Minnesota Department of Natural Resources
Investigational Report 569, April 2018

Impacts of Walleye fry stocking on year-class strength in lakes with Walleye spawn-take operations

by

Dale E. Logsdon
Minnesota Department of Natural Resources, Division of Fish and Wildlife
50317 Fish Hatchery Road
Waterville, Minnesota 56096, USA

Charles S. Anderson
Minnesota Department of Natural Resources, Division of Fish and Wildlife
500 Lafayette Road
St. Paul, Minnesota 55155, USA

Abstract — Oxytetracycline (OTC) immersion marking was used to evaluate the practice of "putting back" Walleye fry by stocking fry into Minnesota egg-source lakes at a rate equal to at least 10% of the eggs removed. Our results indicate that the current put-back practice results in substantially more fry stocked than would be necessary to compensate for the additional fry that would have hatched in absence of the egg-take operations. Although the wild hatch rates observed in the study lakes were quite variable, they were substantially lower than the 10% value (Johnson 1961) that is the basis of the put-back practice. This study also revealed that stocked Walleyes can comprise a substantial proportion of the year-classes in the egg-source lakes. Our recruitment response modeling did not show a consistent relationship between fry density and subsequent year-class strength, but the weight of the evidence did identify the occurrence of density-dependent growth and recruitment, and supported recognition of diminishing year-class benefits at higher fry densities (Beverton-Holt curve) or even a risk of suppression of year-class strength (Ricker curve) as plausible. Consequently, we recommend that stocking in the egg-source lakes no longer be based on a percentage of the egg-take (or convenience for disposing of surplus fry), but instead be conducted at levels targeted to achieve intermediate total fry densities and subsequently modified based on changes to growth, recruitment, and forage abundance over time.

This project was funded in part by the Federal Aid in Sport Fish Restoration (Dingell-Johnson) Program.
Completion Report, Study 644, D-J Project F-26-R Minnesota.

INTRODUCTION

With approximately 270 million Walleyes stocked annually in Minnesota waters, the Minnesota Department of Natural Resources (MNDNR) operates one of the largest Walleye-stocking programs in the United States. In order to fulfill its annual stocking needs, the MNDNR collects over 600 million eggs from a total of 13 different spawning runs. The lakes that support these spawning runs are some of the most important fisheries in the state. Consequently, the MNDNR compensates for the egg removal by stocking back into these lakes the number of fry equal to at least 10% of the eggs removed. The actual number of Walleyes stocked into these lakes often exceeds 10%, however, because fry in excess of State stocking needs are also returned to the egg-source lakes. It was not clear what effect, if any, stocking had on growth or year-class strength of the recipient populations.

The 10% "put-back" value is based loosely on in-situ observations of deposited Walleye eggs at several locations within the Lake Winnibigoshish system (Johnson 1961). In contrast to the 50% to 88% hatch rates that typically occur in MNDNR fish hatcheries (N. Vanderbosch, MNDNR, personal communication), Johnson (1961) estimated that hatch rates ranged from only 0.6% to 36% in Lake Winnibigoshish. The 10% put-back value approximates the average of Johnson's estimates and has been interpreted as a prediction of the total number of additional fry that would have hatched in the lake in absence of the egg-take operation. Because Lake Winnibigoshish is located within the boundaries of the Leech Lake Indian Reservation, the MNDNR adopted the 10% put-back policy for reservation waters following a formal agreement with the Leech Lake Band in 1972. Elsewhere, the 10% put-back was adopted as common practice.

Although put-back stocking has been common practice in Minnesota since the 1970's, the effects on the resident Walleye populations have never been adequately evaluated because there was neither a perceived need nor the technology to do so. The resulting stocking densities in egg-source lakes can be quite high (up to 6,200 fry/littoral acre) but application of Johnson's average hatch rate to estimates of egg production indicated that natural reproduction far exceeded the number of fry that were stocked back into the systems. Prior to the advent of oxytetracycline (OTC) marking, the small size at stocking also prevented a means to mark the fry and thus restricted the ability to identify the stocked Walleyes and their contribution to the recipient populations.

Approval for OTC marking of potential food fish was granted in 2004 (FDA 2015) following several years of successful marking trials that verified its effectiveness for marking Walleye fry (Brooks et al. 1994; Fielder 2002; Lucchesi 2002). Pond and laboratory experiments in Minnesota also demonstrated that large numbers of newly hatched Walleye fry could be marked with little disruption to typical hatchery operations or adverse effects on the survival or growth of the fish (Logsdon et al. 2004).

Some of the early stocking of OTC-marked fry in Minnesota was into the Red Lakes where the resulting year classes were composed of up to 97% marked fish (Logsdon et al. 2016). Subsequent studies on Leech and Woman Lakes resulted in year classes composed of 39% to 86% marked fish (D. Schultz, MNDNR, personal communication). A high return rate of stocked Walleyes was expected in the Red Lakes since the spawning stock was very low and a large number of fry were stocked into the system. However, mark returns were expected to be much lower on Leech and Woman Lakes because spawning stocks were abundant and natural reproduction is known to occur regularly. The observed return rates for all three of these lakes indicated that stocked fry can survive well enough among wild fry to compose a large proportion of individual year classes.

The high proportion of marked Walleyes in age-0 samples also allowed the use of Petersen mark-recapture techniques to estimate total fry abundance and, by subtraction of stocked fry, wild fry abundance. Division of wild fry abundance by estimates of egg production returned system-wide hatch rates for Red, Leech, and Woman Lakes between 0.02% and 0.89% (Logsdon 2006; D. Schultz, personal communication). These resulting values, as such, were at least an order of magnitude below the 10% value that the put-back fry stocking is based on. Subsequent catches of the stocked Walleyes in our gill nets also indicated that strong year-classes can be formed at much lower fry densities than are typically stocked into our egg-source lakes. For example, the strong 1999 and 2001 year-classes in the Red Lakes were produced from total fry densities less than 650 total fry/littoral acre (Logsdon et al. 2016), whereas the 2005 and 2006 year-classes in Leech Lake were produced with less than 450 total fry/littoral acre (D. Schultz, personal communication).

Although fry are typically stocked into our egg-source lakes at substantially higher densities than those which produced strong year-classes in Red and Leech Lakes, the egg-source lakes do not provide a proportionally higher catch rate of Walleyes in gill nets or by anglers. These observations suggest the existence of a carrying capacity; above which, the addition of more fry results in compensatory increases in mortality rather than increased recruitment. If the relationship between total fry density and eventual recruitment is asymptotic, the 10% put-back practice may prove to be an inefficient approach to allocating fry; if the relationship is dome-shaped, the practice could also be detrimental to the Walleye populations in the egg-source lakes.

Because the goal of put-back stocking is to prevent detrimental effects of our Walleye production operations on the populations in our egg-source lakes, we sought to 1) quantify natural reproduction across the range of spawning stock densities observed in four typical egg-source lakes, 2) identify the contribution of stocked fry to the total fry density in the four lakes, 3) monitor the effects of total fry density on growth and survival, and 4) determine put-back strategies that, when combined with natural reproduction, optimize growth and survival so as to maximize year-class strength.

METHODS

Study Sites

Vermilion, Winnibigoshish, Woman, and Otter Tail Lakes were selected as study lakes for this research because 1) they all provide important Walleyes fisheries, 2) have long served as egg-source lakes, and 3) are large enough to provide adequate samples sizes for abundance estimates. In addition, Lakes Vermilion and Winnibigoshish are in the MNDNR Large Lakes Program that includes annual sampling and a dedicated fisheries specialist for each lake.

Lake Vermilion is a 40,557 acre lake in the Canadian Shield area of St. Louis County that is composed of irregular-shaped basins with many bays and islands. For management purposes, Lake Vermilion is often considered as consisting of an East Basin (28,813 acres) and a West Basin (11,744 acres) with the division occurring at Oak Narrows. The West Basin has slightly clearer water, more centrarchids, and more vegetation than the East Basin; whereas the East Basin has typically had higher Walleye abundance than the West Basin. The egg-collection station is operated on the Pike River, a tributary to the East Basin, where 70 to 160 million eggs are removed each year for hatchery production. Put-back stocking during the 8 years prior to this study ranged from 15 to 25 million fry (1,100 to 1,700 fry/littoral acre) distributed across both basins. An 18 to 26 inch protected slot limit (PSL) and four-fish bag limit has also been in place for Walleyes in Lake Vermilion since 2006 and, in more recent years, both Rusty Crayfish and Double-Crested Cormorants have become established in the East Basin.

Lake Winnibigoshish is a 58,544 acre lake located in the Chippewa National Forest in northern Cass County. Lake Winnibigoshish consists of a single basin that is connected to the Cut Foot Sioux chain of lakes (2,768 acres) where the MNDNR egg-collection station is located. The Cut Foot Sioux station is the largest egg-collection operation in Minnesota and accounts for between 160 and 233 million eggs each year. Recent put-back stocking ranged from 18 to 32 million fry (900 to 1,600 fry/littoral acre) prior to the study and all fry are stocked into Cut Foot Sioux and Little Cut Foot Sioux lakes. A 17 to 26 inch PSL was initiated for Walleyes in 2000 but relaxed to an 18 to 23 PSL with only 1 over 23 inches in 2015. Zebra mussels are present in Lake Winnibigoshish.

Woman Lake is a 5,520 acre lake that is also located in northern Cass County. Woman Lake consists of a large central basin with four bays and connections to Girl Lake (428 acres), Child Lake (285 acres), and Little Woman Lake (31 acres). The egg-collection station is located on the Boy River, a tributary to the southwest end of Woman Lake, where between 50 and 95 million eggs are collected annually. Recent put-back stocking ranged from 6 to 11 million fry (1,900 to 4,600 fry/littoral acre) with the highest stocking occurring during years when the egg quota was increased at the Boy River egg-collection station to accommodate stocking of nearby Leech Lake. Fry stocking for Woman Lake occurs in the main basin only. Rusty crayfish are also present in Woman Lake.

Otter Tail Lake is a 13,725 acre oval-shaped basin located in west-central Minnesota. Otter Tail Lake is connected to Walker Lake (578 acres) via a short segment of the Dead River, which is a tributary on the northwest side of Otter Tail Lake. The egg-collection station is located on the Dead River immediately upstream of Walker Lake. The egg take typically consisted of between 55 and 76 million eggs, and put-back stocking has recently ranged between 0 and 14 million fry (0 to 2,000 fry/littoral acre). Zebra mussels have recently been discovered in Otter Tail Lake.

Egg Production

Adult sampling.—Walleyes age 1 and older were sampled by MNDNR staff each September with experimental gill nets. The gill nets consisted of 15.3 m panels of each: 19 mm, 25 mm, 32 mm, 38 mm, and 51 mm bar measure mesh. The nets were allowed to fish for approximately 24 hours prior to retrieval and all collected Walleyes were 1) individually weighed, 2) measured for length, 3) the gonads inspected to determine sex and maturity, and 4) a scale sample and both sagittal otoliths removed. During 2008-2012, the ovaries of the mature females were also removed, preserved in formalin, and later forwarded to the Brainerd MNDNR Fisheries Research Station or the University of Wisconsin Stevens Point (UWSP) for egg enumeration.

Lakes Vermilion and Winnibigoshish are both part of the Minnesota large-lake monitoring program and have a history of annual gill-net sampling (Wingate and Schupp 1985). Lake Vermilion has been sampled in the fall, but Winnibigoshish has been sampled in the summer. Anderson's (1998) q_{abg} model was developed to estimate Walleye abundance from fall gill-net catches; so, beginning in 2007, supplemental fall sampling has been conducted on Lake Winnibigoshish. Woman is another lake that was traditionally netted in the summer, but only once every three years. Beginning in 2007, Walleye sampling on Woman Lake was changed to annual fall sampling, and in 2008 the number of gill nets increased from twelve to fifteen. Otter Tail Lake has traditionally been netted in the fall, but only once every three years. The frequency of netting on Otter Tail was increased to annual beginning in 2008.

