899	0.777	0.622	0.553	0.822	0.608
	b	0.688	0.610	0.589	0.481	0.923	0.500	0.865	0.784	0.623	0.692	0.826	0.597
Water Volume Through Net (cu.m)	a	67.07	53.49	55.79	42.63	92.56	49.34	86.29	74.57	59.70	53.06	78.95	58.37
	b	66.00	58.59	56.58	46.14	90.71	47.94	83.04	75.27	61.33	66.40	79.29	57.82
Depth of Bottom Net (m)	a		1.03		2.12		1.0		1.03		1.27		1.43
	b		1.00		2.12		0.85		1.12		1.09		1.27
Duration of Sampling (min.)	a	10:00	10:00	10:00	10:00	10:00	10:00	10:00	10:00	10:00	10:00	10:00	10:00
	b	10:00	10:00	10:00	10:00	10:00	10:15	10:00	10:00	10:15	10:00	10:00	10:05
Number of Larvae	a	0	0	0	0	0	0	0	3	3	0	1	3
	b	1	0	0	0	2	0	0	2	2	0	0	2
Number of Eggs	a	0	0	0	0	0	0	0	0	0	0	0	0
	b	0	0	0	0	0	0	0	0	0	0	0	0
Total Number of Eggs and Larvae		1		0		2		5		5		6	
Total Volume (cu. m)		245.15		201.14		280.55		319.17		240.49		274.45	
Density (#/cu. m)		.004		-		.007		.016		.021		.022	

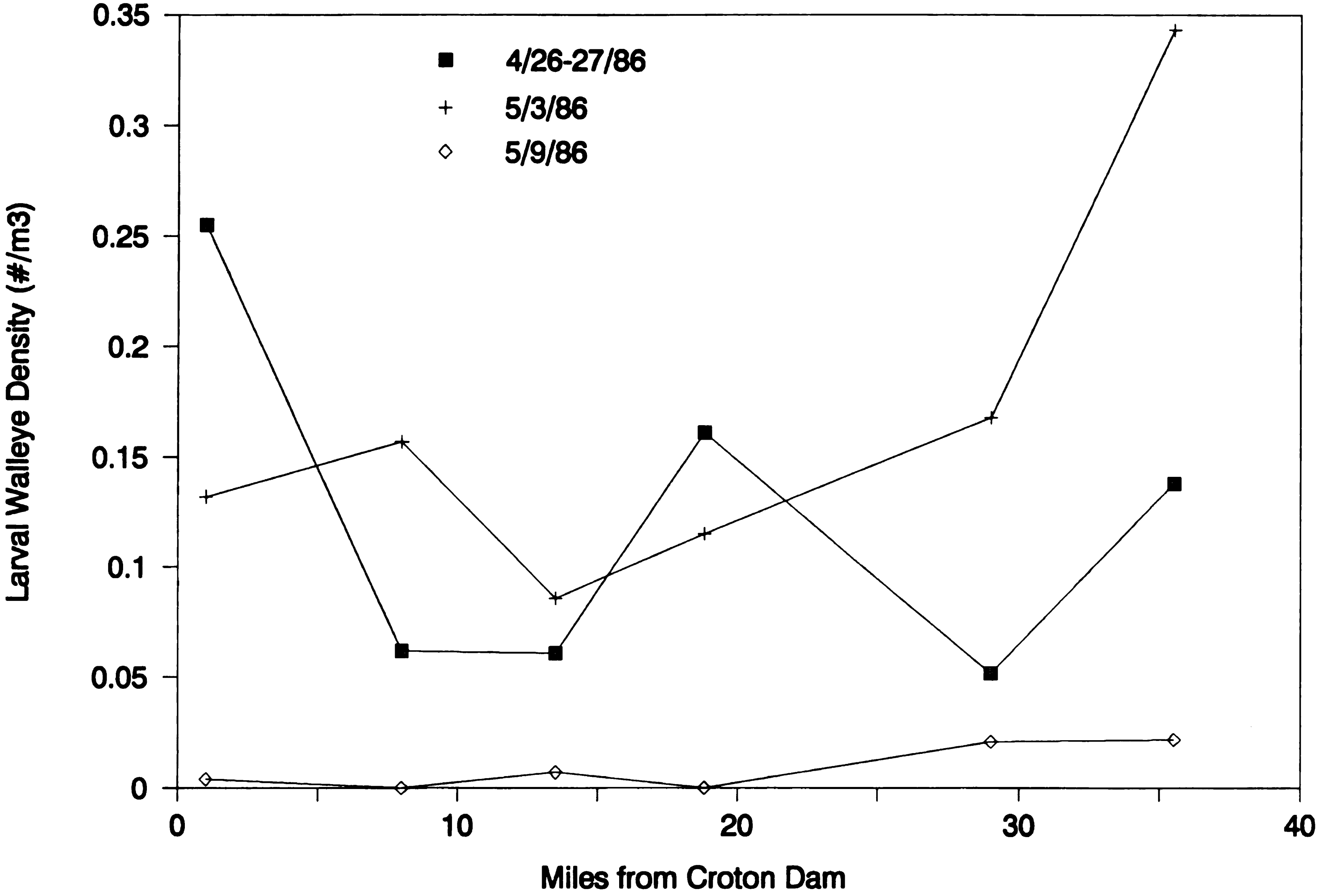


Figure 19. Total densities of larval walleyes and eyed-up eggs at six stations on the Muskegon River.

per m^3 to 0.343 per m^3 and it appears that the peak densities of larval walleyes shifted downstream during the sampling period and that most of the larvae had drifted out of the study area or had died by the second week in May.

