

SEX RATIOS OF YOUNG-OF-THE-YEAR WALLEYE FROM REARING PONDS AND LAKES IN MINNESOTA¹

Paul D. Eiler

Minnesota Department of Natural Resources
Section of Fisheries
500 Lafayette Road
St. Paul, MN 55155

Abstract. --Sex ratios were determined for young-of-the-year walleye collected from 40 rearing ponds in Minnesota during fall, 1983 to 1989. Sexing 9,966 fish from 69 collections yielded 53.01% males overall. Sixteen collections had sex ratios significantly different from 1:1, ranging from 29% to 42% males in three collections and from 61% to 89% males in 13 collections. Sex ratios were significantly different among years for 4 of 12 ponds having data from two or more years. Sex ratios also differed significantly among ponds in the same management area stocked from the same spawn source. The pooled percent males increased from north to south when collections were grouped by management area and spawn source, and appeared higher when northern spawn sources were used (no statistics were applied). Pond temperatures tended to increase from north to south, and were higher by the time fry from northern spawning runs were stocked, providing tentative evidence of a correlation between temperature and sex ratio. The different spawning conditions and methods of some northern areas might also account for the effect of northern spawn. Temperature units (degree-days above 0° C) in six ponds monitored in 1987, during the walleye's 9-d-old to 50-d-old age interval (post-hatch), did not correlate with the percentage identified as males in fall. In contrast, temperature units in three ponds monitored in 1988, during the walleye's 17-d-old to 77-d-old age interval, were positively related to percent males.

Young-of-the-year walleye were also collected during 1983-1989 from five large lakes receiving little or no stocking. Sexing a total of 3,874 fish from 26 collections yielded 52.61% males overall.

Immersing fry aged 1-8 d for three 2-h periods in 800 µg/L of 17 alpha-methyltestosterone or 17 beta-estradiol had no effect on sex ratios observed in fall.

Introduction

The Minnesota Department of Natural Resources (MN DNR) maintains an extensive culture and stocking program for wall-

eye *Stizostedion vitreum*, a coolwater fish that is popular with anglers. Eggs and sperm are obtained in spring from spawning adults and combined to produce fertilized eggs that are incubated in hatcheries. With-

¹ This project was funded in part by Federal Aid in Sport Fish Restoration (Dingell-Johnson) Program. Completion report, Study 139, D-J Project F-26-R Minnesota.

in a few days after hatching, fry are stocked into natural or artificial ponds to be reared until fall, when they are harvested and stocked into lakes for future angling, though some lakes receive fry directly.

Female walleye grow at a faster rate than males and reach a larger ultimate size (Craig 1987). This divergence is apparent after age 3 (Olson 1968). Anglers and fisheries managers have reasoned that the sex ratio of stocked walleye would affect the average size of walleye caught and the quality of fishing. To address this issue, Olson (1968) collected young-of-the-year (y-o-y) walleye from rearing ponds and found that males significantly outnumbered females in 19 of the 36 collections, but that females never predominated. Males composed 41-92% of each collection, and 61.9% of all 5,710 fish sexed. In contrast, y-o-y walleye collections from large lakes that receive little or no stocking, because natural reproduction maintains their populations, tended to have equal numbers of each sex or significantly more females. Males composed 42-53% of the fish in the five lake collections. Ponds stocked with the same lot of fry sometimes yielded significantly different sex ratios, and any one pond often had significantly different ratios in different years. It seemed likely to Olson that characteristics of the pond, including environmental factors and population density, controlled the sex ratio of walleye. Presumably, these biotic and abiotic factors varied sufficiently among water bodies and years to interact with genetic control to produce the observed sex ratios. He could not identify, however, from among the several water quality variables measured, specific factors that influenced the sex ratio or the mechanism by which they operated.

Hunter and Donaldson (1983) reviewed evidence pertaining to the specific mechanisms by which sex is determined in fish. Though a genetic basis is assumed to exist, no single model could be reconciled with all available data. For most species studied, one of a number of polygenic systems appeared to fit the data most closely, where-

by the balance of male and female genes inherited on autosomal chromosomes could override sex chromosomes. The majority of fish do not have cytologically distinguishable sex chromosomes. For those species that do, they noted that the XY:XX system was apparently the most common, but that both male and female digamety systems had been demonstrated, as well as variations of these models that included multiple sex chromosomes. Even in species with heterosomal systems, sex determination may be labile to extrinsic factors.

The genetic basis of sex in walleye has not yet been determined. Though Baumgartner et al. (1986) have identified the walleye karyotype, they could not detect specific sex chromosomes. Malison et al. (1986) determined that in yellow perch *Perca flavescens*, a species in the same family as walleye, females are the homogametic sex. This is probably also true for walleye. The extent of genetic or environmental control over the sex of walleye is still unknown.

Several animals are subject to environmental sex determination (reviewed by Korpelainen 1990). Among vertebrates, temperature is most frequently cited as the environmental determinant of sex. Bull and Charnov (1989) presented three patterns of sex ratio response by reptiles to egg incubation temperature, but the adaptiveness of these patterns was unclear. Conover and Heins (1987) presented evidence that temperature and other environmental factors interact with genotype to control the sex of the Atlantic silverside *Menidia menidia*. Offspring produced in the early breeding season (late April and early May) were mostly females, but those of the late breeding season (July) were mostly males (Conover 1984). In experiments by Conover and Kynard (1981), eggs and larvae of Atlantic silverside incubated at low fluctuating temperatures (11-19° C) that were characteristic of the early breeding season produced significantly higher proportions of females than did sibling larvae incubated at higher temperatures (17-25° C) that were representative of the late breeding season. Differential

mortality could not account for the differences in sex ratio between treatments, implying that temperature directly affected sex determination. The longer average growing season experienced by females could account for their attaining a larger average size by fall. Large size was more important to the reproductive success of females than males. Temperature was thought to have served as a cue to the length of the growing season, and temperature-dependent sex determination was considered to be adaptive for this reason.

Concern over the preponderance of male walleye observed in Minnesota rearing ponds has led to an interest in developing techniques to control the sex of y-o-y walleye. Sex has been experimentally controlled in a variety of teleost fishes, but no such study has been published for walleye.

A commonly used method for controlling sexual phenotype has been the administration of sex steroids, before or during gonadal differentiation, resulting in partial or complete anatomical and histological inversion (termed "reversal" by many) of the gonad to the opposite gender (Malison et al. 1986). Effective treatments have included immersing eggs or larvae in solutions of these hormones and adding the hormones to the diet. The time period during which treatments are effective is species-specific (Malison et al. 1986). Sex inversion by steroid administration has been achieved with the medaka *Oryzias latipes*, several tilapia (*Tilapia* or *Oreochromis* spp.), several salmonids (for reviews see Yamamoto 1969; Schreck 1974; Donaldson and Hunter 1982; Hunter and Donaldson 1983; Varadaraj 1990), channel catfish *Ictalurus punctatus* (Davis et al. 1990), yellow perch (Malison et al. 1986), silver carp *Hypophthalmichthys molitrix* (Mirza and Shelton 1988), blue-spotted grouper *Epinephelus fario* (Kuo et al. 1988), and largemouth bass *Micropterus salmoides* (Garrett 1989).

Of species whose sex has been successfully manipulated, the yellow perch is most closely related to walleye. Malison et al. (1986) harvested yellow perch from produc-

tion ponds and brought them into the laboratory when they measured 20-35 mm total length. Feeding for 84 d on a diet containing 17 beta-estradiol induced complete sex inversion in most males. Diet containing 17 alpha-methyltestosterone induced spermatogenesis in females. The following spring some of these sex-inverted genetic females were sacrificed and sperm was removed from their gonads. The sperm fertilized normal ova in the laboratory and produced all-female offspring.