Spawner biomass.—The abundance of mature female Walleyes in each lake was estimated from the gill-net catches of the previous fall using Anderson's (1998) gill-net catchability model (q_{abg} model). Catchability ($q[l]$) was first calculated for each 10-mm length-group using the formula

$$q(l) = 1.32 \cdot \alpha(l) \textstyle\sum_{meshes} \beta_m \gamma(x) \text{ / acres}$$

where l is the midpoint of the length-group, $\alpha(l)$ is the encounter probability per length group for the entire gill net, β_m is the contact coefficient per mesh size, and $\gamma(x)$ is the retention function for each mesh size where x is the fish/mesh perimeter ratio, and acres is the area in acres of the basin where the netting took place. The abundance estimate (N) was then calculated for each basin with the formula

$$\hat{N} = \sum_{lengths} \mathrm{CPE}_l / q(l)$$

where CPE is the catch per effort of mature female Walleyes per 10 mm length interval, and $q(l)$ is the catchability coefficient. Woman and Otter Tail Lakes were considered single basins, resulting in a single estimate for each lake. Separate estimates were calculated for the two basins of Lake Vermilion as well as the separate basins of Lake Winnibigoshish and Cut Foot Sioux. Biomass estimates ($\hat{B}$) were also calculated from the q_{abg} model for each basin using the formula

$$\hat{B} = \sum_{lengths} N_l a l^b$$

where N_l is the population estimate of Walleyes at each length group, a is the antilog of the y intercept from the regression of log(weight) on log(total length), and b is the regression coefficient from the regression of log(weight) on log(total length). Total lake estimates of both abundance and biomass were calculated for the Lake Vermilion and Winnibigoshish systems as the sum of the individual basin estimates. Confidence intervals of the estimates for all lakes were calculated using bootstrap methods described by Haddon (2001) where population and biomass estimates calculated from individual net catches served as the pool for resampling. This pool of values was resampled with replacement to produce bootstrap samples of size n, where n = the number of nets fished during the survey. One thousand bootstrap estimates were generated, and the confidence intervals were calculated as the 5th and 95th percentiles of the distribution of bootstrap estimates.

Fecundity.—Preserved ovaries were first weighed whole and then 5 samples of eggs between 11 and 63 grams each were randomly removed from each ovary, weighed to the nearest 0.001 gram, and enumerated. Tissue associated with the ovarian wall of every fifth fish in the samples was also separated from the egg mass and weighed separately. Then the mean number of eggs per mg was multiplied by the entire weight of the ovaries, minus that of the ovarian tissue, to estimate the total number of eggs per female. Total eggs were estimated in a similar manner for those fish without weighed ovarian tissue except that total ovary weights were reduced by the mean ovarian tissue weight (by percent) of fish in the weighed sub-sample. The relative fecundity rate was calculated as the number of eggs divided by the total weight of the female at capture. Population-wide egg production was then calculated by applying the mean relative fecundity rate of the sample to the corresponding fall estimates of adult female biomass.

For comparison, we also calculated fecundity from eight assorted samples of Walleyes collected during the spring spawning runs. The eggs were easier to count when collected in the spring but sample sizes were restricted due to an unwillingness to sacrifice many large Walleyes in a public setting. The samples from the spawning runs consisted of nine to ten females that possessed firm, swollen abdomens but did not express eggs when massaged. Fecundity was measured gravimetrically for six of the samples (Pike River 2011, Dead River 2011, Boy River 2009 & 2011, and Cut Foot Sioux 2010 & 2011) where females were first measured and weighed, then both ovaries were removed and preserved in formalin. The eggs were later stripped from the preserved ovaries and weighed. Nine randomly selected samples between 0.4 and 0.6 grams were then removed from the egg mass, enumerated, and weighed to the nearest 0.001 gram. The mean number of eggs per mg was then extrapolated to the weight of the entire egg mass to estimate the total number of eggs in the ovaries. Fecundity was determined both gravimetrically and volumetrically for samples collected at Cut Foot Sioux in 2008 and 2009. Females were first measured and weighed, then both ovaries were removed and stripped of their eggs. The total volume of eggs from each female was first measured to the nearest 5 ml in a graduated cylinder. A random sample of eggs was then collected from the cylinder and the maximum number of eggs that would fit without deformation was placed in a single row in the bottom of a calibrated Von Bayer V-trough (Piper et al. 1982). This was repeated three times for each female. Egg rates (eggs/volume) were then determined from a chart adapted from Piper et al. (1982) and the mean of the three rates was multiplied by the total volume of eggs to determine the total number of eggs from each female. The eggs from each female were then preserved in formalin and later weighed and enumerated using the aforementioned procedure to provide gravimetric estimates of fecundity for comparison.

Stocking

Incubation, marking, and distribution of fry.—Walleye eggs collected by MNDNR are typically fertilized and water-hardened on site, then volumetrically enumerated (similar to description above) and distributed to one or more of the eleven Minnesota state fish hatcheries for incubation in McDonald jars. Eggs collected at Pike River and subsequently stocked as fry into Lake Vermilion are incubated at the Pike River State Fish Hatchery, eggs collected from Cut Foot Sioux Lake and stocked as fry into the Lake Winnibigoshish system are incubated at the Grand Rapids State Fish Hatchery, eggs collected at the Boy River and stocked as fry into Woman

Lake are incubated at the Bemidji State Fish Hatchery, and eggs collected at the Dead River and stocked as fry into Otter Tail Lake are incubated at the Walker Lake State Fish Hatchery.

All of the fry stocked into the study lakes during 2008-2015 were treated by immersion for six hours in a buffered solution of OTC. The procedure used to treat the fry was similar to that first described by Brooks et al. (1994) but, with the exception of those marked at Walker Lake Hatchery in 2010, used a concentration of 700-mg active OTC/L (Fielder 2002; Lucchesi 2002; Logsdon et al. 2004). Walleye fry were erroneously treated with 532-mg active OTC/L at the Walker Lake Hatchery in 2010 because the percent active OTC was not accounted for during mixing of the solution. Pennox 343® was used as the source of OTC (76% active OTC) and sodium phosphate dibasic was used as the buffer during all treatments. Although sodium phosphate dibasic has successfully been used to buffer OTC solutions elsewhere, the extremely low alkalinity of the Pike River supply water created difficulties in stabilizing the solution pH during our first OTC treatment there in 2008. Subsequent solutions at the Pike River Hatchery were mixed with the City of Tower municipal well water to enhance their buffering capacity. Solutions used at the other hatcheries were mixed with water from the same source as that used to incubate the eggs. To reduce handling stress associated with the treatment, the fry were combined with the solution in 19 L containers six hours prior to stocking, transported during the immersion period, and then released directly from the transport containers into the lakes.

Distribution of the treated fry within the lakes followed the procedures previously established by the local MNDNR Area Fisheries Office for stocking put-back fry. The fry stocked into Lake Vermilion were distributed among its two basins; those stocked into the Winnibigoshish system were stocked into Cut Foot Sioux and Little Cut Foot Sioux Lakes; those into the Woman Lake system were stocked into the main basin; and those stocked into the Otter Tail Lake system were distributed among Otter Tail and Walker Lakes. In addition to stocking the egg-source lakes, samples of fry from each of the treatments were also stocked into rearing ponds to provide fish for efficacy evaluation of the OTC-marking procedure.

Stocking quotas.—The principal design of this study was to mark the fry stocked into the study lakes so that Petersen mark-recapture methods could be used to quantify total annual fry abundance in each lake and ultimately determine the recruitment responses across the range of fry densities in a manner similar to that which is commonly used to model stock-recruitment relationships. A problem commonly encountered in stock-recruitment analysis, however, is the inability to describe the shape of the recruitment response relationship due to inadequate contrast in spawning stock abundance levels (Hilborn and Walters 1992). We expected wild fry abundance to fluctuate naturally due to changes in spawner abundance and incubation conditions, but the 10% put-back stockings could have reduced the annual variability in total fry density since the egg-take is based on MNDNR needs rather than a set proportion of the population's egg production. Consequently, we attempted to manipulate total fry densities across a broader range of pre-determined values (250–2,000 fry/littoral acre) by varying the number of fry stocked into the study lakes.

The 250–2,000 fry/littoral acre range roughly brackets the 1,000 fry/littoral acre stocking density that is typically used to sustain Walleye populations in Minnesota lakes that lack natural reproduction (MNDNR 2017) while including the lower densities that have been observed to produce strong year classes in Red and Leech lakes and the higher densities typically stocked due to the 10% put-back practice. To represent this range of values, we sought to achieve total fry densities of 250, 500, 1,000, 1,500, and 2,000 total fry/littoral acre within each lake across the first 5 years of the study (manipulation phase of study; 2008-2012). To facilitate the identification of year effects on growth and recruitment, we also sought to vary the total fry densities among the lakes within each of the experimentally stocked years.

Because of this experimental design, the annual stocking quotas for the study lakes during the first 5 years of the study were dependent upon 1) the annual variability in wild fry production, 2) the target fry densities already achieved in each study lake, 3) the current target fry densities of the other study lakes, 4) the age-0 sample sizes necessary for Petersen fry abundance estimates, 5) the current status of the fishery, and 6) public acceptance of the proposed stocking. Since we would not be able to calculate the abundance of wild fry until after stocking and subsequent recapture of OTC-marked fry, we had to predict wild fry production a priori. The method that we used to predict wild fry abundance for the upcoming year was to apply the mean of observed hatch rates to the total egg production estimates from the previous fall's gill netting minus the upcoming spring egg-removal quota. Thus, the wild "hatch rates" that we used were different than those which are typically referred to by hatchery staff because the wild hatch rate values that we used were actually a function of egg deposition, fertilization, and hatching. For the first year of the study (2008) we used the mean of the wild hatch rates observed on Leech and Red Lakes (0.22%); thereafter we used the running means from the individual study lakes.

Once the predicted wild fry abundance values were calculated, the number of stocked fry necessary to reach each of the target values was determined. The resulting wild and stocked fry values were then used to calculate the age-0 sample size (n) necessary to obtain Petersen population estimates with 10% precision (Robson and Regier 1964) using the formula

$$n = \frac{392 \cdot \hat{N}_{total} \cdot \hat{N}_{wild}}{N_{stocked} \cdot \left(\hat{N}_{total} - 1\right) + (392 \cdot \hat{N}_{wild})}$$

where $\hat{N}_{wild}$ is the predicted wild fry abundance for the upcoming spring, $N_{stocked}$ is the number of marked fry to be stocked into the lake, and $\hat{N}_{total}$ is the sum of $\hat{N}_{wild}$ and $N_{stocked}$. The resulting sample sizes were compared to historical age-0 catch rates in the study lakes, and those stocking rates that resulted in samples sizes that were unlikely to be achievable were excluded from selection. To assure that the stocking rates in our experimental design did not inadvertently reduce a Walleye population to a point that it would produce a long-term reduction in fishing quality (or be perceived by the public as such), we agreed with local lake associations that stocking levels would revert to either 10% of the fry hatched from the egg-take or 1,000 fry/littoral acre for at least two years immediately following two consecutive years that age-0 CPE fell below the 25th percentile of age-0 CPE observed during the 10 years preceding the study. After accounting for required sample sizes and low age-0 CPE contingency stocking, the target values for the study lakes were then selected from those available based on how well they helped distribute the range of total fry densities both within a lake among years and among the lakes within a year. Stocking quotas were then determined by subtracting the predicted wild fry abundance from the total fry target values. Marked fry were also stocked into the study lakes during 2013-2015 (post-manipulation phase of study) to provide additional data on hatch rates and the effects of fry density on age-0 growth, but stocking rates were determined by the MNDNR Area Fisheries offices based on existing policy or perceived need.

Natural Reproduction

Age-0 sampling.—The stocked and wild age-0 Walleyes were later sampled and the actual abundance of fry at the time of stocking calculated from the OTC-mark returns. The method used to collect the age-0 Walleyes depended somewhat upon the standardized methods previously adopted by the local MNDNR Fisheries Areas. Lake Winnibigoshish was sampled with mid-summer bottom trawling whereas Vermilion and Woman Lakes were sampled with fall electrofishing. Otter Tail Lake did not have a history of standardized age-0 Walleye sampling so it was also electrofished each fall for the duration of this study. Whenever possible, the aforementioned sample sizes were attained by sub-sampling those age-0 Walleyes collected during standardized sampling. If the standardized sampling catch was insufficient, then supplemental sampling was conducted to make up the difference. The samples of age-0 Walleyes were immediately placed on ice, then frozen, and later forwarded to the Waterville MNDNR Fisheries Research Station, the Walker MNDNR Area Fisheries Office, or UWSP for OTC-mark detection.