Other fish species captured in drift nets during the spring of 1986 included 129 white sucker larvae and eight white sucker eyed-up eggs, 31 yolk sac johnny darters (Ethostoma nigrum) and one juvenile chinook salmon (Oncorhynchus tshawytscha). The white sucker peak drift density appeared to lag behind that of the larval walleyes. Many white sucker adults were spawning at Croton Dam toward the end of the walleye run and were electroshocked during the egg-take.

Corbett and Powles (1986) studied larval walleyes and larval white suckers in Apsley Creek, Ontario and observed that larvae were unable to maintain their position in slow-water zones during periods of diminished light when they apparently lost their ability to orient visually. Peak drift in the stream studied by Corbett and Powles (1986) occurred between 2100 and 0100 hours at mid-depth stations. They also observed that larvae were kept in suspension in areas of Apsley Creek with relatively strong currents. As the current velocity decreased the larvae sank down in the water column.

Priegel (1970) used one meter diameter drift nets to capture larval walleyes in Spoehr's Marsh on the Fox River,

Wisconsin and found that peak larval walleye drift out of the marsh occurred between 1300 and 1400 hours. He also noted that most fry were taken from mid-water depths. Relatively few fry were taken in surface, bottom or shore nets. Priegel noted that numbers of fry captured in the drift nets increased with an increase in velocity of water moving through the marsh because the fins of the fry were not developed enough to allow them to move about freely. Although peak drift out of the marsh occurred in the afternoon, peak movement downstream occurred from 0100 to 0300 hours, similar to the peak movements found by Corbett and Powles.

Corbett and Powles found that larval walleyes, using visual and tactile cues, could hold their position in slow moving areas with currents of 0.5 cm/sec or less. Houde (1969) also determined that in laboratory experiments most larval walleyes could hold their position at current velocities of 0.5 cm/sec but all newly hatched larvae drifted uncontrollably at current velocities greater than 7.0 cm/sec. The water velocity entering drift nets at all stations in the Muskegon River was much higher than 7.0 cm/sec and ranged from 17.2 cm/sec to 122.0 cm/sec. Since current velocities in the Muskegon River were much greater than those recorded by Corbett and Powles for Apsley Creek, temporal or spatial differences in larval drift may not have been as pronounced in the Muskegon River. Also, the role of abundant detrital drift in dislodging eggs or larval walleye from Muskegon River substrate is unknown.

Corbett and Powles made no attempt to quantify larval walleye densities in Apsley Creek but they captured 300 larval walleyes while continuously fishing for two days in early May. Priegel (1970) captured up to 229 larval walleyes in a one meter diameter net set for 15 minutes at the outlet of Spoehr's Marsh, Wolf River in 1960-1967, and of 52 samples that contained walleyes the average number of fry per sample was 17.1. The average number of larvae and eyed-up eggs, in the 56 Muskegon River samples with walleyes, was nearly nine walleyes or eggs per net while the maximum number was 42. Again, the nets were only placed in the water for approximately 10 minutes and the net opening was smaller than that used by Priegel. It is difficult to compare these raw numbers of fry captured elsewhere to raw numbers of fry captured in the Muskegon River due to differences in current and gear type but there seems to have been a substantial number of young walleyes that hatched in the Muskegon River during the Spring of 1986. This indicates that problems with juvenile recruitment may not be related to egg quality, quality of spawning substrate, or hatching success.

In some respects the walleye population studied by Priegel (1970) in Lake Winnebago and the Wolf River system is similar to the walleye population in the Muskegon River system. In the spring, adult walleyes travel from Lake Winnebago 40 miles (64 km) up the Fox River or 97 miles (156 km) up the Wolf River to spawn in adjacent marshes. The fry hatch in the marshes and drift down to Lake Winnebago or other upriver lakes. According to Priegel, walleye fry can live on their yolk sacs for 3-5 days before they must start feeding. Since their fins are not well enough developed to actively feed in areas with strong currents, the walleye fry needed to drift to one of the downstream lakes where food supplies are abundant. Priegel determined that walleye fry generally were able to travel from spawning sites on the Wolf River to Lake Winnebago in less than three days whereas walleye fry in the Fox River were only able to drift to the lake if the water velocity was above average. If the discharge was below average, fry would be trapped in eddies below low head dams on the Fox River.

More recently, Jude and Schultze (1988) attempted to assess the contribution of naturally produced walleye in Saginaw Bay and its tributaries. Part of the spawning Saginaw Bay walleye population migrates up Saginaw Bay tributaries. Jude and Schultze captured walleye larvae at six stations on the Saginaw River and two stations on the Tittabawassee River and Shiawassee River which combine to form the Saginaw River. Large numbers of larval walleyes were collected and it was estimated that 450,000 walleye larvae passed one sampling station during one 24 hour period. However, no walleyes were collected at the mouth of the Saginaw River and Jude and Schultze concluded that few walleyes were reaching nursery areas in Saginaw Bay. They speculated that natural recruitment problems could be related to contaminants, eutrophication, too long a distance from spawning site to nursery area, food availability, predation, or reversal of water flow at the mouth of the Saginaw River which would prevent the larvae from reaching nursery areas.

All of the walleye fry captured in the Muskegon River still had yolk sacs and none of them had started to feed. It is likely that they also need to drift into slow moving areas in either Muskegon Lake, the lower Muskegon River area or bayous of the Muskegon River for two reasons. First, zooplankton populations tend to be low in areas with flowing water and zooplankton that are found have usually washed into flowing water from slow moving areas (Ward and Whipple 1918, Welch 1952). Second, larval walleyes could not pursue prey as readily in swift moving, turbulent waters as in still waters.