Both diet and immersion treatments have controlled sex in salmonids. Johnstone et al. (1979a) produced nearly all-female brook trout *Salvelinus fontinalis* by including estradiol in their diet for 40 d, beginning at first feeding. Johnstone et al. (1978) included 17 beta-estradiol in the diet of Atlantic salmon *Salmo salar* and rainbow trout *Oncorhynchus mykiss*, and produced all-female fish. When 17 alpha-methyltestosterone was used all-male fish were produced. Fertilization of normal ova by sperm from masculinized genetic females produced all-female offspring, indicating that the female rainbow trout is homogametic (Johnstone et al. 1979b). Goetz et al. (1979) demonstrated that to produce inversion in coho salmon *O. kisutch*, immersion of eyed eggs and alevins in aqueous solutions of the steroids was necessary, in addition to diet treatments. Hunter et al. (1982) achieved the same results and demonstrated that male coho salmon are the heterogametic sex, consistent with the results of earlier karyological studies of salmonids. Hunter et al. (1986) subsequently showed that feminization of coho salmon and chinook salmon *O. tshawytscha* could be accomplished by the immersion treatment alone. Newly hatched alevins were immersed in solutions of 17 beta-estradiol at concentrations ranging from 200 to 1600 ug/L for two 2-h periods, 1 week apart. This produced 66-96% females, but results were not dose-related.

The facilities to hold y-o-y walleye and feed them an artificial diet, as required for the above treatment of yellow perch, were not available to us. We did have facilities to

immerse fry in solutions of sex steroids, and we used this method of treatment to attempt to control the sex of walleye. The expectation was that sexual phenotype and resulting sex ratios of y-o-y walleye would be consistent with the hormones used.

In addition, we wished to determine if walleye sex was influenced by rearing temperature, as for *Menidia*. Rearing ponds in Minnesota occur over a range of latitude and topography that we expected would provide a range of rearing temperatures for any given calendar interval. Dates of spring spawning runs of adult walleye tend to be earliest in the southern portion of the state, and to be progressively later in more northerly locations. Fry from a northern (late) spawning run are often stocked into southern ponds, which should be warmer than at the time the southern-run fry would have been stocked. By this manipulation the range of rearing temperatures should be increased. By verifying the expected geographic trend in pond temperatures, and surveying ponds for sex ratio, pond location, and source of spawn, a relation between sex ratio and pond temperature might be identified. The expectations were that percent males would correlate with pond temperatures, pond temperatures would increase from north to south, and, therefore, percent males would increase from north to south and when fertilized eggs or fry were moved southward.

Based on Olson's data, males were expected to outnumber females for all ponds taken together. In large lakes in Minnesota, which receive little or no stocking, the numbers of each sex were expected to be equal, or else females would outnumber males. To make this comparison, sex ratio data for y-o-y walleye from large lakes were obtained.

Methods

During 1987 attempts were made to control the sex ratio of y-o-y walleye by immersing fry in solutions of sex steroids and by increasing the temperature that fry

experienced in rearing ponds. Temperatures were monitored in 13 ponds to identify associations among temperature, pond location, and sex ratio. No special treatments were performed in 1988, but temperatures were monitored in four ponds. A larger-scale survey was conducted to examine the relation between sex ratio of y-o-y walleye and location of pond and spawn source, and to compare ratios between ponds and lakes.

During the second week of April 1987, spawn was collected from adult walleye in the Detroit Lakes Area and fertilized eggs were incubated in Meehan jars at the local hatchery. Fry hatching on 1-3 May were placed into six Big Redd incubators (Big Redd Incubators, Inc., Longville, MN) and received hormone immersion treatments on 4 May, 6 May, and 7 May. Addition of 17 alpha-methyltestosterone to two incubators, 17 beta-estradiol to two incubators, and no hormone to two others, provided three hormone treatments. Dosages and treatment durations were suggested by those used by Hunter et al. (1986) for Pacific salmon. Water supply to the incubators was stopped, and 8 mg of steroid were added to the ten-liter incubators to maintain a nominal concentration of 800 $\mu\text{g/L}$ for 2 h. Resumption of water exchange reduced concentrations to near zero 3 h later. When 5-7 d old, fry from three incubators were stocked into three local ponds (Detroit Lakes Area), each pond receiving fry from a different treatment. Three southern ponds (Waterville Area) were stocked with fry 6-8 d old in the same way. The two locations provided two gross levels of temperature treatment, providing six treatments in all.

Fertilized eggs obtained from a later spawning run in the Grand Marais Area of northeast Minnesota were incubated at the French River hatchery near Duluth. They were transferred to Big Redd incubators at Detroit Lakes immediately after hatching on 13 May. Similar hormone immersion treatments were administered at ages 1, 5, and 8 d. Fry from three incubators were stocked into three ponds in the Fergus Falls Area (immediately south of the Detroit Lakes

Area) when 9 d old. At age 10 d, fry from four incubators (an extra control) were stocked into four Waterville Area ponds. Fry from this later spawning run were expected to experience higher temperatures as a result of the later stocking date.

The hormone immersions and temperature manipulations comprised 12 treatments, and 13 ponds were stocked. Stocking rates were 12,300 fry per hectare.

Temperatures in the 13 ponds were monitored to reveal any relation to geographic location, to quantify the temperature treatment that the fry received, and to relate the temperature treatment to the sex ratio of y-o-y walleye. Temperature and dissolved oxygen profiles were recorded on one or more occasions. A temperature record of each pond was obtained with minimum-maximum thermometers placed just above the bottom at about 0.75 m depth. Temperature extremes were recorded at intervals of 1-7 d, into July. Interval mean temperature was computed as the average of the two readings recorded during the interval. Temperature units (degree-days above 0° C) were computed for each time interval as interval mean temperature times length of the interval in days, and accumulated each interval. Both temperature and temperature units were also averaged over the ponds in a management area.

During 1988, steroid immersion treatments were not used. Instead, four ponds, each in a separate management area, were chosen to test again for a temperature-effect. Incubation and fry stocking followed each area's normal procedure. The Detroit Lakes, Fergus Falls, and Glenwood Areas obtained spawn locally, and the Waterville Area hatchery received fertilized eggs from Grand Marais. For each pond, at least one profile of temperature and dissolved oxygen was taken. Continuously recording thermographs were installed about two weeks after the fry were stocked. The sensor was placed about 10 cm above the sediment in water 1 m deep. After retrieving the thermographs in August, readings were taken every 2 h from the continuous record. For

each pond and each day, the average of these readings yielded a daily mean temperature. The cumulative sum of daily mean temperatures yielded temperature units.

To relate pond temperature data to geographic location, comparisons of temperature data among ponds were made during common calendar intervals. To relate pond temperature data to sex ratio, temperature units were calculated and compared for a common walleye age interval.

Because Olson (1968) determined that gonads had differentiated by the time that walleye were 50 d old and 40 mm long, I attempted to collect walleye from 8 of the 13 ponds that received treated fry in 1987, to determine their growth rate and infer when differentiation would occur. A beach seine, measuring 3.2 m x 1.5 m x 15.2 m, was used in mid-June when fry were 25-46 d old.

A survey was conducted to repeat Olson's work (1968), except that the locations (Fisheries Management Area Headquarters) of the spawn source and the pond were included in the analysis of sex ratios to determine if geographic trends existed. In addition, the spawning method was recorded, since it varied among years and locations. Collections of y-o-y walleye were obtained during 1988 and 1989 from rearing ponds in the Detroit Lakes, Fergus Falls, Spicer, and Waterville Areas. Sex ratio data from previous pond harvests (Spicer, 1983-1987, and Fergus Falls, 1986) were also obtained. These fry received no special treatment; incubation, hatching, and stocking followed normal procedures for the area. Sex ratios from these collections were intended to be representative of those produced by the state's normal extensive walleye culture program. For comparison with pond data, sex ratio data were obtained for y-o-y walleye collected in summer and fall 1983-1989 from large lakes in Minnesota receiving little or no stocking.

Trap nets were used to harvest y-o-y walleye from the treatment and survey ponds during September, October, or November. Fish destined for sexing were preserved in

10% formalin or by freezing. Two hundred fish were desired from each pond, as this number would limit the 95% confidence interval for percent males from that pond to a maximum range of 14 percentage points.

Sex was determined by gross gonadal morphology, as described by Eschmeyer (1950) and Don Olson (Minnesota DNR, personal communication 1987). I sexed pond-reared walleye collected from 1987 through 1989 from all areas except Spicer. Vince Jenniges (MN DNR, Spicer, MN, personal communication 1989) sexed most from the Spicer Area. Walleye collected in 1986 from the Fergus Falls Area were sexed by Glenn and Mathias (1988), and those from the large lakes were sexed by the respective MN DNR Large Lake Specialists. Jenniges and I collaborated in sexing several Spicer Area collections in 1989 to verify that we were consistent. Olson and I each sexed the 83 fish from Bradbury Pond in 1987 to verify consistency between our studies. To verify accuracy, six fish of each apparent sex were submitted unlabeled to the MN DNR Pathology Laboratory to determine the sex of gonadal germinal tissue.