Oxytetracycline mark detection.—The samples from the study lakes, along with their respective known-treated samples from the efficacy ponds, were inspected for OTC marks using the methods described in Logsdon et al. 2004. The sagittal otoliths were first secured to a microscope slide with cyanoacrylate cement and then polished with 1,000 grit sandpaper until the innermost circuli first became visible under 100 X magnification with transmitted light. Inspection for a mark was then conducted under an epifluorescent microscope with 100-200 X magnification, fluorescent lighting, 505 nm dichroic mirror, 420-490 nm exciter filter, and 520 nm barrier filter. Marks were identified as such based on the presence of a golden-yellow circular band appearing among the first four inner circuli.

Fry abundance.—The abundance of fry in the study lakes immediately following stocking ($\widehat{N}$) was estimated using the Chapman modification of the Petersen single-census method (Ricker 1975).

$$\widehat{N} = (M + 1)(C + 1)/(R + 1)$$

where M is the number of marked fry stocked into the lake, C is the number of age-0 Walleyes from the samples that were inspected for the presence of an OTC mark, and R is the number of inspected Walleyes with a visible mark. Only whole-lake estimates of fry abundance were conducted due to the likelihood of movement of the stocked Walleyes between basins during the periods between stocking and sampling. Estimates of the abundance of wild fry at the time of stocking were calculated by subtracting the number of stocked fry from the total fry abundance estimate. Wild hatch rates, as previously described, were then calculated by dividing the wild fry abundance by the total egg production estimates from the previous fall's netting minus the number of eggs removed for hatchery incubation.

Growth, Survival, and Recruitment

Growth.—The effect of total fry density on first-year growth of the cohort was investigated with a multiple linear regression model with separate intercepts and slopes for each lake and a common year effect:

$$TL_{ijk} = \mu_i + \beta_i FRY_{ij} + \tau_j + \varepsilon_{ijk}$$

where TL_{iik} is the total length of the k-th age-0 Walleye from lake i in year j; μ_j is the intercept for lake j; FRY_{ij} is total number of fry/littoral acre from lake i in year j; τ_j is effect of the year in which the fry were stocked; and ε_{ijk} is the residual error.

Survival.—The abundance of Walleyes at age 2 was considered a benchmark during this study because it was reasoned that age-2 walleyes were large enough to be captured representatively in the gill nets (Anderson 1998) but not of acceptable size to anglers long enough to have been significantly reduced in abundance by harvest. Consequently, the survival rate from the time of stocking to capture at age-2 was calculated for comparison among lakes and years by dividing the q_{abg} model estimate of age-2 abundance by the Petersen estimate of total fry abundance.

Annual survival rates during the first 3 years of life were also calculated from the abundance estimates at ages 0-3, but were calculated via natural exponentiation of the instantaneous mortality rate to account for the differences in time periods between abundance estimates (Ricker 1975; Miranda and Bettoli 2007). The time period between the estimates of fry abundance and abundance during fall gill netting at age 1 was 1.3 years, whereas the time period between all other abundance estimates derived from fall gill netting was 1.0 year.

Instantaneous mortality estimates were calculated for each year of life using

$$\hat{Z}_t=(log_e N_t - log_e N_{t+1})/\hat{I}_t$$

where N_t is the abundance of Walleyes from the year-class of interest at the beginning of an interval of length $\hat{I}_t$ and N_{t+1} is the abundance of Walleyes that survive to the end of the interval. Annual survival rates ($\hat{S}$) were then calculated from Z using the formula

$$\hat{S}=e^{-Zt}$$

This method standardizes the interval used to calculate S to 1.0 year for the first-year estimates to allow direct comparisons of annual survival across years.

Recruitment.—Relative strength of the stocked year-classes (YCS) was described using a mixed-effects (Kutner et al. 2004) version of Maceina and Pereira's (2007) model of a cohort's catch over ages 1-3. Maceina and Pereira's (2007) 2-way ANOVA model predicts the log-transformed CPE of a cohort from age and cohort treated as fixed-effect categorical factors, whereas the mixed-effect version treats cohort as a random effect and also adds sample year as a random effect to account for variation in gill-net catchability among years using the formula

$$\log_e(\mathrm{CPE}_{ij}+0.1)=\mu+\alpha_i+\gamma_j+\psi_{i+j}+\varepsilon_{ij}$$

where CPE_{ij} is the number of fish, of age i from year-class j that were caught divided by the number of nets fished; μ is the y-intercept; α_i is the fixed effect of age on catch rates for ages i=1,…,3; γ_j is the random effect of cohort on catch rates for year-classes j=2008,….,2012 assumed to be distributed as Normal($0,\sigma_{\mathrm{YCS}}$) on the $\log_e$ scale; ψ_{i+j} is the random effect of sample-year on catch rates assumed to be Normal($0,\sigma_{\mathrm{catch}}$); and $\varepsilon_{\mathrm{ij}}$ is a random error term assumed to be Normal($0,\sigma^2$).

The $\log_e$ scale YCS estimates are the predicted realizations of the random effect for each cohort (these are often referred to as "BLUPs", which stands for Best Linear Unbiased Predictor); these estimates have an expected mean of zero, and when back-transformed by exponentiation to the original scale the YCS estimates will have an expected median value of one. For comparisons among lakes, the $\log_e$ scale YCS estimates were standardized to common scale by dividing them by the estimated σ_{YCS} value.

Because the effect of parental stock density on recruitment is thought to be exerted through the abundance of larvae that they produce as mitigated by density-competition or predation (Ricker 1975), we began by fitting a null model, then a linear model through the origin (Ogle 2016) and two commonly used stock-recruit relationships; the Beverton-Holt (Beverton and Holt 1957, cited by Ogle 2016) and Ricker (1975) models, with total fry density substituted for parental stock size.

The null model assumes recruitment is independent of fry density with the form

$$R = a$$

The linear model assumes that the rate of recruitment remains constant across all levels of total fry density and has the form of

$$R = aFRY$$

whereas the Beverton-Holt model assumes that recruitment will approach an asymptote at high levels of total fry density and has the form of

$$R = \frac{aFRY}{1 + bFRY}$$

and the Ricker model assumes a dome-shaped relationship where maximum recruitment occurs at an intermediate level of total fry density with the form of

$$R = aFRYe^{-bFRY}$$

where R is recruitment as measured by the YCS, FRY is total fry density, a is a parameter controlling the slope at low fry density, and b is a parameter controlling degree of density-dependence. The models were first fit with least-squares regression, the latter three using nonlinear least-squares as implemented in the FSA package in R (Ogle 2016), and compared using Akaike information criterion (AIC; Burnham and Anderson 2002).

A General Additive Model (GAM) was also used to independently identify the general response of recruitment to various levels of total fry density:

$$\log_e(\mathrm{YCS}) = \beta_0 + s(\text{Total Fry Density}) + \varepsilon$$

The model was fit with the multiple generalized cross validation (mgcv) package in R, which fits a penalized regression spline for the predictor variable based on the resulting degrees of freedom that minimizes the generalized cross validation (GCV) score (Wood 2017).

Following Hilborn and Walters (1992) and Madenjian et al. (1996), additional explanatory variables were then incorporated into to the Ricker model in the form of

$$R = aFRYe^{-bFRY+c_lX_l+..+c_oX_o}$$

where $X_{i..o}$ are the additional explanatory variables and $c_{l..o}$ are parameters with units $1/X_{i..o}$. For these comparisons, the fitting was done on the linearized form of the model with

$\log_e(R/FRY)$ as the response variable, thus assuming a log-normal error structure. Subbey et al. (2014) reported that incorporating environmental covariates into recruitment models can be challenging when using datasets without long time series. Consequently, we limited the additional explanatory variables in the extended Ricker models to three which we felt had the greatest likelihood to influence Walleye recruitment: 1) growing degree days above 5°C (GDD), 2) total Walleye biomass, and 3) Yellow Perch CPE. Models were compared using Akaike information criterion (AIC; Burnham and Anderson 2002).

Temperature has broad-ranging effects on the physiological processes of fish in general (Smith 1982) and more specifically on the incubation duration (Thompson 1996; Busch et al. 1975), recruitment (Busch et al. 1975; Hansen et al.1998; Rose 1999; Hansen et al. 2015), and subsequent production and yield of Walleyes (Christie and Regier 1988; Lester et al. 2004). In absence of in-situ water temperature measurements, we substituted GDD (Lester et al. 2004) calculated from air temperatures collected at nearby weather stations to capture broad-scale interannual variability in temperatures.

Total Walleye biomass was also included in the extended model to account for inter-cohort suppression through cannibalism and competition. Ricker (1975) included an index of parental stock twice in his stock-recruit model. The first occurrence represents the maximum reproductive capability of the population, whereas the second occurrence is an exponential parameter that reduces this maximum in proportion to the initial size of the cohort (the overcompensation that results in a dome-shaped response). Substituting fry density for parental stock abundance, as we did in this study, would therefore fail to capture variability in the direct effects of cannibalism (Chevalier 1973; Hansen et al. 1998) and competition (Forney 1977; Hansen et al 1998) on the sub-recruits as the adult population changes. Since inter-cohort suppression is likely caused by both juveniles (Li et al. 1996) and adults (Hansen et al 1998), the Walleye biomass parameter included in the extended Ricker Model during our study included an estimate of all age-1 and older Walleyes.

Yellow Perch CPE was included in the extended model because Yellow Perch abundance can affect Walleye growth and survival in several different ways. As a primary prey species (Maloney and Johnson 1955) the availability of suitable-sized Yellow Perch can enhance survival of Walleyes through increased feeding efficiencies. Enhanced growth from more efficient feeding can reduce susceptibility to gape-limited predators (Forney 1976) and improve overwinter survival (Forney 1980), whereas the condensed foraging excursions afforded by abundant prey may also reduce the time exposed to those predators large enough to consume them. Abundant Yellow Perch populations can also buffer cannibalism and predation on Walleyes by providing alternative forage to potential predators (Forney 1974; Rudstam et al. 2016). Selection of an appropriate Yellow Perch index was complicated during this study because the ages of Yellow Perch from the gill-net surveys are not routinely determined. We do know from previous surveys that our gill-net mesh sizes are such that the catches are frequently dominated by age-3 Yellow Perch. Consequently, we reasoned that CPE of Yellow Perch when the year-class of Walleyes was age 3 could serve as an index of the abundance of Yellow Perch available to that year-class of Walleyes since their birth if it could be assumed that predation at younger ages did not alter the relative strength of the Perch cohort prior to capture at age 3.

RESULTS

Egg production

Spawner biomass.—Estimates of adult female biomass varied substantially among both lakes and years (Table 1). Lake Winnibigoshish was the largest lake in the study and had both the highest mean adult female biomass (55,746 kg) and the highest mean adult female biomass relative to surface area (2.25 kg/ha). The other study lakes followed in order of size with Vermilion averaging 33,245 kg (2.03 kg/ha), Otter Tail averaging 9,621 kg (1.66 kg/ha), and Woman averaging 2,992 kg (1.18 kg/ha). No strong trends in adult female biomass were apparent within a lake across time or among lakes by year (Table 1).

TABLE 1. Estimated spring biomass of adult females, by year, in each of the study lakes. Standard errors are presented in parenthesis.