Prior to 1969, spawning walleyes were stopped at the Newaygo dam and spawning populations were estimated as high as 139,000 fish in 1954. When the Newaygo dam was removed in 1969 another 13.5 miles (22 km) was available to spawning walleyes. While the quality of spawning substrate probably did not decrease, the distance that fry needed to travel did increase. Also, the sediments stored behind the Newaygo Dam and fill material added to the lower river system when the freeway (U.S. 31) was built may have physically impacted the river, or flows, in such a way that now walleye fry may have difficulty making the journey.

Juvenile Walleyes in the Muskegon River System

Sampling for juvenile walleyes in the Muskegon River and Muskegon Lake was much more intensive but only seventeen juveniles were captured from May to November of 1986. The first six juvenile walleyes were captured with an electroshocking unit on June 25 in the lower river area (Figure 20). Four more were captured during the first two weeks of July in trap nets, also in the lower Muskegon River. All of these captures occurred shortly after the MDNR released juvenile walleyes from the rearing ponds further upstream and the walleyes were probably moving downstream. Three juvenile walleyes were captured in the night trawls conducted in Muskegon Lake, in September, October and November. In addition, two YOY walleyes and one two-year-old walleye were captured along with thirteen adult walleyes in a MDNR boomshocking sampling trip on October 29, 1986. The last YOY walleye captured was found in the lower river in November of 1986.

In general, the gear and methods used to capture walleyes in the Muskegon River system were effective in

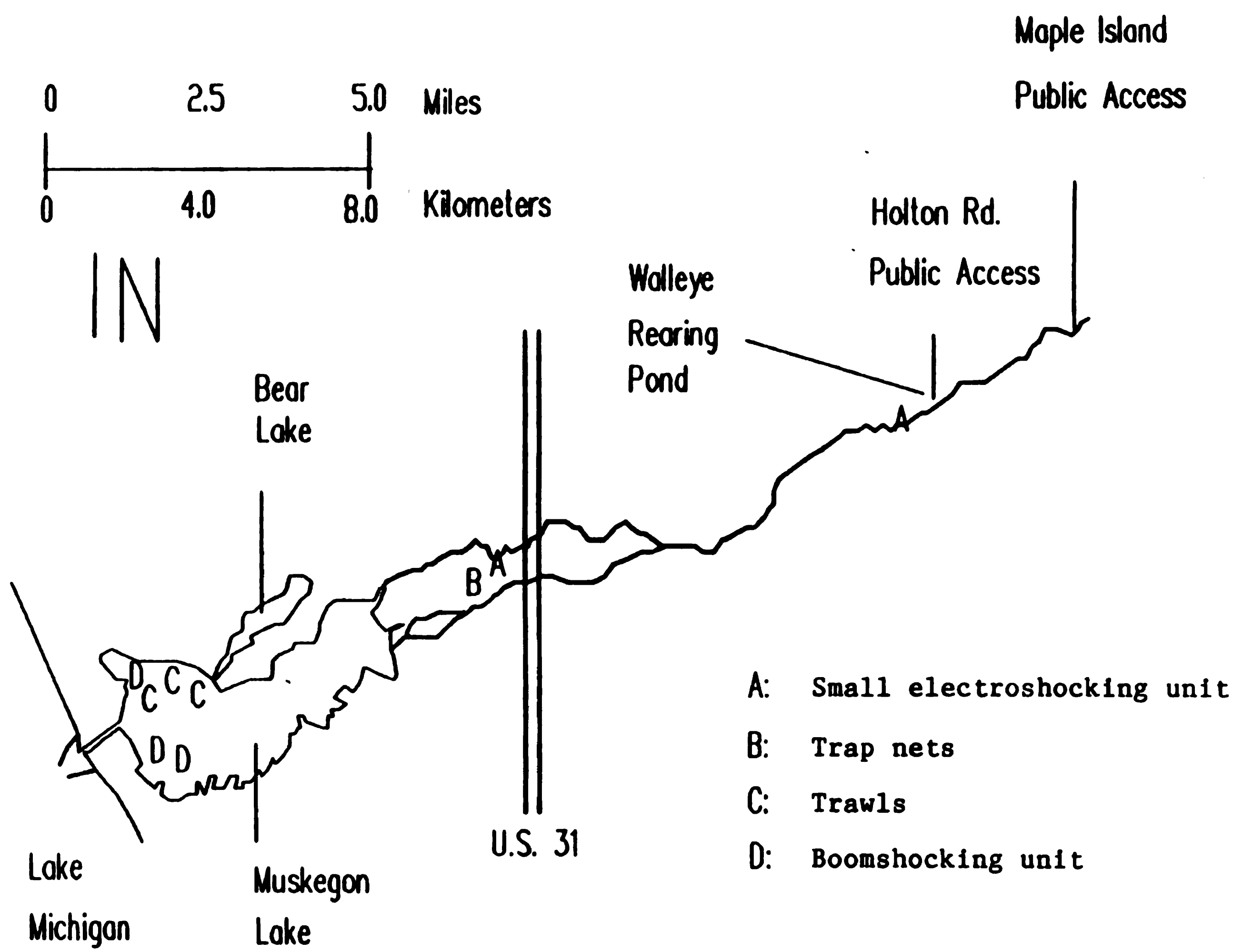


Figure 20. Locations where juvenile walleyes were captured in 1986.

capturing both juvenile and adult fish of a variety of species listed in Table 14. Given that the gear used is effective, the small number of juvenile walleyes captured could indicate that (1) these fish are distributed very sparsely throughout the system or (2) they are concentrated in large numbers in a few areas not sampled or (3) there is an exceptionally high mortality of the larval of early juvenile fish or (4) some combination of these events was occurring simultaneously.