Analysis of sex ratios paralleled the procedures used by Glenn and Mathias (1988). Sex ratios observed for each pond-year collection were tested against hypothesized 1:1 sex ratios using chi-square goodness-of-fit tests employing the Yates correction for continuity (Zar 1984). When a pond's sex ratio was sampled in more than one year, a chi-square test for heterogeneity was applied to determine if sex ratios differed among years. Collections were grouped by management area and source of spawn (local, or northern MN), and heterogeneity tests were applied to each group. A single heterogeneity test was performed on all collections to see if sex ratios differed among them. Alpha was set at 0.05 for all tests. Data published by Olson (1968) were reanalyzed in the same way for comparison. In Table 2 of Glenn and Mathias (1988), the female number and percentage were incorrectly substituted for the male values for Darow Pond, Minnesota (Fergus Falls Area,

1986). I corrected this transcribing error and reanalyzed their data; results were confirmed by C.L. Glenn (Brandon University, Brandon, Man., Canada, personal communication 1990). Analysis of the sex ratio data from the large Minnesota lakes was similar.

Length and weight were recorded when walleye from the Minnesota ponds were sexed. Mean length and weight were calculated separately for males and females within each pond-year collection. Differences between male and female means were tested for significant differences from zero using two-tailed, two-sample *t*-tests ($\alpha = 0.05$).

Results

Jenniges and Olson agreed with me on the sex of walleye we examined, indicating that this study could include Jenniges' data and mine, and that it could be compared to Olson's. Gonadal histology was consistent with prior sex determinations based on gross gonadal morphology, indicating that sex determinations in this study and Olson's were probably accurate.

Y-o-y walleye collected in fall 1987 from the ponds receiving treated fry were sexed to determine the effects of steroid immersions and rearing temperatures. None of the seven Waterville Area ponds yielded enough fish to determine the sex ratio. The proportion that was males in five of the six remaining ponds did not differ from 50% (Table 1). Bradbury Pond had significantly more than 50% males, and a higher proportion of males than any other pond. Percent males was not consistent with the steroid used, suggesting that the steroid immersions had no effect. There was also no apparent relation between percent males and temperature units during the walleye's 9-d-old to 50-d-old age interval (Table 1). Gonads had probably differentiated by the end of this interval, since mean total lengths then exceeded 40 mm. (Seining in mid-June collected walleye from [three] [3?] of the 13 ponds; mean total lengths were 43 mm at age 40 d, 45 mm at age 46 d, and 56 mm at

Table 1. Fry treatments and sex of young-of-the year (y-o-y) walleye collected in fall 1987 from rearing ponds in Minnesota. Temperature units (degree-days above 0° C) were accumulated during the 9-d-old to 50-d-old age interval.

Pond	Location ^a	Spawn source ^a	Steroid immersion ^b	Stocking date	Temperature units	Y-o-y walleye sexed		
						No.	% males	95% C.I.
Lunde	DL	DL	C	8 May	782	200	50	44-57
Miller	DL	DL	T	8 May	806	199	49	42-56
Dewey	DL	DL	E	8 May	783	242	53	47-59
Bradbury	FF	GM	C	22 May	882	83	80	71-88
Monson	FF	GM	T	22 May	890	203	54	47-61
Babcock	FF	GM	E	22 May	890	209	53	46-60

^a Minnesota DNR Fisheries Management Area Headquarters:

DL = Detroit Lakes, MN

FF = Fergus Falls, MN

GM = Grand Marais, MN

^b C = control

T = 17 alpha-methyltestosterone

E = 17 beta-estradiol

age 46 d.)

Temperature and dissolved oxygen profiles taken in mid-June 1987 revealed that some ponds were stratified, and that thermometers placed in shallow water did not fully describe pond temperatures. Bradbury Pond had an oxygen concentration of less than 1 ppm below a depth of 1 m. Miller, Babcock, and Monson ponds were stratified but contained plants and at least 3 ppm oxygen to deeper levels, and Lunde and Dewey Ponds were not stratified. Temperatures of the epilimnia and upper metalimnia were similar in all ponds, ranging from 27° C to 23° C. Temperatures of the deeper oxygenated waters of Miller, Babcock, and Monson ponds ranged from 21° C to 16° C. Walleye may have been restricted to the warm surface waters of Bradbury Pond, but may have had access to cooler waters in the other stratified ponds. For this reason, the temperature units shown in Table 1 may be relatively accurate for Bradbury, Lunde, and Dewey ponds, but may be overestimates of the temperature units actually experienced by the fry in Miller, Babcock, and Monson ponds. Relating percent males to temperatures is therefore difficult for these ponds.

Y-o-y walleye were collected in fall from the ponds monitored in 1988, to relate percent males to rearing temperature, as in 1987. Fish from Stammer Pond were stocked locally and were not made available for sexing, but nearly 200 fish were sexed from each of the remaining three ponds. Percent males was positively related to temperature units during the fry's 17-d-old to 77-d-old age interval (Table 2). This was consistent with our hypothesis, but contrasted with the previous year's results.

Stratification was less of a confounding factor in 1988. Because Lunde and Stammer Ponds did not stratify, their thermograph records were representative of rearing temperatures. Temperatures in Bradbury Pond on 17 June 1988 decreased with depth from 23° C at the surface to 21° C at 2 m depth (where 1 ppm oxygen was recorded), and to 19° C at the bottom. A larger range was recorded on 16 June 1987 (27° C to 14° C). On 23 June 1988 temperatures in Pepin Pond decreased from 26° C at the surface to 25° C at 2.5 m (where 1 ppm oxygen was recorded), and to 23° C at the bottom. Walleye in the latter two ponds may have ranged deeper than the thermo-

Table 2. Sex of young-of-the-year (y-o-y) walleye collected in fall 1988, from Minnesota rearing ponds, and temperature units (degree-days above 0° C) accumulated during the 17-d-old to 77-d-old age interval.

Pond	Location ^a	Spawn source ^a	Stocking date	Temperature units	Y-o-y walleye sexed		
					No.	% males	95% C.I.
Lunde	DL	DL	3 May	1333	200	46	39-53
Bradbury	FF	FF	5 May	1456	194	63	56-70
Pepin	WV	GM	16 May	1549	195	77	72-83

^a Minnesota DNR Fisheries Management Area Headquarters:

DL = Detroit Lakes, MN

FF = Fergus Falls, MN

GM = Grand Marais, MN

WV = Waterville, MN

graphs, but this would not have changed the relative rearing temperature relation of the three ponds in Table 2. For this reason, the temperature units shown in Table 2 should be relatively accurate in representing the temperature units experienced by the developing walleye. This further supports the positive relation between temperature units and sex ratio.

Comparing pond temperature records during a common calendar interval may reveal the potential scope for the control of sex ratios by ponds. From 20 May through 2 July 1987, temperatures in the 13 monitored ponds ranged from about 14° C to about 27° C. The Waterville ponds (southernmost area) were usually warmer than the Detroit Lakes ponds (northernmost area) by 2-3° C. Temperatures of ponds in the Fergus Falls Area were usually intermediate, but closer to those for Detroit Lakes, a pattern reflecting geographic locations. Temperature units for the same period, when averaged for the ponds in each area, also reflect locations; final Waterville Area values (950 degree-days) exceeded those for Detroit Lakes (863 degree-days) by about 10%.

The temperature records obtained in 1988 with continuously recording thermographs may be compared from 28 May through 31 July (Figure 1). Lunde, the northernmost pond (Detroit Lakes Area),

was consistently the coolest, as expected, beginning day 160 (8 June). Pepin, the southernmost pond (Waterville Area), was generally the warmest, as expected, beginning day 170. Prior to 8 June Bradbury Pond (Fergus Falls Area) was warmest and Pepin Pond was coolest, indicating that latitude alone does not control pond temperature. Bradbury Pond may have stratified soonest, permitting the most rapid warming of the epilimnion. Pepin Pond has the greatest depth and surface area of the four, and its stratification may have been relatively delayed, causing delayed warming. Stammer Pond (Glenwood area) and Lunde Pond are the shallowest and did not achieve stable stratifications. Temperature units accumulated by these four ponds during the same period are shown in Figure 2. The plots from Lunde and Pepin ponds diverge and have values consistent with their location at latitudinal extremes. The plots for Bradbury Pond and Stammer Pond are reversed from what might be expected based on their latitudes, again demonstrating the influence of basin morphology and stratification.