Year	kg	kg/ha
	Vermilion	
2008	36,409 (6,370)	2.22 (0.39)
2009	27,245 (6,495)	1.66 (0.40)
2010	22,804 (3,453)	1.39 (0.21)
2011	16,467 (3,540)	1.00 (0.22)
2012	36,431 (9,407)	2.22 (0.57)
2013	36,901 (6,890)	2.25 (0.42)
2014	48,960 (11,068)	2.98 (0.67)
2015	40,742 (14,196)	2.48 (0.86)
	Winnibigoshish	
2008	60,039 (9,373)	2.42 (0.57)
2009	55,027 (14,361)	2.22 (0.87)
2010	56,070 (8,805)	2.26 (0.54)
2011	68,954 (8,975)	2.78 (0.55)
2012	48,637 (8,367)	1.96 (0.51)
2013	74,933 (8,010)	3.02 (0.49)
2014	40,213 (5,486)	1.62 (0.33)
2015	42,097 (7,381)	1.70 (0.45)
	Woman	
2008	4,018 (936)	1.59 (0.06)
2009	3,484 (1,197)	1.37 (0.07)
2010	990 (337)	0.39 (0.02)
2011	3,152 (1,202)	1.24 (0.07)
2012	1,981 (681)	0.78 (0.04)
2013	3,765 (944)	1.49 (0.06)
2014	4,054 (1,299)	1.60 (0.08)
2015	2,495 (547)	0.98 (0.03)
	Otter Tail	
2008	6,443 (1,770)	1.11 (0.11)
2009	6,632 (1,251)	1.15 (0.08)
2010	11,500 (3,163)	1.99 (0.19)
2011	17,191 (2,136)	2.97 (0.13)
2012	6,299 (1,632)	1.09 (0.10)
2013	9,182 (1,767)	1.59 (0.11)
2014	9,679 (3,218)	1.67 (0.20)
2015	10,039 (1,769)	1.73 (0.11)

Fecundity.—The number of eggs present in the ovaries of fall-captured females followed a strong linear relationship with the total weight of the fish at the time of capture (Figure 1; Table 2). The females with the highest relative fecundity rates consistently occurred in the Otter Tail Lake samples, where the annual mean rates ranged from 89,786 to 94,133 eggs/kg adult female. Mean annual relative fecundity rates for the other lakes ranged from 67,673 to 76,037 for Lake Vermilion, 70,749 to 78,304 for Lake Winnibigoshish, and 70,063 to 84,808 for Woman Lake.

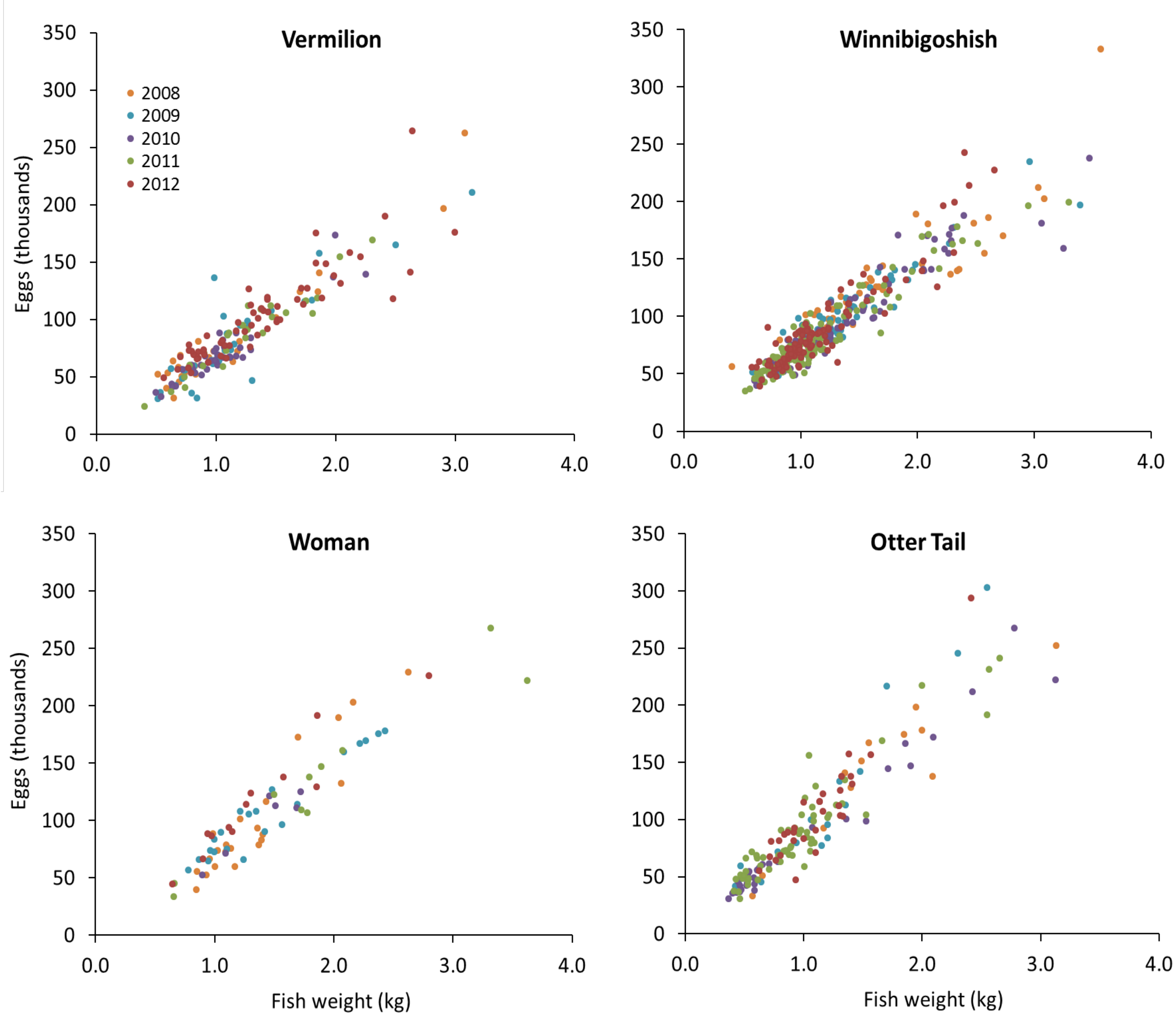

FIGURE 1. Fecundity estimated from the egg counts of female Walleyes collected in fall gillnets. Dates represent spawning year.

TABLE 2. Summary of relative fecundity estimates calculated from females captured with gill nets in the fall previous to spawning. The values for *a*, *b*, and r^2 represent the intercept, slope, and coefficient of determination, respectively, of the least-squares regression of egg abundance on total weight of the female carrying the eggs.

Spawning Year	*n*	Eggs/kg adult female			
			From regression		
		Mean (SE)	*a*	*b*	r^2
		Vermilion			
2008	24	74,960 (2,852)	-375	74,081	0.94
2009	30	70,957 (3,341)	4,124	67,189	0.81
2010	36	67,673 (1,307)	-2,590	70,213	0.87
2011	26	70,076 (1,639)	-972	71,303	0.91
2012	60	76,037 (1,478)	16,146	62,623	0.78
		Winnibigoshish			
2008	50	78,304 (1,870)	12,130	68,577	0.86
2009	54	74,464 (1,313)	12,157	64,989	0.87
2010	104	71,373 (778)	6,549	65,929	0.90
2011	129	70,749 (767)	3,038	67,828	0.91
2012	106	75,507 (1,088)	-5,791	80,675	0.87
		Woman			
2008	22	71,482 (3,165)	-38,758	102,812	0.88
2009	21	74,413 (1,900)	1,647	73,061	0.92
2010	6	70,153 (3,486)	-19,115	84,839	0.89
2011	10	70,063 (3,337)	-77	71,311	0.92
2012	12	84,808 (878)	2,651	83,286	0.91
		Otter Tail			
2008	16	89,823 (3,598)	10,416	82,560	0.89
2009	18	93,670 (4,377)	-24,897	118,150	0.92
2010	31	89,786 (3,677)	4,227	80,163	0.94
2011	60	92,631 (2,182)	4,989	86,272	0.87
2012	31	94,133 (2,647)	-27,794	120,173	0.86

Little difference occurred between the gravimetric and volumetric estimates of the samples that were measured with both methods. However, the mean fecundity estimates calculated from spring collected ovaries were generally lower and less correlated with female body weight than the fecundity calculated from fall-collected ovaries of the same spawning year (Table 3).

Egg production and removal.—Application of the relative fecundity rates to the spawner biomass estimates produced estimates of population-wide egg production ranging from approximately 69 million to 5.6 billion eggs in the study lakes (Table 4). The Walleye population in Woman Lake produced the fewest number of eggs but consistently had the highest proportion of available eggs removed for hatchery incubation. The two largest lakes, Winnibigoshish and Vermilion, produced substantially more eggs than Woman or Otter Tail lakes but had a much lower proportion removed for hatchery incubation.

TABLE 3. Summary of relative fecundity estimates calculated for their respective spawning years when samples of females were both captured with gill nets in the fall previous to spawning (Fall) and captured at the egg-collection stations during the spring spawning run (Spring). The values for a, b, and r^2 represent the intercept, slope, and coefficient of determination, respectively, of the least-squares regression of egg abundance on total weight of the female carrying the eggs.

				Eggs/kg adult female				
						From regression		
Spawning Year	Season	Method	n	Mean	(SE)	a	b	r^2
				Vermilion				
2011	Fall	Weight	26	70,076	(1,639)	-972	71,303	0.91
	Spring	Weight	10	62,469	(2,684)	-30,686	81,977	0.93
				Winnibigoshish				
2008	Fall	Weight	50	78,304	(1,870)	12,130	68,577	0.86
	Spring	Weight	10	60,312	(4,865)	11,431	53,547	0.42
	Spring	Volume	10	61,738	(5,261)	2,385	60,893	0.45
2009	Fall	Weight	54	74,464	(1,313)	12,157	64,989	0.87
	Spring	Weight	10	41,090	(4,321)	15,152	31,830	0.44
	Spring	Volume	10	40,143	(3,180)	5,349	37,088	0.65
2010	Fall	Weight	104	71,373	(778)	6,549	65,929	0.90
	Spring	Weight	10	53,937	(2,166)	-4,259	56,784	0.96
2011	Fall	Weight	129	70,749	(767)	3,038	67,828	0.91
	Spring	Weight	10	62,899	(5,146)	30,655	45,125	0.45
				Woman				
2009	Fall	Weight	21	74,413	(1,900)	1,647	73,061	0.92
	Spring	Weight	10	63,308	(3,684)	-8,794	69,016	0.86
2011	Fall	Weight	10	70,063	(3,337)	-77	71,311	0.92
	Spring	Weight	9	70,137	(2,607)	-5,799	75,127	0.96
				Otter Tail				
2011	Fall	Weight	60	92,631	(2,182)	4,989	86,272	0.87
	Spring	Weight	10	60,448	(2,652)	-12,580	69,249	0.88

TABLE 4. Estimates of population-wide egg production, eggs removed for hatchery use, and number of eggs remaining in the population. Standard errors are presented in parentheses. Some additional but unquantifiable variability likely exists due to measurement error in number of eggs removed.

		Millions of eggs removed		
Year	Millions of eggs produced	No.	% of total	Millions of eggs remaining
		Vermilion		
2008	2,729 (488.6)	97.7	4 (0.6)	2,632 (488.6)
2009	1,933 (469.8)	116.8	6 (1.5)	1,816 (469.8)
2010	1,543 (235.6)	111.1	7 (1.1)	1,432 (235.6)
2011	1,154 (249.6)	126.4	11 (2.4)	1,028 (249.6)
2012	2,770 (714.3)	97.2	4 (0.9)	2,673 (714.3)
2013	3,066 (579.6)	150.5	5 (0.9)	2,915 (579.6)
2014	3,613 (823.9)	127.0	4 (0.8)	3,486 (823.9)
2015	3,007 (1,051.4)	96.6	3 (1.1)	2,910 (1,051.4)
		Winnibigoshish		
2008	4,702 (742.5)	133.3	3 (0.4)	4,568 (742.5)
2009	4,098 (1,071.8)	163.5	4 (1.0)	3,934 (1,071.8)
2010	4,000 (629.7)	264.8	7 (1.0)	3,735 (629.7)
2011	4,878 (637.1)	168.9	6 (0.5)	4,710 (637.1)
2012	3,672 (605.8)	206.0	6 (0.9)	3,466 (605.8)
2013	5,619 (608.0)	103.4	2 (0.2)	5,516 (608.0)
2014	2,985 (409.7)	144.1	5 (0.7)	2,706 (409.7)
2015	3,125 (549.9)	189.7	6 (1.1)	2,794 (549.9)
		Woman		
2008	287 (68.1)	45.7	16 (3.8)	242 (68.1)
2009	259 (89.3)	65.7	25 (8.7)	194 (89.3)
2010	69 (23.9)	43.3	62 (21.4)	26 (23.9)
2011	221 (84.9)	56.0	25 (9.8)	165 (84.9)
2012	168 (59.3)	27.7	17 (5.8)	140 (59.3)
2013	296 (74.9)	70.3	24 (6.0)	225 (74.9)
2014	304 (97.9)	53.0	18 (5.6)	251 (97.9)
2015	187 (41.5)	18.2	10 (2.2)	169 (41.5)
		Otter Tail		
2008	579 (160.7)	52.5	9 (2.5)	526 (160.7)
2009	621 (120.7)	49.7	8 (1.6)	572 (120.7)
2010	1,033 (287.1)	61.0	6 (1.6)	972 (287.1)
2011	1,592 (201.3)	58.4	4 (0.5)	1,534 (201.3)
2012	593 (157.5)	66.7	11 (3.0)	526 (157.5)
2013	899 (177.4)	43.4	5 (1.0)	856 (177.4)
2014	900 (300.9)	58.7	7 (2.2)	841 (300.9)
2015	934 (167.8)	77.4	8 (1.5)	856 (167.8)