Introduction to Potential Impacts of Alewife on Juvenile Walleyes

Schneider and Leach (1979) claim that the decline in the Muskegon River spawning population can be traced to poor recruitment. They note that the most likely cause of low recruitment was the invasion and continued high abundance of alewives. Alewife populations exploded in the Muskegon and adjacent river systems in about 1958 roughly coinciding with the decline of the walleye population (Schneider and Leach 1979). Schneider and Leach (1979) note that the peak densities of alewives in Muskegon Lake occur from late May to August overlapping with the critical period for walleye fry and fingerlings. Schneider and Leach (1979) felt that this exotic species may have impacted young walleye populations through predation or competition.

Table 14. Species of juvenile and adult fish captured in the Muskegon River system, in 1986, using gear targeted at larval and juvenile walleyes.

Species	Adult	Lar./Juv.
Walleye (Stizostedion vitreum)	X	X
Yellow perch (Perca flavescens)	X	X
Log perch (Percina caproides)	X	
Blackside darter (Percina maculata)	X	
Johnny darter (Etheostoma nigrum)	X	X
American brook lamprey (Lampetra lamonttei)	X	
Bowfin (Amia calva)	X	
Longnose gar (Lepisosteus osseus)		X
Gizzard shad (Dorosoma cepedianum)	X	X
Alewife (Alosa pseudoharengus)	X	X
Chinook salmon (Oncorhynchus tschawytscha)	X	X
Brown trout (Salmo trutta)	X	X
Rainbow trout (Oncorhynchus mykiss)	X	X
Northern pike (Esox lucius)	X	X
Grass pickerel (Esox americanus)	X	X
Central mudminnow (Umbra limi)	X	X
Carp (Cyprinus carpio)	X	
Blacknose dace (Rhinichthys atratulus)	X	
Golden shiner (Notemigonus crysoleucas)	X	
Fathead minnow (Pimephales notatus)	X	
Pugnose minnow (Opsopoeodus emiliae)	X	X
Rosyface shiner (Notropis rubellus)	X	
Spottail shiner (Notropis hudsonius)	X	X
Lake chubsucker (Erimyzon sucetta)	X	
Redhorse sucker (Moxostoma spp.)	X	X
White sucker (Catostomus commersoni)	X	X
Channel catfish (Ictalurus punctatus)	X	
Brown bullhead (Ictalurus nebulosus)	X	X
Tadpole madtom (Noturus gyrinus)	X	X
Pirate perch (Aphredoderus sayanus)	X	X
Trout perch (Percopsis omiscomaycus)	X	X
Burbot (Lota lota)		X
Banded killifish (Fundulus diaphanus)	X	
Brook silverside (Labidesthes sicculus)	X	X
Largemouth bass (Micropterus salmoides)	X	X
Smallmouth bass (Micropterus dolomieu)	X	X
Black crappie (Pomoxis nigromaculatus)	X	X
White crappie (Pomoxis annularis)	X	X
Warmouth (Chaenobryttus gulosus)	X	X
Rock bass (Ambloplites rupestris)	X	X
Green sunfish (Lepomis cyanellus)	X	
Longear sunfish (Lepomis megalotis)	X	
Bluegill (Lepomis macrochirus)	X	X
Pumpkinseed (Lepomis gibbosus)	X	X
Freshwater drum (Aplodinotus grunniens)	X	X

Other investigators have documented alewife predation on larval fish. Kohler and Ney (1980) found that alewives consumed larval fish up to 26 mm TL and found larval yellow perch (*Perca flavescens*), *Lepomis sp*., *Micropterus sp*., largemouth bass (*Micropterus salmoides*) and white bass (*Morone crysops*) in alewife stomachs. During a period from mid-June to early July, larval fish frequency of occurrence in alewife stomachs reached 40%-70% but cannibalism was infrequent relative to total fish consumption. Also, Schneider and Leach (1979) reported that larval alewife up to 32 mm total length have been found in the stomachs of adult alewives captured in southern Lake Michigan.

Schneider and Leach (1979) felt that competition between YOY walleyes and adult alewives may have been the primary interaction limiting walleye recruitment. Wells (1970) noted that alewife populations may have shifted zooplankton populations in southern Lake Michigan. He noted that selective predation by alewives caused a decline in populations of the largest cladocerans and the largest calanoid copepods while median-sized and small species of zooplankton increased in number. Larval walleyes have difficulty feeding on smaller zooplankton species (Mathias and Li 1982)

In an effort to document competition or predatory interactions between YOY walleyes and alewives, stomach content analyses were done on alewives captured in small

mesh trap nets and trawls. One hundred and eighty-nine adult alewives were captured in the trap nets from June 11, 1986 to July 11, 1986. Stomachs from a subsample of 94 of these 189 were analyzed. Seventeen of the alewives were females and 77 were males. Alewives ranging in size from 120 mm to 220 mm fed most heavily (percentage of species by number) on cladocerans followed by Tricoptera larvae. There were also large percentages (by number) of Chironomidae larvae, Ostracoda, calanoid copepods and unidentified insect remains. A single brook silverside (Labidesthes sicculus) larva was found in the stomach of one alewife captured on July 11, 1986. Also, the remains of an unidentified larval fish were found in the stomach of another alewife captured on June 12, 1986.

As previously noted, alewives were captured incidently during the search for juvenile walleyes. Trap nets are not an ideal sampling method because alewives have relatively rapid rates of digestion. Gannon (1976) found that invertebrates in alewife stomachs were digested beyond recognition in 2.5-4.5 hours at 15 degrees Centigrade. Daphnia were no longer discernable after 2.5 hours and all Crustacea were entirely digested after 4.5 hours. Kohler and Ney (1980) citing personal communication with T. Edsall (Great Lakes Fishery Laboratory, Ann Arbor, MI) claim that smelt larvae were digested beyond recognition by alewives in less than two hours at 18.3 degrees Centigrade.