Forty rearing ponds in four fisheries management areas provided sex ratio data for the rearing pond survey (Table 3). Data from the above treatments were included. Sex ratios were determined for a total of 69 pond-year collections taken from 1983 through 1989, though sample sizes were

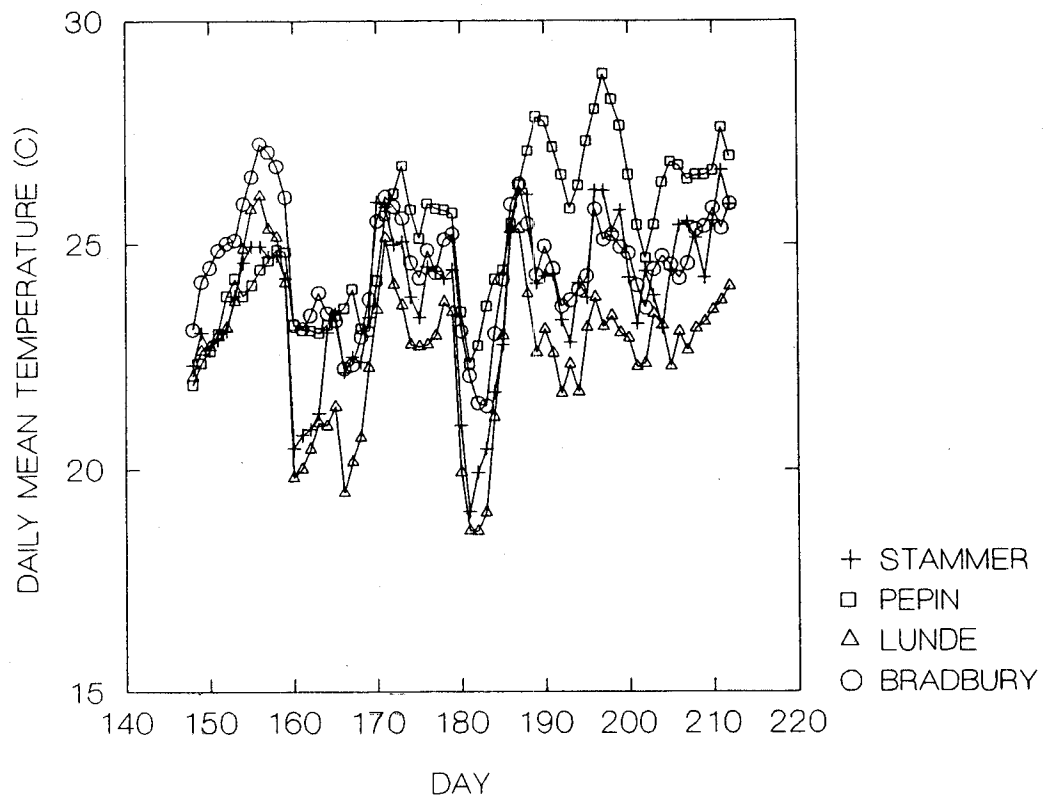


Figure 1. Daily mean temperatures in four rearing ponds, 28 May-31 June 1988.

sometimes smaller than desired. Table 4 presents the percentage of y-o-y walleye identified as males, and the results of chi-square tests for goodness-of-fit with a 1:1 sex ratio. Sixteen collections had sex ratios that differed significantly from 1:1 ($\chi^2 > 3.841 = \chi^2_{0.05,1}$), ranging from 29% to 42% males in three collections and from 61% to 89% males in 13 collections. Twelve ponds were sampled in more than one year; sex ratios of four were heterogeneous among years ($P(\chi^2) < 0.05$), indicating that annual sex ratios were dissimilar (Table 5). Sex ratios were also heterogeneous among collections grouped by pond management area and spawn source (either local or a more northern management area). For this reason, it was not proper to compare these groups statistically. Pooling all collections together, a total of 9,966 y-o-y walleye were sexed, yielding 53.01% males. Heterogene-

ity of sex ratios among the individual collections made it improper to test the pooled data for goodness-of-fit with a 1:1 ratio.

Analyzing Olson's (1968) data in a similar way facilitated comparison. He sexed y-o-y walleye collected from 23 ponds over three years (1963-1965). Males significantly outnumbered females in 18 of the 36 collections. Females never significantly outnumbered males. Sex ratios differed significantly among years for six of 12 ponds sampled in more than one year. Sexing 5,710 fish yielded 61.9% males overall. The pooled data were not tested further because of heterogeneity among the collections.

Glenn and Mathias (1988) had sexed y-o-y walleye taken over three years from 26 culture ponds in two states and four provinces. After correcting one ratio from a Minnesota pond and applying the Yates'

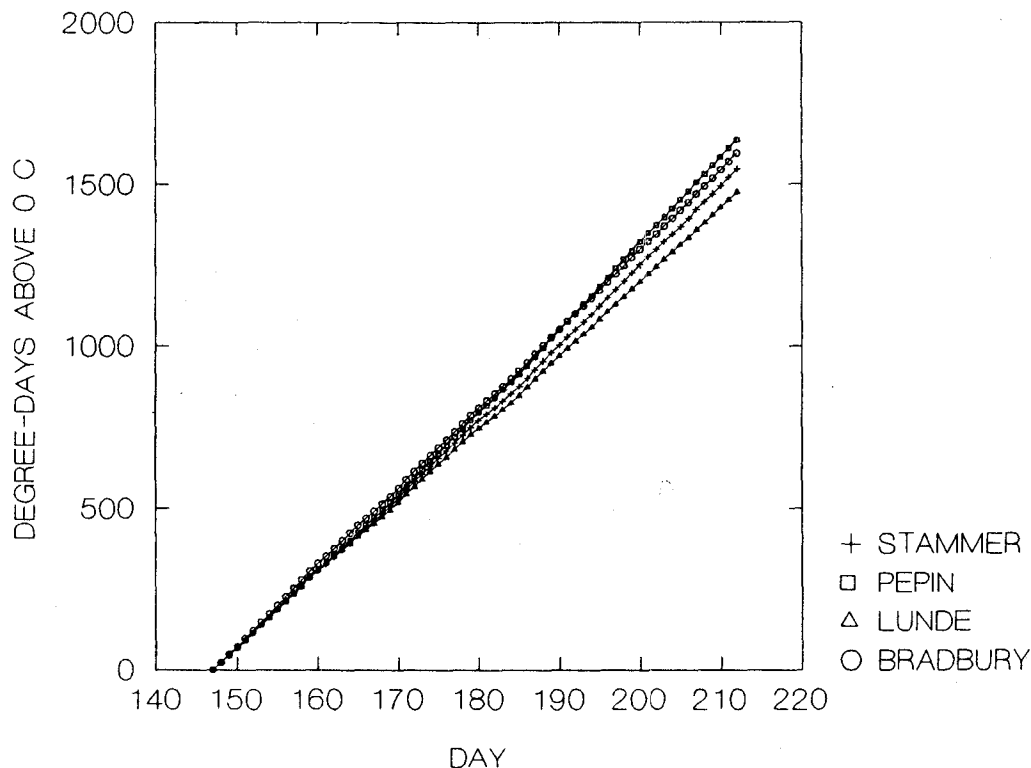


Figure 2. Cumulative degree-days over time in four rearing ponds, 28 May-1 July 1988.

continuity correction to all collections, re-analysis showed that females significantly outnumbered males in [three] [3] of their 31 collections and males never significantly outnumbered females. Sex ratios were not heterogeneous among collections ($\chi^2 = 41.69$; $df = 30$; $P = 0.076$), thus the collections were pooled and tested as a single population. The overall result, 48.2% males from 2,164 fish sexed, was not significantly different from a 1:1 sex ratio ($\chi^2 = 2.599$; $df = 1$; $P > 0.10$).

Five large lakes in Minnesota that maintain walleye populations by natural reproduction (Table 6) provided y-o-y sex ratio data from 1983-1989. Males were significantly more numerous in three of the 26 collections, but neither sex predominated in the rest (Table 7). Heterogeneity among collections grouped by lake, gear, or year made it inappropriate to test the groups'

pooled sex ratios for goodness-of-fit with a 1:1 ratio. Sexing a total of 3,874 fish yielded 52.61% males, a figure nearly identical to that from ponds.