Fry abundance

Stocking.—Approximately 242 million OTC-treated fry were stocked during this study. Stocking densities during the fry-manipulation phase of the study ranged from 720 to 1,000 fry/littoral acre into Lake Vermilion, 150 to 690 fry/littoral acre into Winnibigoshish, 580 to 1,530 fry/littoral acre into Woman Lake, and 150 to 1,730 fry/littoral acre into Otter Tail Lake (Table 5). All stocking rates during the fry-manipulation phase were conducted in an attempt to achieve pre-determined total fry density rates except for stockings of approximately 990 fry/littoral acre into Woman Lake during both 2010 and 2011. Those two Woman Lake stockings were "contingency" stockings that were triggered by two consecutive years of low age-0 catch rates. Fry stocking densities in the post-manipulation phase ranged from 670 to 900 fry/littoral acre into Lake Vermilion, 620 to 1,040 into Lake Winnibigoshish, 290 to 580 into Woman Lake, and 590 to 1,030 fry/littoral acre into Otter Tail Lake. Relatively high stocking mortality (~10-20%) was observed during the first two years of the study (2008 and 2009) in Lake Vermilion and the first year (2009) in Lake Winnibigoshish. The estimated number of dead fry were replaced with additional OTC-marked fry.

In an attempt to reduce further mortality of stocked fry, several changes were implemented to the treatment and transportation process. The changes included 1) removing excess fry to reduce crowding in the raceways; 2) collecting the fry with frame nets and blotting excess water with a sponge instead of capturing with a seine and rolling the fish dry; 3) exposing the treatment jugs to ambient lighting to incite phototactic swimming and reduce crowding on the bottom of the jugs; and 4) improving the timing of treatment, loading, and stocking so that the fry were stocked immediately after the six hour immersion period. Elevated stocking mortality was not observed following the changes to treatment and stocking protocols.

Mark efficacy.—The intensity of the marks varied across treatments but, with a couple of notable exceptions, were suitable to identify which fish in the samples had been stocked as fry. The first exception occurred during the initial treatment of fry at the Pike River Hatchery where only 6% of the inspected Walleyes from the efficacy pond exhibited easily discernable marks (Table 6) and no marks were visible on Walleyes sampled from Lake Vermilion. The exact cause of this poor mark efficacy is unknown, but the low pH and alkalinity of the hatchery source water required substantially more sodium phosphate dibasic to buffer the solution than has been required at other hatcheries across the state. We also observed a fine precipitate in the bottom of the jugs during this treatment that did not occur again after switching the source of mixing water to the City of Tower municipal well.

A large number of fish with faint and absent marks were also observed from a sample of Walleyes treated at the Pike River Hatchery in 2011 and reared in New London Pond 15 (Table 6). However, Walleyes from the same treatment that were stocked into Lawler Pond all had clear or intense marks. In addition, the percentage of marked fish in the samples from Lake Vermilion in 2011 (same treatment as Pond 15 and Lawler Pond) exceeded the expected mark percentage that was predicted from historical hatch rates (Table 7) and their marks were also bright. The only apparent difference between the samples from Pond 15 compared to those from Lawler Pond and Lake Vermilion was that the Pond 15 samples had been thawed and refrozen prior to inspection. Similar faint or absent marks were observed on other efficacy samples that had thawed due to careless handling and were subsequently refrozen (Leech Lake Pond 7 in 2010, New London Pond 14 in 2011) but the marks from their respective study lakes were both plentiful and bright. The only sample from a study lake subjected to the extra thaw/freezing cycle was that from Lake Vermilion in 2015. The 2015 Lake Vermilion samples had fewer marks than expected and the marks that were present were extremely faint and too indistinct to be reliable.

TABLE 5. Distribution of OTC-marked fry during the study. Stocking quotas during 2008 to 2012 (Manipulation phase) were manipulated in an attempt to achieve pre-determined total fry densities. The other fry stocking quotas (Post-manipulation phases) were based on the 10% put-back plus surplus fry or the perceived management needs of the lake. Some unquantifiable variability likely exists due to measurement error in egg removal and stocked fry abundance.

Year	Fry stocked (millions)	Percent of egg take	Stocking density (fry/littoral acre)
	Vermilion		
2008	10.8	11	720
2009	11.6	10	770
2010	6.0	5	400
2011	15.0	12	1,000
2012	11.6	12	770
2013	11.6	8	770
2014	13.5	11	900
2015	10.0	10	670
	Winnibigoshish		
2008	3.0	2	150
2009	12.6	8	620
2010	10.4	4	510
2011	14.0	8	690
2012	2.7	1	130
2013	21.0	20	1,040
2014	12.5	9	620
2015	14.7	8	730
	Woman		
2008	3.7	8	1,530
2009	1.4	2	580
2010	2.4	6	990
2011	2.4	4	990
2012	3.3	12	1,370
2013	1.4	2	580
2014	0.7	1	290
2015	1.2	7	500
	Otter Tail		
2008	1.0	2	150
2009	4.1	8	600
2010	5.0	8	730
2011	5.6	10	820
2012	11.8	18	1,730
2013	4.0	9	590
2014	6.0	10	880
2015	7.0	9	1,030

TABLE 6. Intensity of marks observed on walleyes harvested from efficacy ponds. Values represent the percentage of walleyes per sample assigned to each mark intensity category.

			Mark intensity			
Year	Efficacy Pond	*n*	Absent	Faint	Clear	Intense
Pike River Hatchery (Vermilion)						
2008	New London Ponds 7 & 15	70	28	66	6	0
2009	New London Pond 14	50	0	12	62	26
2010	New London Pond 15	58	0	3	67	29
2011[a]	New London Pond 15	50	42	54	4	0
2011	Lawler Pond	79	0	0	54	46
2012	New London Pond 12	50	0	14	48	38
2013	New London Pond 16	50	0	0	34	66
2014	New London Pond 16	50	0	8	50	42
2015	New London Pond 17	49	0	39	16	45
Grand Rapids Hatchery (Winnibigoshish)						
2008	Leech Lake Pond 5	59	0	49	41	10
2009	Leech Lake Pond 3	23	0	9	61	30
2010[a]	Leech Lake Pond 7	48	40	33	27	0
2011	Leech Lake Pond 8	50	0	36	50	14
2012	Leech Lake Pond 7	0	No fingerlings recovered from pond			
2013	Lily Pond	120	1	0	11	88
2014	Lily Pond	97	0	6	64	30
2015	Lily Pond	0	No fingerlings recovered from pond			
Bemidji Hatchery (Woman)						
2008	Curly's & Kinn's Ponds	200	0	21	59	21
2009	Pony	100	0	31	60	9
2010	Leech Lake Pond 3	100	0	27	58	15
2011	Curly's Pond	100	0	9	87	4
2012	Park Pond	26	0	8	62	31
2013	Hiram Pond	101	0	12	79	9
2014	Hiram Pond	93	0	29	70	1
2015	Lyden Pond	100	Reported as 100% good quality marks			
Walker Lake Hatchery (Otter Tail)						
2008	New London Ponds 9 & 10	76	1	29	42	28
2009	New London Pond 10	50	0	8	42	50
2010[b]	New London Pond 9	24	4	71	21	4
2011[a]	New London Pond 14	50	2	54	38	6
2012	Chance Pond	50	0	18	42	40
2013	Johnson Pond	22	0	41	45	14
2014	East Olaf & Lakeway Ponds	66	0	0	0	100
2015	Lakeway Pond	49	0	0	45	45

[a] Samples had been thawed and refrozen prior to examination

[b] Fry erroneously treated at 532-mg active OTC/L instead of 700-mg active OTC/L

TABLE 7. Mark-recapture information for the study lakes where M = the number of OTC treated fry stocked into the lake, C = the number of fingerlings inspected for a mark, Observed R = the percentage of inspected fingerlings with a mark, and Predicted R = the percentage of inspected fingerlings expected to have a mark based on historical hatch rate data (see methods). Standard errors are presented in parentheses. Some additional but unquantifiable variability likely exists due to measurement error in the number of fry stocked.

Year	M in millions	C	R (%)		Estimated total fry abundance in millions	Estimated total fry/littoral acre
			Observed	Predicted		
Vermilion						
2008	10.8		Poor marks			
2009	11.6	496	25	36	46.9 (3.65)	3,124 (243)
2010	6.0	564	37	41	16.0 (0.87)	1,066 (58)
2011	15.0	382	60	55	25.0 (1.04)	1,665 (69)
2012	11.6	404	62	34	18.7 (0.73)	1,247 (48)
2013	11.6	570	12	41	94.6 (10.52)	6,306 (701)
2014	13.5	548	47	24	28.6 (1.29)	1,907 (86)
2015	10.0		Poor marks			
Winnibigoshish						
2008	3.0	808	5	33	56.4 (8.28)	2,790 (409)
2009	12.6	853	83	31	15.3 (0.24)	755 (12)
2010	10.4	857	88	30	11.9 (0.15)	586 (7)
2011	14.0	567	74	34	18.8 (0.46)	932 (23)
2012	2.7	327	49	52	5.5 (0.31)	274 (15)
2013	21.0	313	4	84	471.0 (118.8)	23,285 (5,876)
2014	12.5	184	64	86	19.4 (1.06)	961 (52)
2015	14.7	186	85	82	17.2 (0.51)	849 (25)
Woman						
2008	3.7	226	60	93	6.2 (0.33)	2,558 (138)
2009	1.4	505	83	38	1.7 (0.03)	697 (14)
2010	2.4	294	97	56	2.5 (0.02)	1,022 (10)
2011	2.4	152	96	76	2.5 (0.04)	1,035 (17)
2012	3.3	213	71	87	4.6 (0.20)	1,925 (84)
2013	1.4	346	97	54	1.5 (0.01)	601 (6)
2014	0.7	636	89	38	0.8 (0.01)	325 (4)
2015	1.2	230	44	63	2.7 (0.20)	1,115 (81)
Otter Tail						
2008	1.0	278	29	62	3.4 (0.32)	504 (47)
2009	4.1	262	56	57	7.3 (0.39)	1,067 (58)
2010	5.0	392	72	50	6.9 (0.21)	1,010 (31)
2011	5.6	449	67	51	8.4 (0.28)	1,226 (41)
2012	11.8	123	67	86	17.6 (1.11)	2,582 (162)
2013	4.0	277	64	50	6.2 (0.28)	915 (41)
2014	6.0	258	86	59	7.0 (0.18)	1,025 (26)
2015	7.0	201	89	66	7.9 (0.20)	1,157 (29)

No fingerlings were recovered from the efficacy stockings into Leech Lake Pond 7 in 2012 and Lily Pond in 2015, but the percentage of marked fish from the respective study lakes was similar to that predicted and the marks were bright. Much fainter marks occurred on the Walleyes that were erroneously treated with a lower OTC concentration at the Walker Lake Hatchery in 2010. Although the marks were faint, they were discernable as long as the otoliths were sanded lightly and inspected frequently under the UV light. The percentage of marked fish from Otter Tail Lake in 2010 exceeded predictions.