Kohler and Ney (1980) lifted vertical gill nets every four hours in Clayton Lake and felt that most of the alewife feeding occurred at night. If this is the case in Muskegon Lake, then most of prey items ingested by alewives during the night would have been digested before my nets were pulled (usually no earlier than 0930 or 1000 hrs.).

Also, there is no way to know how long the alewives were in the net before the net was pulled. It is possible that stomach contents would reflect only those items ingested while the alewives were in the net. If the net acted as an attractant or deterrent for food items then this method would bias food selection by alewives.

Alewife Predation

Although no direct evidence can be provided by stomach content analysis, there is probably no significant alewife predation on juvenile walleyes in the Muskegon River system for temporal and spatial reasons. The peak densities of alewives in Muskegon Lake typically occur from late May to August and alewives were captured in trap nets from mid-June to mid-July of 1986. During this time, any juvenile walleyes scattered throughout Muskegon Lake were probably large enough to avoid alewife predation.

The growth rates of pond walleyes were used to predict the size of wild walleyes that may have survived. On June 25, 1986, six juvenile walleyes were captured approximately

1/2 mile west of the U.S. 31 bridge, roughly two miles upstream of Muskegon Lake (Figure 20). These walleyes were captured shortly after the release of juvenile walleyes from the Muskegon River rearing pond. These six walleyes ranged in size from 62 to 67 mm TL with an average total length of 64 mm TL. Walleye fry were stocked in the rearing ponds during the first week of May, 1986 and if the average size was 8.0 mm TL (same as the wild fry) then linear interpolation of the growth rate from May 1, to June 25 indicates that these walleye grew roughly 1.02 mm TL/day. The peak number of larval walleyes (282 of 505) collected in the Muskegon River were captured on May 3, 1986 and the average total length of the larval walleyes was 8.0 mm TL. If the walleye captured were released from the pond and had growth rates similar to wild growth rates then the average length of any surviving wild fish on June 1, 1986 would have been roughly 38 mm TL. The average length of wild walleyes would have been 47 mm TL by June 10, 1986 when the first alewife was collected.

The growth rate of juvenile walleyes raised in the ponds may not be the same as the growth rate of wild juveniles. An estimated growth rate of 1.02 mm TL/day is less than wild growth rates measured in Lake Gogebic, Michigan, for the same period of life. Growth rates of Lake Gogebic walleyes were estimated to be 1.8 mm TL/day in 1941 and 2.4 mm TL/day in 1947 during the early juvenile stages

(Eschmeyer 1950). Therefore, surviving wild juveniles were probably larger than stocked juvenile walleyes.

As previously noted Schneider and Leach (1979) reported that larval fish up to 32 mm have been found in adult alewives captured in Lake Michigan. If 32 mm approaches the maximum size limit of larval fish susceptible to alewife predation then YOY walleyes would not have been subject to predation by alewives.

Alewife Competition

Even though alewife populations have been noted to shift zooplankton population compositions from relatively large species to small species, it is difficult to determine whether or not direct competition between alewives and juvenile walleyes is significantly impacting juvenile walleyes in Muskegon Lake. A shift in zooplankton populations from relatively large species to small species could negatively impact larval walleyes. Mathias and Li (1982) studied the feeding behavior of larval walleyes in rearing ponds and in laboratory aquariums and determined that larval walleyes are selective sight feeders and that feeding success was dependent on their vision, their ability to pursue and capture prey as well as on the size of the prey and its ability to escape. They determined that the preferred zooplankton was 1.2 mm and that under normal conditions rotifers and nauplii were too small for larval walleyes to see and catch. However, when there were high densities of these smaller zooplankton some were ingested with the respiratory current.

At the time when alewives were first captured in the lake, the average estimated length of any surviving wild juvenile walleyes was 47 mm TL. According to Ney (1978) fish may become the major component of walleye diets by the time they reach 30 mm TL. Stomach content analysis of six juveniles (averaging 64 mm TL) captured with electroshocking gear, on June 25, 1986 in the Muskegon River indicates that fish were the only food items in the four stomachs that were not empty. Although it is possible that alewives and YOY walleye compete for other larval fish, during a limited period of time, competition for zooplankton and insects is probably not limiting to juvenile walleyes in Muskegon Lake because YOY walleyes should be feeding primarily on fish at the time alewives reach peak densities.

In addition YOY alewives may provide a source of forage for juvenile and adult walleyes throughout the year. Adult alewives spawn in Muskegon Lake in early summer and juvenile walleyes should be feeding primarily on fish when alewives hatch. Also, since juvenile alewives were abundant in late year trawls, it is possible that they provide a source of forage, throughout the year, for Muskegon Lake walleyes.

Alewife-Yellow Perch-Walleye interactions

Alewives may have contributed to the decline of walleye recruitment through means other than predation or competition. If walleye recruitment in the Muskegon River system is linked to yellow perch recruitment and yellow perch recruitment is adversely affected by alewife populations then alewife may exhibit indirect control over walleye populations.

Yellow perch populations spawn later than walleye populations and therefore larvae may be influenced by alewife predation or competition. Some investigators feel that yellow perch populations have been negatively impacted by alewife populations. Larval perch are a major food item of adult alewives and a sharp reduction in the perch population occurred after alewives gained prominence in the Great Lakes (Brazo 1973). Smith (1970) and Wells and McLain (1973) noted that a decline in yellow perch populations corresponded with an increase in alewife populations and that alewives negatively impacted recruitment of yellow perch through predation or competition.