The sizes of male and female y-o-y walleye differed within some of the collections taken during 1983-1989 from Minnesota rearing ponds. Mean total length of females significantly exceeded that of males in 10 of 67 pond-year collections tested (Table 8). Mean weight of females was significantly higher than mean weight of males in 8 of 62 collections tested and significantly lower in one collection (Table 9).

Discussion

Histology of 12 gonads confirmed that my identifications of them based on morphology were accurate. The perfect agreement among Olson, Jenniges, and me tends to

Table 3. Minnesota rearing ponds for which sex of young-of-the-year walleye has been identified.

Pond number	Pond name	Location ^a	Surface area (ha)	Maximum depth (m)
1	Thompson	Spicer	12.2	1.8
2	Mortenson	Spicer	4.1	3.7
3	Henry	Spicer	77.0	2.4
4	Lindgren I	Spicer	30.4	2.1
5	Chesness	Spicer	2.8	3.0
6	Monson	Spicer	17.0	2.7
7	Fields	Spicer	8.1	2.7
8	Lindgren II	Spicer	28.4	1.5
9	NL Pond 7	Spicer	1.9	1.5
10	NL Pond 8	Spicer	1.9	1.5
11	Anderson	Spicer	4.9	1.8
12	Doll	Spicer	1.6	3.0
13	Everson	Spicer	4.1	1.8
14	Golden	Spicer	24.3	6.1
15	Church	Spicer	24.3	3.0
16	E. Sibley	Spicer	6.1	1.8
17	Just	Spicer	55.5	4.0
18	Schackman	Spicer	24.3	.5
19	Allen	Spicer	32.4	.5
20	Wohlin	Spicer	12.2	2.7
21	E. Eagle	Fergus Falls	2.8	2.1
22	Bradbury	Fergus Falls	6.5	3.7
23	Grass	Fergus Falls	8.1	5.2
24	Darow	Fergus Falls	6.1	4.0
25	Helgeson	Fergus Falls	41.3	5.5
26	Babcock	Fergus Falls	3.6	4.3
27	Rankler	Fergus Falls	20.3	3.7
28	Monson	Fergus Falls	4.1	4.6
29	Dewey	Detroit Lakes	8.9	2.7
30	Lunde	Detroit Lakes	11.7	2.1
31	Miller	Detroit Lakes	3.6	3.7
32	Clear	Waterville	113.8	1.5
33	Armstrong	Waterville	50.6	1.8
34	Pepin	Waterville	163.2	3.7
35	Bishop	Waterville	10.9	1.2
36	Abby	Detroit Lakes	115.8	3.0
37	Wood	Waterville	23.1	0.9
38	Frank	Spicer	54.7	2.1
39	Sperry	Spicer	62.0	1.2
40	Carlson	Spicer	12.6	1.5

^a Minnesota DNR Fisheries Management Area Headquarters.

confirm their accuracy and Olson's (1968) data. The large lake sex data in this study have not been verified histologically, but I believe that they are similarly accurate. However, because so few gonads were examined in this way, it cannot be said with certainty that gender incongruity between somatic and germinal elements (partial sex

inversion) did not occur, or that some undeveloped females were not misidentified as males. Glenn and Mathias (1988) also used histological verification.

Immersing walleye fry in solutions of sex steroids had no discernible effect on sexual phenotype, based on the resulting sex ratios. Immersion treatments had also failed

Table 4. Sex of young-of-the-year walleye collected in fall from rearing ponds in Minnesota. Sex ratios were tested for goodness-of-fit with a 1:1 ratio.

Pond number	Year	Spawn source ^a	Spawn method ^b	Number sexed	Percent males
1	1983	S	d	60	72 *
2	1983	S	d	33	45
3	1983	S	d	56	75 *
4	1983	S	d	132	52
5	1983	E	w	93	42
6	1983	E	w	60	50
7	1983	S	d	104	50
8	1983	S	d	177	53
9	1983	S	d	53	47
10	1983	S	d	111	56
11	1984	S	d	89	60
3	1984	S	d	85	29 *
2	1984	S	d	213	54
12	1984	S	d	196	48
5	1984	S	d	170	50
13	1984	S	d	441	42 *
7	1984	S	d	422	49
12	1985	S	d	72	64 *
6	1985	S	d	463	51
5	1985	S	d	175	48
14	1985	E	w	92	89 *
15	1985	E	w	126	58
16	1985	E	w	46	70 *
4	1986	S	d	149	52
3	1986	S	d	343	52
12	1986	S	d	437	52
6	1986	S	d	144	54
7	1986	F,E	d	116	46
5	1986	F,E	d	101	44
17	1986	F,E	d	86	48
18	1987	S	d	83	71 *
19	1987	S	d	36	67
20	1987	S	d	128	49
21	1986	F	d	71	52
22	1986	F	d	73	62
23	1986	F	d	67	39
24	1986	F	d	75	57
25	1986	F	d	75	43
26	1986	F	d	70	50
27	1986	F	d	75	47
22	1987	G	w	83	80 *
26	1987	G	w	209	53
28	1987	G	w	203	54
29	1987	D	d	242	53
30	1987	D	d	200	50
31	1987	D	d	199	49
22	1988	F	d	194	63 *
26	1988	F	d	240	55
30	1988	D	d	200	46
31	1988	D	d	206	35 *
32	1988	G	w	194	53
33	1988	G	w	86	59
34	1988	G	w	195	77 *
35	1988	S	d	109	61 *

Table 4. Continued.

Pond number	Year	Spawn source ^a	Spawn method ^b	Number sexed	Percent males
7	1988	S	d	104	59
3	1988	S	d	106	53
19	1988	S	d	112	41
6	1988	S	d	103	42
36	1989	D	d	195	52
22	1989	F	d	264	56
37	1989	E	w	123	52
38	1989	S	d	85	52
39	1989	S	d	95	62 *
3	1989	S	d	118	57
2	1989	S	d	126	53
7	1989	S	d	102	54
6	1989	S	d	122	55
40	1989	B,F,D	d	101	74 *
19	1989	B,F,D	d	52	85 *

^a B = Bemidji, D = Detroit Lakes, E = Ely, F = Fergus Falls
G = Grand Marais, S = Spicer.

^b d = semi-dry-pan method, w = wet-pan method.

* Chi-square (Yates continuity correction, 1 df) > 3.841,
P < 0.05.

to control sex of yellow perch fry (T. B. Kayes, Department of Food Science, University of Wisconsin, Madison, WI, personal communication 1987). Differences in egg size and developmental rates may explain why this technique was effective for salmon (Hunter et al. 1986) but not for walleye. Compared to coho and chinook salmon, walleye eggs are smaller, and smaller fry (measuring about 6-8 mm total length) hatch after a shorter incubation time. Through the time that the yolk sac is absorbed (1 week post-hatch for walleye, 2-3 weeks post-hatch for salmon), the walleye is developmentally more primitive and the gonads are not sufficiently advanced to be influenced by the hormone, in contrast to the salmon (T. B. Kayes, personal communication 1987).

Several non-salmonid fishes have been sex-inverted by treatments of longer duration administered to older fish. In yellow perch that were sex-inverted by Malison et al. (1986), somatic elements of the gonads had already begun to differentiate when the 84-d diet treatment was begun at 20-35 mm total

length, though gametogenesis was still influenced. Similarly, hormonal control of the sex of largemouth bass was achieved by Garrett (1989) with a treated diet administered from 5 weeks (20-30 mm standard length) to 11 weeks of age. Davis et al. (1990) feminized channel catfish by including steroid in the diet for 21 d after yolk-sac absorption, but feeding the diet for less than 12 d was ineffective.

Hormonal control of sex in walleye may require that treatments occur during an analogous age or size interval. Olson (1968) found that ovaries and testes were morphologically distinguishable by the time walleye were 40 mm long and 50 d old, which occurred by mid-June in the 1987 study ponds. Inversion of germinal tissue might be accomplished after this date, however, as for yellow perch.

Pond temperatures are obviously influenced by basin morphology, as it affects stratification, in addition to day of the year and latitude. In early June 1988, Bradbury Pond was the warmest of the four monitored

Table 5. Year-to-year consistency of sex ratio of young-of-the-year walleye collected in fall from Minnesota rearing ponds: results of chi-square tests for heterogeneity. Sex ratio is significantly different in at least one year when $P < 0.05$.