Total fry abundance.—Although the observed mark percentage of the samples often varied appreciably from the values predicted from historical hatch rates, the process of calculating the predictions helped to inform stocking and sampling decisions to produce a broad range of total fry abundance estimates with relatively low standard error (Tables 7 and 8). Suitable abundance estimates, however, were not attainable for every lake during all years of the study. Poor marks, as described above, prevented abundance estimates in Lake Vermilion during 2008 and 2015. In addition, two outliers occurred in 2013 when the fry density estimates for Lake Vermilion and Winnibigoshish substantially exceeded the target range of values in the experimental design (6,306 and 23,285 fry/littoral acre, respectively). No explanation could be derived for those high values. The marks were bright on the fingerling samples from both the study lakes and their respective efficacy ponds. In addition, follow-up inspection of a sample of the 2013 Lake Winnibigoshish year-class at age 1 revealed similar mark percentage and brightness as the previous year's fingerling sample. Although we could not identify reasons why these high fry density values could be in error, we felt it prudent to exclude the 2013 outliers from density-dependent growth and recruitment analysis so as to prevent values well beyond the design of this experiment from unduly influencing the results. The remaining fry density estimates ranged from a low of 274 fry/littoral acre in Lake Winnibigoshish to a high of 2,582 fry/littoral acre in Otter Tail Lake; both occurred during 2012 (Table 8).

TABLE 8. Study design matrix showing the estimates of total fry densities achieved, by year, in each of the study lakes.

	Total fry density (fry/littoral acre)							
	Fry-manipulation phase					Post-manipulation phase		
Lake	2008	2009	2010	2011	2012	2013	2014	2015
Vermilion	[a]	3,124	1,066	1,665	1,247	6,306	1,907	[a]
Winnibigoshish	2,790	755	586	932	274	23,285	961	849
Woman	2,558	697	1,022[b]	1,035[b]	1,925	601	325	1,115
Otter Tail	504	1,067	1,010	1,226	2,582	915	1,025	1,157

[a] Absence of reliable mark return data prevented calculation of population estimate.

[b] Contingency stocking of 1,000 fry/littoral acre invoked because of low age-0 catch rates the previous fall.

Natural Reproduction.—Since the wild fry abundance estimates were derived by subtracting the number of stocked fry from the total fry abundance estimates, the samples with inestimable total fry abundance also had inestimable wild fry abundance (Table 9). The estimates of wild fry abundance during the study ranged from a low of 50,150 in Woman Lake during 2013 to a remarkable high of 450,000,022 in Lake Winnibigoshish during 2013. Although Lake Winnibigoshish was the largest lake in the study, its abundance of wild fry was frequently surpassed by that of both Lake Vermilion and Otter Tail Lakes. The wild fry estimates for

Woman Lake were most frequently the lowest of the study lakes in terms of both absolute abundance and density, with four years well below 100 fry/ littoral acre. Winnibigoshish was the only other lake in the study with a wild fry density estimated below 100 fry/littoral acre. All of the estimates for Lake Vermilion exceeded 450 fry/littoral acre, whereas the Otter Tail Lake estimates ranged from 132 to 854 fry/littoral acre.

TABLE 9. Estimated wild fry abundance, density, and hatch rate estimates, by year, in each of the study lakes. Standard errors are presented in parentheses. Some additional but unquantifiable variability likely exists due to measurement error in the number of fry stocked.

	Wild fry		
Year	Abundance in thousands	Fry/littoral acre	Percent hatch
	Vermilion		
2008	Inestimable due to poor marks		
2009	35,272 (3,651)	2,351 (243)	1.94 (0.54)
2010	9,991 (866)	666 (58)	0.70 (0.13)
2011	9,978 (1,039)	665 (69)	0.97 (0.26)
2012	7,117 (727)	474 (48)	0.27 (0.08)
2013	83,023 (10,519)	5,533 (701)	2.85 (0.67)
2014	15,116 (1,290)	1,007 (86)	0.43 (0.11)
2015	Inestimable due to poor marks		
	Winnibigoshish		
2008	53,442 (8,280)	2,642 (409)	1.17 (0.26)
2009	2,663 (240)	132 (12)	0.07 (0.02)
2010	1,450 (151)	72 (7)	0.04 (0.01)
2011	4,844 (465)	239 (23)	0.10 (0.02)
2012	2,835 (312)	140 (15)	0.08 (0.02)
2013	450,000 (118,870)	22,246 (5,876)	8.16 (2.34)
2014	6,933 (1,060)	343 (52)	0.24 (0.05)
2015	2,481 (514)	123 (25)	0.08 (0.02)
	Woman		
2008	2,476 (334)	1,026 (138)	1.03 (0.32)
2009	283 (34)	117 (14)	0.15 (0.07)
2010	67 (24)	28 (10)	0.26 (0.25)
2011	98 (41)	41 (17)	0.06 (0.04)
2012	1,346 (202)	558 (84)	0.96 (0.43)
2013	50 (15)	21 (6)	0.02 (0.01)
2014	85 (11)	35 (4)	0.03 (0.01)
2015	1,491 (196)	618 (81)	0.88 (0.25)
	Otter Tail		
2008	2,444 (320)	358 (47)	0.46 (0.15)
2009	3,186 (395)	467 (58)	0.56 (0.14)
2010	1,895 (214)	277 (31)	0.20 (0.06)
2011	2,772 (277)	406 (41)	0.18 (0.03)
2012	5,829 (1,106)	854 (162)	1.11 (0.39)
2013	2,247 (280)	329 (41)	0.26 (0.06)
2014	1,000 (177)	146 (26)	0.12 (0.05)
2015	899 (199)	132 (29)	0.11 (0.03)

The estimates of wild fry density within the study lakes were much more variable than could be accounted for by estimates of the changes in adult female biomass or egg abundance (Figure 2). This relationship between fry and egg abundance is referred to as wild hatch rate during this study and ranged from a low of 0.02% to a high of 8.16% (Table 9). Because of the linear relationship between fecundity and total female weight, the wild hatch rates are also proportional to the number of fry produced per biomass of adult females after accounting for the eggs removed for hatchery incubation.

Application of the wild hatch rates to the number of eggs removed for incubation in the hatcheries approximates the total number of additional fry that would have hatched naturally in the lakes in absence of the egg-takes. These “replacement fry” values were substantially lower than the number of fry that were actually stocked during this study (Figure 3). The net effect of these stockings was that fry densities in the study lakes were often twice or more higher than would likely have occurred naturally (Figure 4).

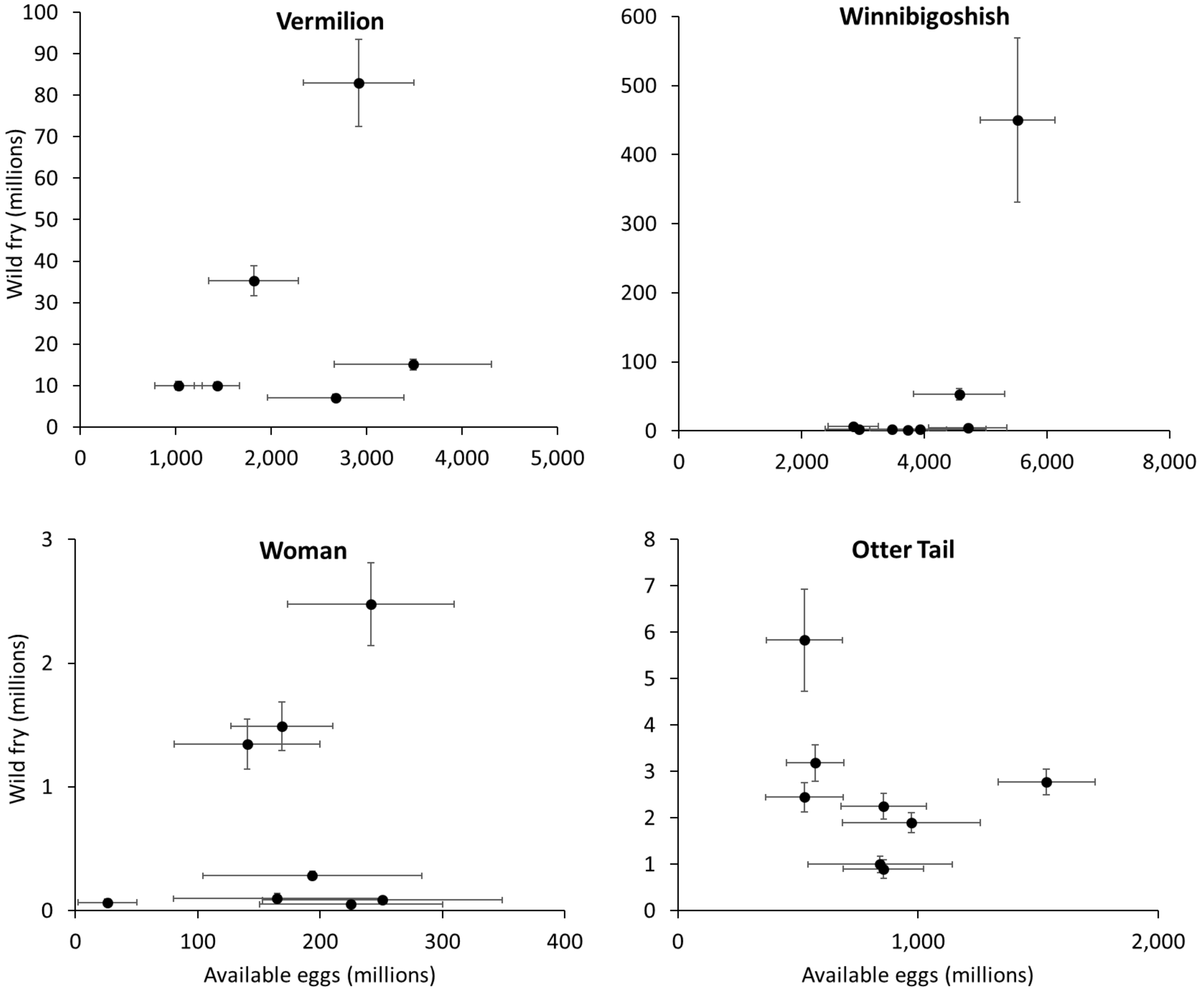

FIGURE 2. Relationship between wild fry abundance and the number of eggs remaining in the population after removal for hatchery incubation (available eggs). Error bars (some hidden by symbols) represent +/- one standard error. Some additional but unquantifiable variability likely exists due to measurement error of egg removal and stocked fry abundance.