The success of walleye year classes has been positively correlated with the success of yellow perch year classes in several systems. Forney (1974) claimed that in Oneida Lake, New York, yellow perch abundance regulated walleye cannibalism and therefore regulated walleye year class strength. Oneida Lake walleyes fed primarily on yellow perch but switched to white bass and juvenile walleyes during times when yellow perch abundance was low. Nelson and Walburg (1977) found a strong correlation between YOY walleyes and yellow perch abundance in two Missouri reservoirs. Abundance of young walleyes was apparently dependent on abundant prey to provide food and reduce cannibalism. Maloney and Johnson (1957) studied walleye and yellow perch populations in two Minnesota lakes and felt that the size of yellow perch populations was an important factor in determining the year class strength of walleyes.

However, no correlation was found between year class strength of walleyes and yellow perch in Clear Lake, Iowa (Carlander and Payne 1977). Also, Kelso and Ward (1977) studied unexploited populations of walleye in West Blue Lake, Manitoba, and although these walleyes fed primarily on yellow perch, the investigators found no evidence of species interactions that would limit year class strength of either species. Kelso and Ward (1977) noted that large fluctuations in year class strength were caused by factors affecting egg and fry survival.

Potential Impacts of Gizzard Shad on Juvenile Walleyes

Schneider and Leach (1979) speculated that gizzard shad contributed to the decline in recruitment of Muskegon walleyes either by predation or competition interactions with YOY walleyes. Gizzard shad were captured in both the trawls and trap nets in Muskegon Lake. Juvenile gizzard shad were only captured in trawls at night while adults were captured in both trawls and trap nets throughout the season. Stomachs were removed from 31 adult gizzard shad captured throughout the year. The zooplankton Bosmina sp. was found in 18 of the stomachs with one stomach containing approximately 250 individuals. Detritus or sand was found in 17 of the stomachs, 17 stomachs contained plant material, 10 contained insects and 13 contained other crustaceans.

According to Scott and Crossman (1973), fully developed gizzard shad are herbivorous feeding on phytoplankton and benthic algae. They also claim that stomachs may contain large volumes of mud which the fish are thought to consume incidently. Juvenile gizzard shad up to 22 mm long have been found to contain, almost entirely, water fleas (Bosmina sp.), copepods and Ostracods (Scott and Crossman 1973). As the gizzard shad grows, the gut becomes specialized to digest and assimilate plant material.

Young gizzard shad can be an important source of forage for game fish (Scott and Crossman 1973). Wolfert (1966) found that alewives and gizzard shad were important sources of food for YOY walleyes in western Lake Erie. The size of gizzard shad and alewife consumed ranged from 35 mm to 64 mm but YOY walleye shifted to other prey items as the gizzard shad and alewife grew to a size that made them unsuitable prey. Juvenile and adult walleyes in Muskegon Lake should have been able to utilize all but the largest gizzard shad and one 80 mm gizzard shad was found in the stomach of a 331 mm juvenile walleye caught in Muskegon Lake, with an electroshocker, on October 29, 1986.

Gizzard shad probably do not significantly impact juvenile walleyes for the same reasons discussed in previous sections. When the distribution of the two species overlaps, YOY walleyes should be large enough to avoid gizzard shad predation. In addition, YOY walleyes should be feeding primarily on larval fish while gizzard shad are feeding on *Bosmina sp.*, plant material and detritus.

CONCLUSIONS

The size of the spawning population of walleyes in the Muskegon River was estimated using mark and recapture data from walleyes tagged at Croton Dam during 1986 and recaptured in the 1987 spawning run. The estimated number of adult walleyes spawning at Croton Dam in 1986 was 43,222 +/- 25,372 after adjustments were made for recruitment and differential mortality of fish kept for eggs versus fish tagged and released immediately.

Tagged walleyes were released below Newaygo Dam in 1948 and 1950. Anglers returned similar percentages of tags in 1948, 1986 and 1987 but the returns from 1986 and 1987 indicate that walleyes did not move as far or leave the system as often as earlier studies indicate. Walleyes recaptured from the 1948 and 1950 studies ranged as far south as St. Joseph and as far north as Betsie Bay with 40% of the recaptures coming from outside the Muskegon River system. Walleyes recaptured in 1986 and 1987 ranged as far south as the Grand River and as far north as White Lake and only 3.3% of the returns came from outside the Muskegon River system.

Earlier investigators felt that adult walleyes from the entire east coast of Lake Michigan homed to the Muskegon River to spawn then left the River system. It seems that walleye still run upstream to spawn but indications are that less are leaving the system after spawning.

Rates of exploitation were higher for smaller fish than larger fish and higher for females tagged and released immediately than for females kept for eggs. However, these comparisons may have been biased by larger fish moving out of the system at a higher rate than smaller fish.

Estimated survival rates were highest for large males and lowest for large females tagged and released immediately. The calculated survival rate for females kept for eggs is relatively high but this estimate was not very precise due to the relatively low number of tags returned by anglers. Also, the estimated survival rate of fish kept for eggs may only represent the survival rate of fish that survive the initial shock of the egg-take operation.

Estimates of survival rates of Muskegon walleyes were calculated with mark and recapture data and estimates were probably low due to the influence of differential mortality of marked fish, differential emigration of unmarked fish or immigration of unmarked fish. These three factors bias the estimates by decreasing the proportion of marked to unmarked fish.

Estimated annual mortality of Muskegon walleyes was relatively high compared to other populations and mortality due to fishing was much less than natural mortality. However, estimates of the annual mortality of Muskegon walleyes were probably biased. Also, natural mortality will be biased by incomplete reporting of angler returns and differences in angler cooperation with various studies will effect comparisons between studies.