Pond	Number of years ^a	Overall chi-square	P
2	3	0.7639	0.6825
3	5	30.35	0.0000
4	2	0.0195	0.8890
5	4	2.109	0.5501
6	5	4.876	0.3003
7	5	4.800	0.3085
12	3	5.032	0.0808
19	3	29.15	0.0000
22	4	15.33	0.0016
26	3	0.4671	0.7917
30	2	0.8110	0.3678
31	2	7.919	0.0049

^a Degrees of freedom = number of years - 1.

Table 6. Large lakes in Minnesota receiving little or no stocking for which sex of young-of-the-year walleye was identified.

Lake number	Lake name	Location ^a	Surface area (ha)	Maximum depth (m)
1	Leech	Walker	45,135	46
2	Lake of the Woods	Baudette	128,294	66
3	Cass	Bemidji	6,312	37
4	Upper Red	Bemidji	43,640	6
5	Mille Lacs	Aitkin	53,629	13

^a MN DNR Fisheries Management Area Headquarters.

ponds. As of July 31, its epilimnion had accumulated more temperature units than Stammer Pond, which is located farther south, but which does not stratify. Bradbury Pond is nearly surrounded by wooded hills, and is relatively sheltered from the wind, whereas Stammer Pond is in open prairie.

In both 1987 and 1988, the maximum temperature difference between monitored ponds was equal to or greater than 3° C.

This amount, and the range of temperatures observed, was sufficient to influence the sex ratio of Atlantic silverside in experiments by Conover and Heins (1987). Failure of the Waterville Area ponds to produce walleye in 1987 prevented analysis of the sex ratio effect of this southern stocking location. The apparent high mortality may have resulted from temperatures exceeding 34° C (Hokanson and Koenst 1986) or predation

Table 7. Sex of young-of-the-year walleye from large Minnesota lakes receiving little or no stocking. Sex ratios were tested for goodness-of-fit with a 1:1 ratio.

Lake number	Year	Collecting gear ^a	Number sexed	Percent male	Dominant sex ^b
1	1983	S	304	53	
1	1984	S	159	44	
1	1984	T	60	52	
1	1985	S	375	52	
1	1986	S	405	53	
1	1986	T	149	52	
1	1987	S	268	48	
1	1987	T	60	43	
1	1988	S	79	61	
1	1988	T	208	51	
1	1989	S	52	46	
1	1989	T	97	41	
2	1987	G	150	56	
3	1985	S	195	52	
3	1985	T	56	61	
3	1986	S	136	52	
3	1987	S	84	39	
3	1988	T	54	43	
3	1989	S	75	51	
3	1989	T	119	61	M
3	1989	E	66	59	
4	1984	S	168	67	M
4	1985	S	350	58	M
4	1989	S	99	52	
4	1989	E	40	55	
5	1988	G	66	50	

^a S = seine, July-August.
T = trawl, August.
E = electrofishing boat, August.
G = gillnet, fall.

^b M (male) entries indicate chi-square (Yates continuity correction applied, 1 df) > 3.841, $P < 0.05$.

by other species.

There is tentative evidence of a positive relation between temperature units and sex ratio in 1988, but no relation is apparent in 1987. The rearing temperature record for 1988 is more accurate, because continuously recording thermographs were used and stratification confounded the data to a lesser degree. The range in temperature units is also slightly greater. In addition, the age interval for which data were available corresponded better in 1988 (age 17 d to age 77

d) to the period when yellow perch sex was inverted (Malison et al. 1986) than it did in 1987 (age 9 d to age 50 d). Taken together, these differences give greater credibility to the positive relation between temperature units and percent males observed in 1988, save for the fact that only three data points are available. This correlation is consistent with field observations of the tidewater and Atlantic silverside and experiments with the Atlantic silverside (Middaugh and Hemmer 1987; Conover and Heins 1987).

Table 8. Significantly different lengths (mm) of female and male y-o-y walleye collected in fall, 1983-1989, from rearing ponds in Minnesota. Differences were not significant ($P > 0.05$) in 57 collections not listed.

Pond	Year	Female		Male		T	df	P
		Mean	SE	Mean	SE			
2	1984	125.8	0.69	123.4	0.63	2.56 ^e	211	0.011
3	1988	128.9	1.95	124.3	0.98	2.13 ^u	58.5	0.037
7	1984	103.8	0.34	102.7	0.36	2.12 ^e	420	0.032
7	1989	105.6	1.10	101.6	0.96	2.74 ^e	100	0.007
8	1983	147.3	1.65	143.1	1.38	1.96 ^e	176	0.049
11	1984	146.2	2.29	139.5	1.69	2.42 ^e	87	0.017
15	1985	121.6	3.68	112.6	2.82	1.97 ^e	124	0.049
31	1988	120.8	1.08	117.2	1.21	2.22 ^u	170.9	0.026
37	1989	133.3	1.08	129.1	0.95	2.95 ^e	121	0.004
39	1989	119.4	1.47	114.7	0.95	2.80 ^e	93	0.006

^e variances equal.

^u variances unequal.

Table 9. Significantly different weights (g) of female and male y-o-y walleye collected in fall, 1983-1989, from rearing ponds in Minnesota. Differences were not significant ($P > 0.05$) in 53 collections not listed.

Pond	Year	Female		Male		T	df	P
		Mean	SE	Mean	SE			
2	1984	14.4	0.25	13.4	0.22	2.86 ^e	211	0.005
7	1989	8.4	0.30	7.3	0.23	2.81 ^e	100	0.006
8	1983	23.5	0.99	21.1	0.68	2.00 ^u	150.4	0.045
11	1984	23.9	1.28	20.1	0.91	2.48 ^e	87	0.015
12	1986	5.2	0.08	5.6	0.10	-3.05 ^u	424.5	0.003
31	1988	13.7	0.69	11.9	0.46	2.22 ^u	202.4	0.026
32	1988	18.7	0.32	17.6	0.37	2.34 ^e	191	0.019
37	1989	18.2	0.42	16.4	0.37	3.16 ^e	121	0.002
39	1989	13.4	0.54	11.6	0.30	2.90 ^u	57.2	0.005

^e variances equal.

^u variances unequal.

Potential inaccuracies in the temperature units in 1987 might mask a relatively high value in Bradbury Pond that would correspond to its high proportion identified as males. Walleye may have been more restricted to the epilimnion than in other ponds, being excluded from the cooler

depths by lack of oxygen. Fry in Miller, Monson, and Babcock Ponds may not have been so confined, and thus may have been exposed to fewer temperature units than indicated in Table 1.

When size of the sexes differed significantly in this study's rearing pond survey,

females were nearly always longer or heavier (18 of 19 such cases), though such differences were slight. Olson (1968) stated that growth rates of the sexes did not differ in their first summer, and Glenn and Mathias (1988) stated that neither sex was consistently larger. Malison et al. (1988) demonstrated in the laboratory that female yellow perch grew significantly faster than males by consuming significantly more ration and converting it with significantly greater efficiency. Slightly faster first-year growth by female percids may be evidence of their greater reproductive need for large size, as for silverside, but may be independent of rearing temperature.

Life history differences suggest that temperature-dependent environmental sex determination would be less adaptive for walleye than for silverside. Atlantic silverside reproduce at age 1 and tidewater silverside may reproduce in their first year. Because increasing body size yields a proportionately larger increase in egg number than sperm number, Conover (1984) argued that it is adaptive for silverside to respond to temperature cues about the remaining length of the growing season and resultant potential body sizes by producing more females early in the season and more males late in the season. There would seem to be less selective advantage for a first-season divergence of growth between male and female walleye, since the age of maturity in Minnesota is at least two for males and three for females (Thorn 1984; S.E. Persons, MN DNR, Grand Marais, MN, personal communication 1991). Because more growing seasons occur before maturity, any first-season adaptive response of walleye sex ratio to temperature would probably be less dramatic.

Sex ratios of y-o-y walleye varied greatly from pond to pond, and from year to year for the same pond, in this study's survey. When sex ratios differed significantly from 1:1, males were usually more numerous (13 of 16 such cases). Males composed 53% of all fish sexed from the rearing ponds. These results are similar to Olson's (1968), but are

less extreme. Glenn and Mathias' collections (1988) were somewhat different: females usually outnumbered males, resulting in 48.2% males overall (not significantly different from 50%). The lack of heterogeneity among their collections is probably the result of smaller sample sizes (20-99, compared to 45-313 for Olson, and 33-463 in this study). Recent sex ratio data from large Minnesota lakes are similar to the pond data, whereas the two previous studies found either no difference from a 1:1 ratio or a predominance of females.