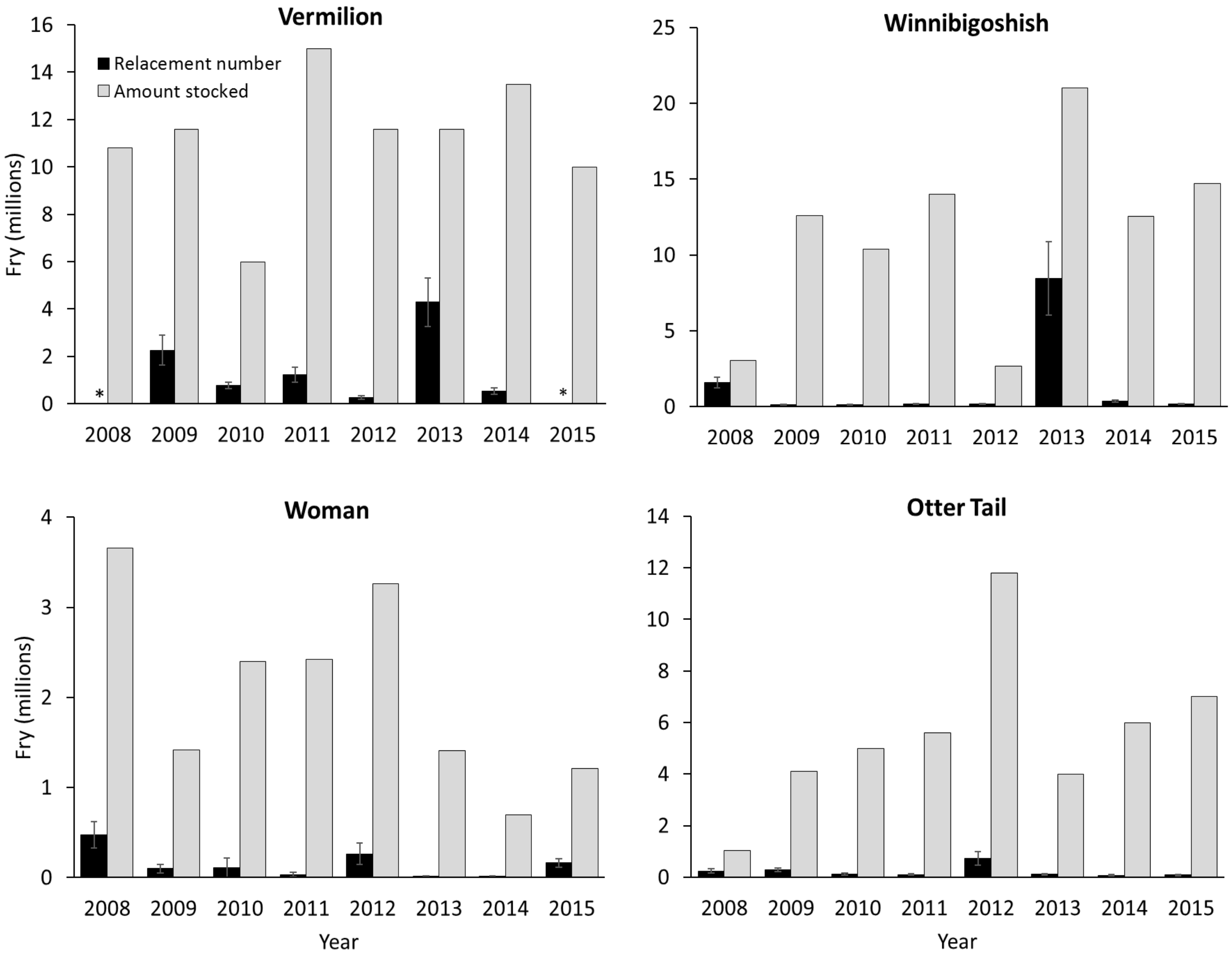

FIGURE 3. Estimated replacement number compared to the actual number of fry stocked. The replacement number is an estimate of the number of additional wild fry that would have hatched in the study lakes had eggs not been removed for hatchery incubation. Error bars represent +/- one standard error. Some additional but unquantifiable variability likely exists due to measurement error of egg removal and stocked fry abundance. Asterisks represent missing estimates.

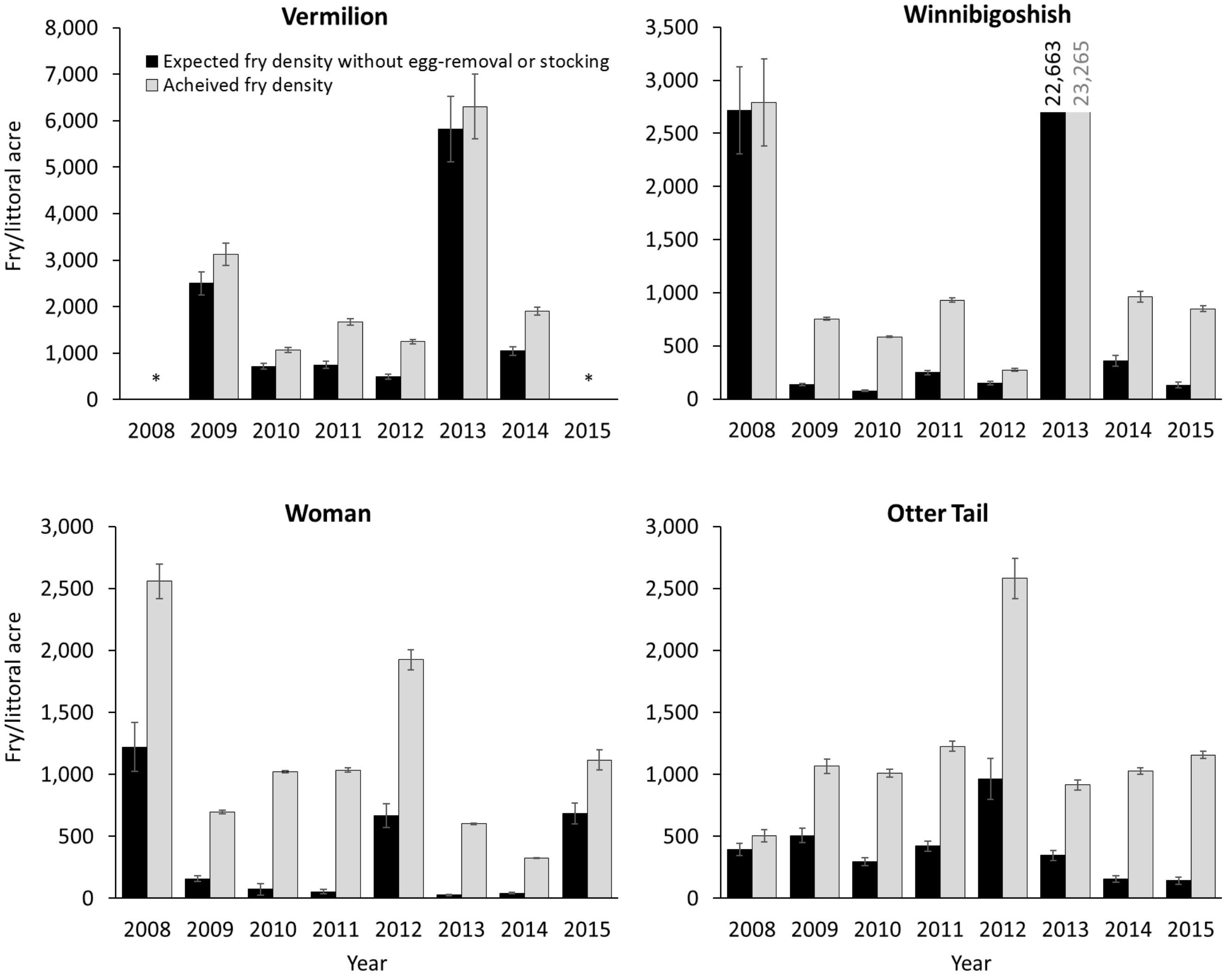

FIGURE 4. The density of fry that would be expected in the study lakes without the egg removal or stocking compared to estimates of achieved total fry density. The fry abundance in absence of egg removal and stocking was estimated by adding wild fry abundance to the sum of the wild hatch rate and number of eggs removed. Error bars represent +/- one standard error. Some additional but unquantifiable variability likely exists due to measurement error of egg removal and stocked fry abundance. Asterisks represent missing estimates.

Recruitment

Growth.—Mean length-at-capture of age-0 Walleyes ranged between 86 and 155 mm during this study (Figure 5). The means from Lake Winnibigoshish were consistently lower than those from the other lakes simply because the fish were sampled earlier in the year. The age-0 Walleyes from all the lakes showed substantial interannual variability in growth; with fish from all lakes often shifting synchronously as either larger or smaller than the previous year (Figure 5). Although this apparent year effect on age-0 growth occurred frequently, it was not without exception. For example, growth increased from the previous year in Woman Lake during 2009 and 2013 whereas growth in the other lakes decreased during that time period. Growth also decreased from 2014 to 2015 in both Woman and Otter Tail Lakes but increased between 2014 and 2015 in both Winnibigoshish and Vermilion Lakes.

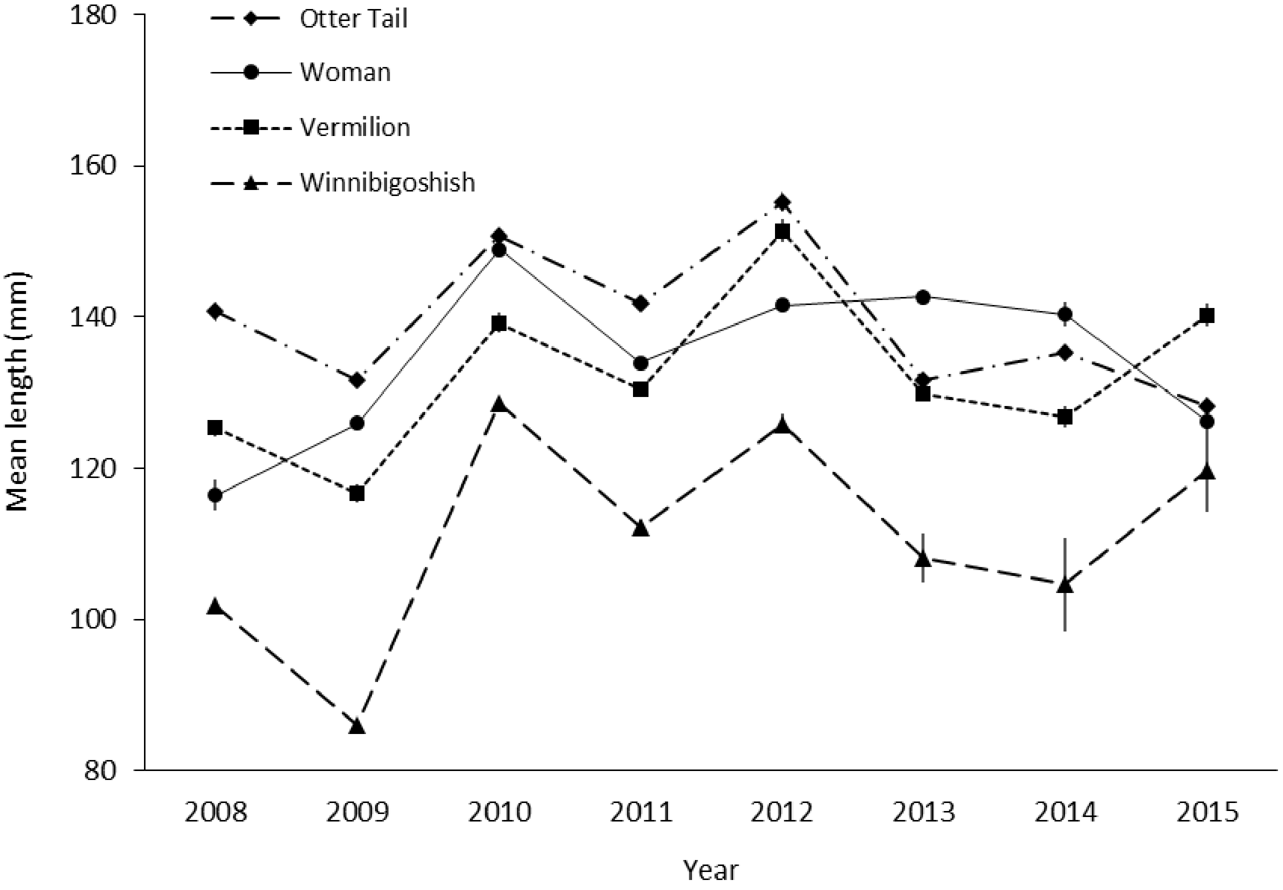

FIGURE 5. Mean length of age-0 walleyes collected during the study. Walleyes were collected from Lake Winnibigoshish by trawl during the summer and from the other lakes by electrofishing during fall. Error bars (often hidden by symbols) represent +/- one standard error.

In Woman Lake, the two year-classes with the highest fry densities had the poorest growth relative to the other study lakes, and the two year-classes with the lowest fry densities had the fastest relative growth. Results of the multiple regression growth model indicated that, when year-effects were accounted for, there was a significant negative relationship (t=-10.119; P<0.001) between fry density and age-0 length at capture in Woman Lake (Figure 6). Walleyes from Otter Tail Lake also exhibited a negative relationship between fry density and age-0 growth (t=-2.485; P=0.013), whereas age-0 growth of those from Lake Vermilion exhibited a positive relationship with fry density (t=2.785; P=0.005) and those from Lake Winnibigoshish lacked an apparent relationship with fry density (t=0.939; P=0.348).