Back calculated lengths at any given age were larger for the younger fish indicating Lee's phenomenon. This was probably caused by faster growing, faster maturing members of the younger age classes joining the spawning earlier than other members of their age class.

Estimated lengths at each age of walleyes from the Muskegon River system were usually larger than lengths at each age of walleye from other systems indicating that Muskegon walleye grew faster and larger than walleyes from several other systems.

The weight-versus-length relationship ($W=aL^b$) was calculated using length and weight data for all gravid adults. The "b" value from gravid Muskegon River walleyes was higher than those calculated for gravid walleye populations from other areas. This indicates that Muskegon walleyes were heavier at each length than walleyes from other systems.

Average weights were back calculated using a weight versus length relationship and Muskegon river walleyes were generally heavier at each age than walleyes from other systems. Also, differences between back calculated weights of gravid and spent females provide the potential to estimate the quantity of eggs that may be extracted from a single fish.

The ultimate length (L_∞), growth coefficient (K), theoretical length at age 0 (t_0) and age at which 95% of the growth is completed $A_{(0.95)}$ were calculated for Muskegon walleyes and compared to other walleye populations. The ultimate length of Muskegon walleyes was close to those calculated for other walleye populations. However, the growth coefficients were higher for Muskegon River walleyes so fish grew to their ultimate length faster. Also, male and female walleyes from the Muskegon River would reach their ultimate length at about the same time.

Several walleyes captured at Croton Dam exceeded the predicted ultimate length and 95% confidence interval. This may have been due to a difference in growth patterns for larger fish, difficulty in correctly determining the age of larger fish or immigration of individuals with different growth rates.

The relationships between fecundity and length and fecundity and weight were slightly more curvilinear than linear. Standard partial regression coefficients (SPRC) indicated that (log) length was a better predictor of (log) fecundity than (log) weight. Fecundity estimates from Muskegon River walleyes captured in 1986 and 1987 were less than estimates from Muskegon River walleyes captured in 1947 but the difference was not statistically significant (alpha = 0.05). The fecundity of Muskegon walleyes was generally greater than the estimated fecundity of similar-sized walleyes from other systems.

Five hundred and five larval walleyes and eyed-up eggs were collected, during the day, in the Muskegon River, with peak densities moving downstream from the last week in April to the second week in May, 1986. The average number of larval walleyes captured per Muskegon River sample was not directly comparable to other areas because of differences in methods. However, there seems to have been a substantial number of larval walleyes that hatched during the spring of 1986. This indicates that problems with juvenile recruitment may not be related to egg survival, quality of spawning substrate, or hatching success.

Larval walleyes must drift into areas where currents are slow or less turbulent, with an adequate food supply or they will not be able to feed. If they are not able to drift into these nursery areas within 3 to 5 days of hatching they will die of starvation. Changes to the river may have had an impact on the ability of walleye fry to drift into nursery areas within 3 to 5 days. The removal of the Newaygo Dam increased the distance larval walleye needed to drift. Also, hydraulic characteristics of the river may have changed with increased sedimentation caused by the removal of Newaygo Dam and construction of the highway (U.S. 31) across the river.

Relatively intensive sampling from May to November of 1986 yielded only 17 juvenile walleyes. None of the juveniles were captured before walleyes were released from MDNR rearing ponds while 10 of the 17 juveniles were captured during the first three weeks after the juveniles were planted. The low capture rate of juveniles could be due to a number of factors including low densities, concentrated numbers in a few areas not sampled, exceptionally high mortality, or a combination of these factors.

Investigators have speculated that the decline of the Muskegon River spawning population can be traced to poor recruitment caused by the invasion of exotic species, namely alewives and gizzard shad. Other investigators have documented that alewives can shift zooplankton from larger species to smaller species and the alewives and gizzard shad may also feed heavily on larval fish. Thus it has been speculated that the alewives and gizzard shad impact walleyes either through predatory or competitive interactions. Although there was no direct evidence to indicate that alewives or gizzard shad are feeding on YOY walleyes the possibility cold not be ruled out. However, due to spatial and/or temporal differences between the distribution of these species it seems that alewife predation on walleyes would not be significant and competition would only occur during a brief period of time and would probably be limited to competition for larval fish of other species.

Alewives may be indirectly impacting walleye recruitment by impacting yellow perch populations. Some investigators have documented a positive relationship between yellow perch year class strength and walleye year class strength. Other investigators have speculated that alewives in the Great Lakes have negatively impacted yellow perch populations. If this is the case in Muskegon Lake and if yellow perch and walleye year class strength are linked, then the alewives could be indirectly impacting walleye recruitment.

The major items found in gizzard shad stomachs were *Bosmina sp*., plant material and detritus. Therefore, gizzard shad are not likely predators of juvenile walleyes. Also, walleye should be feeding on larval fish when the distribution of the two species overlaps and there should not be competition for zooplankton.

FUTURE RESEARCH AND MANAGEMENT IMPLICATIONS

One goal of any long term fisheries management plan for walleyes in the Muskegon River system should be a self sustaining, naturally reproducing population. The Muskegon River spawning run is currently being supported with an intensive stocking program and it seems clear that the demise of the spawning run was due to a lack of recruitment caused by exceptionally high mortality of YOY walleyes. Therefore, the primary focus of any research efforts in the Muskegon River system should be recruitment.