Bradbury Pond (pond no. 22) is noteworthy in that males were more numerous in all four collections (significantly in two, borderline in another). Additional temperature and sex ratio data are needed to verify if a relation exists between this pond's temperature pattern and its apparent trend toward males.

When collections were pooled into groups by pond location and spawn source, heterogeneity within each group indicated the presence of significant sex ratio differences within management areas, even when the spawn source was the same. It was therefore inappropriate to test the pooled ratio of each group for goodness-of-fit with a 1:1 ratio, or to test for differences in pooled ratios among the groups. We had expected percent males to increase from north to south, and when northern spawn was used, but could not now test these hypotheses. Thus no probability statements can be made regarding the relation between sex ratio and pond location or spawn source. The pooled sex ratios are presented in Table 10 as an unqualified summary in the interest of detecting trends, and in doing so, Bradbury Pond has been deleted from the data set (because it seems to produce males in higher proportions than other ponds in the same management area). Percent males increased from Detroit Lakes southward and when spawn was obtained from management areas north of the pond. It appears that ponds in southern areas are most likely to produce excess males, especially when eggs are received from more northern areas. This

Table 10. Summary of sex ratios of young-of-the-year walleye collected from rearing ponds in Minnesota, fall 1983-1989. Data are grouped by location of pond and spawn source. Bradbury Pond in the Fergus Falls Area was omitted because it consistently produced males in higher proportions than other ponds in the area.

Pond location ^a	Spawn source	Number of pond-year collections	Young-of-the-year walleye		
			Number sexed	Number of males	Percent males
Detroit Lakes	local	6	1242	592	47.67
Fergus Falls	local	7	673	339	50.37
Fergus Falls	northern MN	2	412	221	53.64
Spicer	local	36	5554	2870	51.67
Spicer	northern MN	10	873	513	58.76
Waterville	northern MN	4	598	368	61.54

^a MN DNR Fisheries Management Area Headquarters, north to south.

pattern is consistent with, but does not prove, the phenomenon of temperature control of walleye sex. Additional data should be collected from extreme northern and southern areas to verify these trends.

Several events related to life history and behavior could explain some of the variation observed in sex ratios, but would be unlikely explanations for the the above trends. Differential incubation times, or segregation of fry in hatchery or distribution tanks, could cause varying sex ratios in dipped lots of fry, and, hence, in pond sex ratios. Such events have not been investigated. Segregation of the sexes in the pond could result in sex-selective harvest methods and inaccurate sex ratios. This has not been reported for y-o-y walleye, and is unlikely when ponds are seined, as in some male-dominated collections seen by Olson (1968).

Because pond temperature follows the same north-to-south trend as that apparent for sex ratio, it is implicated as a factor controlling sex ratio. The apparent increase in percent males when northern spawn is used may also result from temperature control, since northern runs are later and local ponds receiving northern fry are warmer than when local fry were stocked. Thus, the location of the rearing pond and the date of

stocking directly affect rearing temperatures and may affect sex ratios. It is possible that a genetic factor exacerbates the hypothesized temperature effects, whereby northern stocks are adapted to cooler temperatures and are more affected than southern stocks by the warmer temperatures of southern ponds.

Two mechanisms by which temperature, or some other aspect of the pond environment, may control sex ratio are sex-selective mortality and sex inversion. An alternative mechanism for the effect of northern spawn may be varying spawning conditions among management areas. From Detroit Lakes southward variations of the dry-pan method are used to take spawn and fertilize eggs, whereas the wet-pan method is used in Ely and Grand Marais. In the strict dry-pan method eggs and milt are mixed together before being activated by addition of water, whereas in the wet-pan method they are extruded together into water. Details of the spawning methods, as well as water quality and anti-clumping agents used, also vary among management areas. If walleye are digametic, then the wet-pan method could produce excess males if it favors fertilization by male sperm.

The wet-pan method produced all the pond-reared fish sexed by Olson (1968).

Since then most management areas changed to a "semi-dry-pan" method, whereby some water unavoidably enters the pan. When data from this study are grouped by spawning method, semi-dry-pan and wet-pan groups are nearly equivalent to local and northern spawn groups, respectively (Table 4). For the semi-dry-pan method males composed 51.7% of 8,456 fish sexed from 57 collections. For the wet-pan method males composed 60.3% of 1510 fish sexed from 12 collections, which is closer to Olson's results (61.9% males). This suggests that the wet-pan method produces relatively more males than the semi-dry-pan method, and may partially explain differences among studies, though there are additional uncontrolled variables.

Stocking a lake with excess male walleye could have various effects on the sex ratio of the lake's population, depending on the cause of the excess and the relative amount of natural reproduction in the lake. Stocking excess genetic males (resulting from sex-selective fertilization, harvest, or mortality) would increase the proportion of males in stocked year-classes only. If complete sex reversal has occurred, altering homogametic genetic females to reproductively functional males, then matings with normal females may produce excess female offspring; ratios could vary among year-classes with dominance by males or females. Kayes (personal communication 1987) stressed that the sex *inversion* achieved for yellow perch was anatomical and histological, not necessarily functional. There have been no long term studies to learn if sex-inverted yellow perch (or walleye) behave during spawning in a manner that is effective and consistent with their germinal tissue, even though their gametes are fertile.

This study's overall result of 53% males would seem to cause little functional change in a population compared to 50%, but the more extreme proportions seen in some ponds, and overall by Olson (1968), might do so. Lakes are usually stocked with y-o-y from several ponds, so that an extreme ratio

from one pond might be countered by others. The slightly greater size of females might afford them a survival advantage (Forney 1966; Chevalier 1973) that would tend to offset the effects of male-dominated stocking.

Conclusions

Several conclusions can be drawn from this study. Males tend to be slightly more numerous than females in collections of y-o-y walleye from Minnesota rearing ponds, composing 53% of all fish sexed in this study. Collections from large lakes receiving little or no stocking have sex ratios that are roughly similar to those from rearing ponds. Sex ratios are highly variable from pond to pond, and from year to year for any one pond, but males predominate more often than females. The proportion of male pond-reared walleye that is males tends to increase from Detroit Lakes southward, and when fry originating from management areas north of the pond are stocked, though statistics were not applied to this trend. Pond temperatures increase from north to south, but are also affected by basin morphology. Rearing temperatures may have an effect on sex ratio, higher temperatures yielding more males. The wet-pan method of taking spawn may produce relatively more males than the dry-pan method. Immersing fry in solutions of sex steroids will not control the sex of walleye. When the sexes differ in size during their first year, it is most often the females that are larger.

Management Implications

This study provides a perspective on the control of walleye sex ratios, highlights potential problem areas, and offers at least partial solutions.

The current walleye culture and stocking program of the MN DNR probably does not cause the overall sex ratio in stocked lakes to differ from that of lakes where natural reproduction maintains the population.

Management areas using the wet-pan spawn taking method may produce excessive numbers of males, causing excess males in rearing ponds and stocked lakes. This can be roughly verified by sexing y-o-y walleye from rearing ponds in these areas, or tested by controlled comparisons made between wet-pan and dry-pan methods. If the effect is proven, then a change to the semi-dry-pan method now used in most areas might be recommended to produce sex ratios more like those of natural lakes.

Lakes in the southern portion of the state may be regularly receiving excess males as a result of either temperature (or other environmental) effects or wet-pan spawning, or both.

Stocking a lake with y-o-y walleye from several ponds may help to produce a balanced sex ratio of stocked fish. This is the usual practice.

Obtaining spawn locally and early in the season rather than from later spawning runs in northern areas may minimize the excess males stocked into southern lakes. This is not always practical.

The effect of stocking more males than females on the sex ratio of a lake's walleye population will depend upon the mechanism producing the excess males, the relative mortality of each sex, and the amount of natural reproduction. If mortality of females equals or exceeds that of males and there is relatively little natural reproduction then males will predominate.

Sex of walleye cannot be controlled by immersing fry in solutions of sex steroids.

It may be possible to control the sex of walleye by adding sex steroids to the diet in intensive culture. This would not be practical on the large scale that characterizes Minnesota's extensive walleye culture program.

References

- Baumgartner, A.P., C.L. Chrisman, G.W. Libey, D.B. Lucker, and B.L. Woolcot. 1986. Standard karyotype of the walleye (*Stizostedion vitreum*; $2n = 48$): induction of polyploidy by heat shock. Presentation at the 48th Midwest Fish and Wildlife Conference, Omaha.
- Bull, J.J., and E.L. Charnov. 1989. Enigmatic reptilian sex ratios. *Evolution* 43:1561-1566.
- Chevalier, J.R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. *Transactions of the American Fisheries Society* 102:739-744.
- Craig, J.F. 1987. The biology of perch and related fish. Timber Press, Portland, Oregon.
- Conover, D.O. 1984. Adaptive significance of temperature-dependent sex determination in a fish. *American Naturalist* 123:297-313.
- Conover, D.O., and S.W. Heins. 1987. The environmental and genetic components of sex ratio in *Menidia menidia* (Pisces: Atherinidae). *Copeia* 1987:732-743.
- Conover, D.O., and B.E. Kynard. 1981. Environmental sex determination: interaction of temperatures and genotype in a fish. *Science* 213:577-579.
- Davis, K.B., B.A. Simco, C.A. Goudie, N.C. Parker, W. Cauldwell, and R. Snellgrove. 1990. Hormonal sex manipulation and evidence for female homogamety in channel catfish. *General and Comparative Endocrinology* 78:218-223.
- Donaldson, E.M., and G.A. Hunter. 1982. Sex control in fish with particular reference to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 39:99-110.
- Eschmeyer, P.H. 1950. The life history of the walleye, *Stizostedion vitreum vitreum* (Mitchell), in Michigan. Michigan Department of Conservation, Institute of Fisheries Research, Bulletin 3, Ann Arbor.
- Forney, J.L. 1966. Factors affecting first-year growth of walleyes in Oneida Lake, New York. *New York Fish and Game Journal* 13:146-167.
- Garrett, G.P. 1989. Hormonal sex control of largemouth bass. *Progressive Fish-Culturist* 51:146-148.
- Glenn, C.L., and J.A. Mathias. 1988. Sex ratios of young-of-the-year walleye (*Stizostedion vitreum*) collected from lakes

and rearing ponds of western Canada and northern United States. *Canadian Journal of Zoology* 66:1772-1776.

Goetz, F.W., E.M. Donaldson, G.A. Hunter, and H.M. Dye. 1979. Effects of estradiol-17 β and 17 α -methyltestosterone on gonadal differentiation in the coho salmon, *Oncorhynchus kisutch*. *Aquaculture* 17:267-278.

Hokanson, K.E.F., and W.M. Koenst. 1986. Revised estimates of growth requirements and lethal temperature limits of juvenile walleye. *Progressive Fish-Culturist* 48:90-94.

Hunter, G.A., and E.M. Donaldson. 1983. Hormonal sex control and its application to fish culture. Pages 223-304 in W.S. Hoar, D.J. Randall, and E.M. Donaldson, editors. *Fish physiology*. Vol. 9, part B. Academic Press, New York.

Hunter, G.A., E.M. Donaldson, F.W. Goetz, and P.R. Edgell. 1982. Production of all-female and sterile coho salmon, and experimental evidence for male heterogamety. *Transactions of the American Fisheries Society* 111:367-372.

Hunter, G.A., I.I. Solar, I.J. Baker, and E.M. Donaldson. 1986. Feminization of coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) by immersion of alevins in a solution of estradiol-17 β . *Aquaculture* 53:295-302.

Johnstone, R., T.H. Simpson, and A.F. Walker. 1979a. Sex reversal in salmonid culture Part III. The production and performance of all-female populations of brook trout. *Aquaculture* 18:241-252.

Johnstone, R., T.H. Simpson, and A.F. Youngson. 1978. Sex reversal in salmonid culture. *Aquaculture* 13:115-134.

Johnstone, R., T.H. Simpson, A.F. Youngson, and C. Whitehead. 1979b. Sex reversal in salmonid culture Part II. The progeny of sex-reversed rainbow trout. *Aquaculture* 18:13-19.

Korpelainen, H. 1990. Sex ratios and conditions required for environmental sex determination in animals. *Biological Review* 65:147-184.

Kuo, C-M., Y-Y. Ting, and S-L. Yeh. 1988. Induced sex reversal and spawning of blue-spotted grouper, *Epinephelus fario*. *Aquaculture* 74:113-126.

Malison, J.A., T.B. Kayes, C.D. Best, C.H. Amundson, and B.C. Wentworth. 1986. Sexual differentiation and use of hormones to control sex in yellow perch (*Perca flavescens*). *Canadian Journal of Fisheries and Aquatic Sciences* 43:26-35.

Malison, J.A., T.B. Kayes, B.C. Wentworth, and C.H. Amundson. 1988. Growth and feeding responses of male versus female yellow perch (*Perca flavescens*) treated with estradiol-17 β . *Canadian Journal of Fisheries and Aquatic Sciences* 45:1942-1948.

Middaugh, D.P., and M.J. Hemmer. 1987. Influence of environmental temperature on sex-ratios in the tidewater silverside, *Menidia peninsulae* (Pisces: Atherinidae). *Copeia* 1987:958-964.

Mirza, J.A., and W.L. Shelton. 1988. Induction of gynogenesis and sex reversal in silver carp. *Aquaculture* 68:1-14.

Olson, D.E. 1968. Sex ratios of young-of-year walleyes in Minnesota rearing ponds and lakes. *Progressive Fish-Culturist* 30:196-202.

Schreck, C.B. 1974. Hormonal treatment and sex manipulation in fishes. Pages 3-12 in C.B. Schreck, editor. *Control of sex in fish*. Sea Grant Extension Division, Virginia Polytechnic Institute and State University, Blacksburg.

Thorn, W.C. 1984. Effects of continuous fishing on the walleye and sauger population in pool 4, Mississippi River. Minnesota Department of Natural Resources, Section of Fisheries, Investigational Report 378, St. Paul.

Varadaraj, K. 1990. Production of monosex male *Oreochromis mossambicus* (Peters) by administering 19-norethisterone acetate. *Aquaculture and Fisheries Management* 21:133-135.

Yamamoto, T. 1969. Sex differentiation. Pages 117-175 in W.S. Hoar and D.J. Randall, editors. *Fish physiology*. Vol. 3. Academic Press, New York.

Zar, J.H. 1984. Biostatistical Analysis.
Prentice-Hall, Englewood Cliffs, New
Jersey.

Acknowledgments

D. Pereira and D. Olson designed the steroid immersion and temperature manipulation experiments and provided an initial literature review. Olson assisted with the steroid immersion treatments. V. Jenniges provided ideas and most of the pond sex ratio data. Sex ratio data from lakes was provided by S. Boe, R. Ekstrom, S. Gustafson, and R. Hugill. J. Marcino identified gonadal germinal tissue. Fisheries management crews in the respective areas provided walleye from ponds. Field assistance was provided by T. Domonoske, D. Olson, N. Morris, C. Kavanaugh, D. Pereira, B. Parsons, C. Berberich, and G. Huberty. D. Thompson reviewed the manuscript.

Edited by:

C.S. Anderson, Fisheries Research Supervisor
P.J. Wingate, Fisheries Research Manager

ERRATA

Minnesota Department of Natural Resources
Investigational Report 410, 1991

SEX RATIOS OF YOUNG-OF-THE-YEAR WALLEYE FROM REARING PONDS AND LAKES IN MINNESOTA¹

Paul D. Eiler

Minnesota Department of Natural Resources
Section of Fisheries
500 Lafayette Road
St. Paul, MN 55155

Text Errata

Page/paragraph	Erratum	Correction
4/2	<i>Menidia</i>	<i>M. menidia</i>
6/6	[three] [3?]	three
10/1	[three] [3]	three
19/2	<i>inversion</i>	inversion.

Table Errata

Page	Table	Pond no.	Correction (shown in large bold type)			
7	1		alpha-methyltestosterone			
11	3	18	Shackman	Spicer	24.3	1.5
11	3	19	Allen	Spicer	32.4	1.5
11	3	35	Bishop	Spicer	10.9	1.2

¹ This project was funded in part by the Federal Aid in Sport Fish Restoration (Dingell-Johnson) Program. Completion report, Study 139, D-J Project F-26-R Minnesota.