The first phase of this type of project should be to document the movement of larval walleyes from upstream areas of the Muskegon River to nursery areas in the system. The total number of larvae drifting past various points in the river could be estimated by sampling transects across the river over several twenty-four hour periods and estimating discharge at the transects. If larval walleyes are not surviving until they drift into nursery areas then physical and climatic factors need to be evaluated. For example, larval walleyes may only be able to survive the journey during wet weather years or years when the discharge is above average. On the other hand, habitat alterations to the river system may have made it impossible for larvae to survive the journey in any year in which case some habitat restoration projects may be beneficial. If the larval walleyes are surviving until they drift into bayous or slow moving areas of the lower river then zooplankton populations need to be assessed in these areas with the goal being to evaluate their suitability as a food supply for larval walleyes.

If YOY walleyes are surviving past the larval stage then their interactions with other Muskegon River and Lake species should be assessed. However, the success of this project would clearly be linked to the density of juvenile walleyes in the system and the ability of the investigator to capture them.

The second major area of research should be an evaluation of the effects of the egg-take operation on the adult population. The stocking program has increased the spawning runs but individual fish (primarily females) are suffering high mortality because of it. The effects of this mortality on the population should be assessed. Currently the Muskegon River egg-take supplies the MDNR with all of the eggs hatched, reared and stocked throughout the entire lower peninsula of Michigan. Any impacts of the egg-take operation on the magnitude of the spawning run should be assessed. In addition, using Muskegon River walleyes as a single source of walleyes for the stocking program may influence the genetic composition of lower peninsula walleyes. This aspect of the egg-take operation should also be assessed.

The best way to assess the effects of the egg-take on the Muskegon River walleye population would be to develop a model and predict the outcome of scenarios including no egg-take and relatively intensive egg-take operations, or scenarios ranging from using only small females to using only large females. In order to obtain realistic predictions from the model better estimates of some input variables would be needed. More accurate population estimates could be obtained by designing a study that would minimize the effects of recruitment, differential mortality, immigration and emigration. Also, various mortality estimates would be needed and these rates could be more accurately obtained by designing a study specifically for the purpose of estimating mortality rates.

APPENDIX

ATTENTION WALLEYE ANGLERS

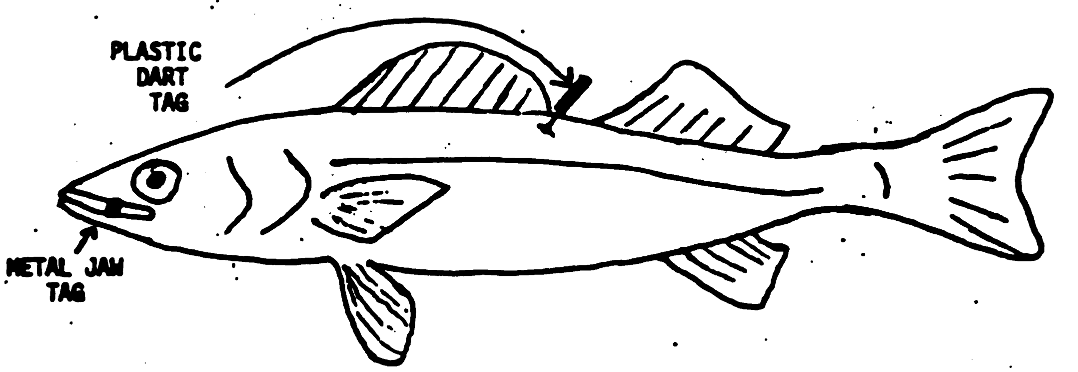
YOUR COOPERATION IS REQUESTED

REWARD FOR TAG RETURNS

MANY WALLEYE HAVE BEEN LIVE CAPTURED, TAGGED AND RELEASED IN MUSKEGON RIVER BELOW CROTON DAM. MICHIGAN STATE UNIVERSITY AND THE MICHIGAN DEPARTMENT OF NATURAL RESOURCES ARE CONDUCTING THIS TAGGING STUDY TO DETERMINE MOVEMENT AND POPULATION OF WALLEYE IN THE MUSKEGON RIVER SYSTEM.

TAG RETURNS FROM ANGLERS WILL BE IMPORTANT TO THE SUCCESS OF THIS STUDY AND A REWARD WILL BE OFFERED FOR RETURNED TAGS. IN ADDITION, A DRAWING WILL BE HELD ON AUGUST 1, 1987, OFFERING PRIZES OF $50, $25 AND $10. A PERSON ENTERS HIS/HER NAME INTO THE DRAWING EACH TIME A TAG WITH APPROPRIATE INFORMATION IS SENT IN.

MOST WALLEYE HAVE BEEN TAGGED WITH A METAL JAW TAG, THOUGH A SMALL PERCENTAGE HAVE BOTH A JAW TAG AND A PLASTIC BACK TAG.



IF AN ANGLER CAPTURES A TAGGED FISH, WE REQUEST YOUR COOPERATION BY RECORDING THE FOLLOWING INFORMATION:

1. FISHERMAN'S NAME AND ADDRESS
2. DATE FISH WAS CAUGHT
3. LOCATION FISH WAS CAUGHT (BE AS SPECIFIC AS POSSIBLE)
4. TAG NUMBERS
5. LENGTH OF FISH (IF POSSIBLE)

RETURN TAGS AND INFORMATION BY MAIL OR IN PERSON TO:

MICHIGAN DEPARTMENT OF NATURAL RESOURCES-FISHERIES DIVISION
GRAND RAPIDS DISTRICT HEADQUARTERS
6TH FLOOR, STATE OFFICE BUILDING
350 OTTAWA ST., N.W.
GRAND RAPIDS, MI 49503

IN RETURN WE WILL SEND YOU A REWARD, INFORMATION CONCERNING THE FISH YOU CAUGHT, AND WE WILL ENTER YOUR NAME IN THE DRAWING. GOOD LUCK FISHING!

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