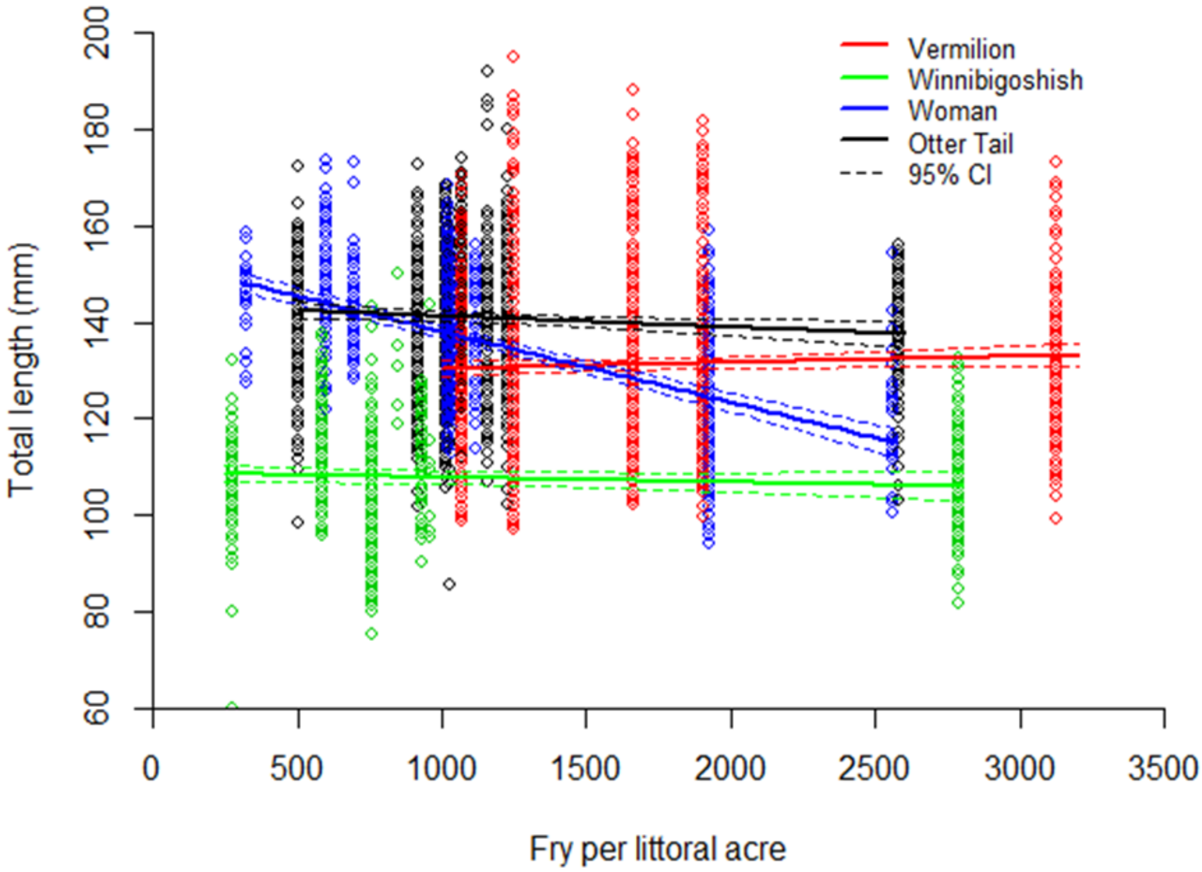

FIGURE 6. Age-0 total length at capture versus total fry density after removing year effects, with partial residuals added. The open circles represent individual fish and the trend lines represent age-0 total length as a function of density in each lake with 95% confidence limits.

Survival.—Less than 5% of the fry survived to fall of their 3rd year of life (age 2) in any of the study lakes (Table 10). The highest survival rates typically occurred in Otter Tail and Vermilion Lakes, but these two lakes were also where the greatest from Vermilion, Woman, and Otter Tail Lakes ranges in survival rates were observed. Walleyes exhibited an apparent decreasing trend in survival with increasing fry density (Figure 7). The trend was less apparent in Lake Winnibigoshish, but the highest fry density there did result in the lowest rate of survival to age 2 observed during the study.

The lowest annual survival rates consistently occurred during the first year of life, with estimates ranging between 1% and 13% (Table 11). Second year survival estimates ranged from 30% to an absurd value of 375%, whereas third year survival estimates ranged from 23% to 79%. In all the study lakes, the highest survival of fry to fall of their 3rd year of life occurred for year-classes with the highest first-year survival. In all but Otter Tail Lake, the lowest survival of fry to fall of their 3rd year of life occurred for year-classes with the lowest first-year survival. Growth rates in the study lakes were such that many of the Walleyes reached sizes acceptable for harvest by anglers prior to fall capture at age 3 (Gerry Albert, MNDNR, personal communication). Consequently, survival rates beyond the first three years may not accurately reflect density-dependent responses to fry abundance because they were likely influenced by fishing mortality.

TABLE 10. Percentage of fry from each of the OTC-fry-stocked year-classes that survived to fall of their 3rd year of life. Standard errors are presented in parentheses. Some additional but unquantifiable variability likely exists due to measurement error in the number of fry stocked.

	Year class							
Lake	2008	2009	2010	2011	2012	2013	2014	2015
Vermilion	[a]	0.52 (0.11)	2.05 (0.37)	1.46 (0.25)	3.08 (0.59)	0.35 (0.09)	0.50 (0.10)	[a]
Winnibigoshish	0.09 (0.03)	1.44 (0.29	2.23 (0.41)	0.53 (0.09)	0.30 (0.11)	0.04 (0.01)	0.10 (0.04)	0.23 (0.05)
Woman	0.13 (0.04)	0.74 (0.21)	1.48 (0.26)	0.61 (0.16)	0.79 (0.16)	5.14 (1.36)	1.66 (0.57)	0.65 (0.21)
Otter Tail	2.33 (0.54)	2.34 (0.37)	4.16 (0.54)	0.49 (0.11)	0.73 (0.12)	2.69 (0.46)	[b]	[b]

[a] Absence of reliable mark return data prevented calculation of survival rates.

[b] Gill-netting not conducted beyond 2015.

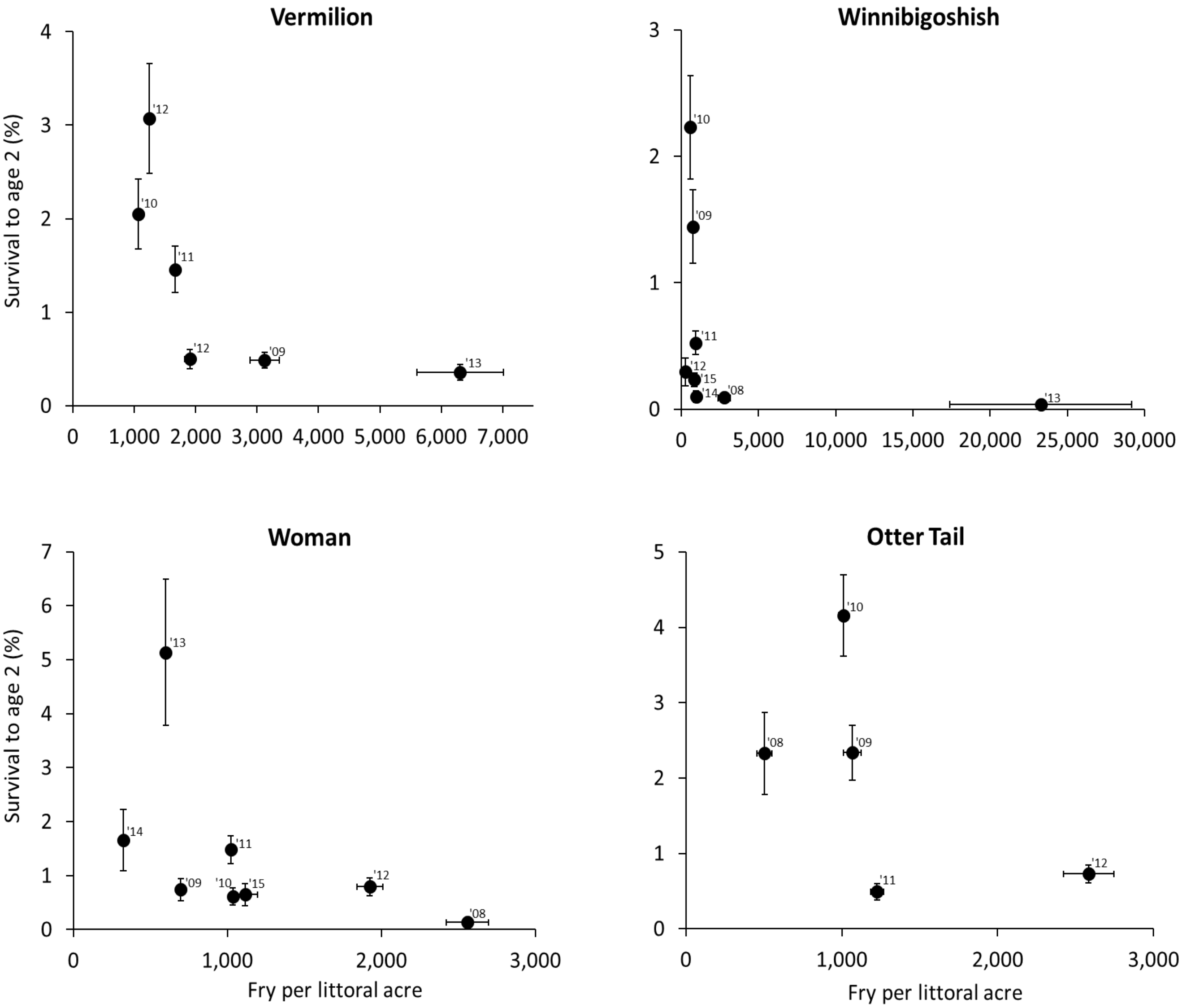

FIGURE 7. Percent of fry surviving to fall of their 2nd year of life vs. total fry density. Annotations represent year class. Error bars represent +/- one standard error. Some additional but unquantifiable variability likely exists due to measurement error of stocked fry abundance.

TABLE 11. Annual survival rates (%) for the first three years of life of Walleyes from the OTC-fry-stocked year-classes. Standard errors are presented in parentheses. Some additional but unquantifiable variability likely exists due to measurement error in the number of fry stocked.

Year	Year class							
of life	2008	2009	2010	2011	2012	2013	2014	2015
				Vermilion				
1	[a]	2 (0.1)	8 (0.7)	5 (0.4)	11 (0.9)	1 (0.1)	4 (0.4)	[a]
2	93 (38.2)	94 (23.0)	59 (14.9)	78 (21.9)	55 (13.3	99 (34.7)	35 (11.1)	0.60 (17.8)
3	79 (18.5)	30 (9.5)	49 (14.6)	29 (7.1)	78 (18.7)	53 (13.1)	41 (12.3)	
				Winnibigoshish				
1	1 (0.1)	1 (0.2)	7 (0.6)	3 (0.3)	1 (0.2)	1 (0.1)	1 (0.1)	2 (0.2)
2	77 (53.9)	375 (166.5)	74 (20.1)	48 (13.8)	77 (42.9)	34 (8.9)	40 (22.8)	31 (10.5)
3	33 (15.2)	34 (9.2)	23 (6.4)	23 (8.3)	76 (37.9)	30 (8.8	44 (24.7)	
				Woman				
1	1 (0.2)	4 (0.5)	6 (0.7)	3 (0.4)	3 (0.3)	11 (1.9)	7 (1.2)	2 (0.3)
2	37 (20.1)	45 (17.5)	52 (16.1)	56 (24.1)	89 (34.9)	91 (39.5)	49 (24.1)	85 (41.7)
3	66 (28.2)	67 (23.0)	30 (8.0)	37 (12.3)	54 (15.5)	21 (7.3)	44 (25.8)	
				Otter Tail				
1	12 (2.2)	13 (1.3)	13 (1.2)	4 (0.4)	2 (0.2)	12 (0.7)	7 (0.6)	[b]
2	35 (13.1	32 (7.3)	62 (13.5)	30 (9.9)	92 (25.1)	43 (8.6)	[b]	[b]
3	38 (13.4)	28 (5.7)	41 (8.8)	63 (21.6)	23 (6.0)	[b]	[b]	

[a] Absence of reliable mark return data prevented calculation of survival rates.

[b] Gill-netting not conducted beyond 2015.

Year-class strength.—Relative year-class strength ranged from 0.22 to 2.25 in the study lakes but failed to exhibit strong synchrony among the lakes across years (Figure 8). The strongest year-class in Winnibigoshish and Woman lakes occurred in 2013, but the 2013 year-class was only moderate in Vermilion and Otter Tail lakes. The 2012 year-class was the strongest in Lake Vermilion but the weakest in Lake Winnibigoshish. The 2009, 2011, 2014 and 2015 year-classes, similarly, showed little pattern among the lakes. The 2008 and 2010 year-classes showed the most consistency across lakes with 2010 producing moderate to strong year-classes and 2008 producing relatively weak year-classes.

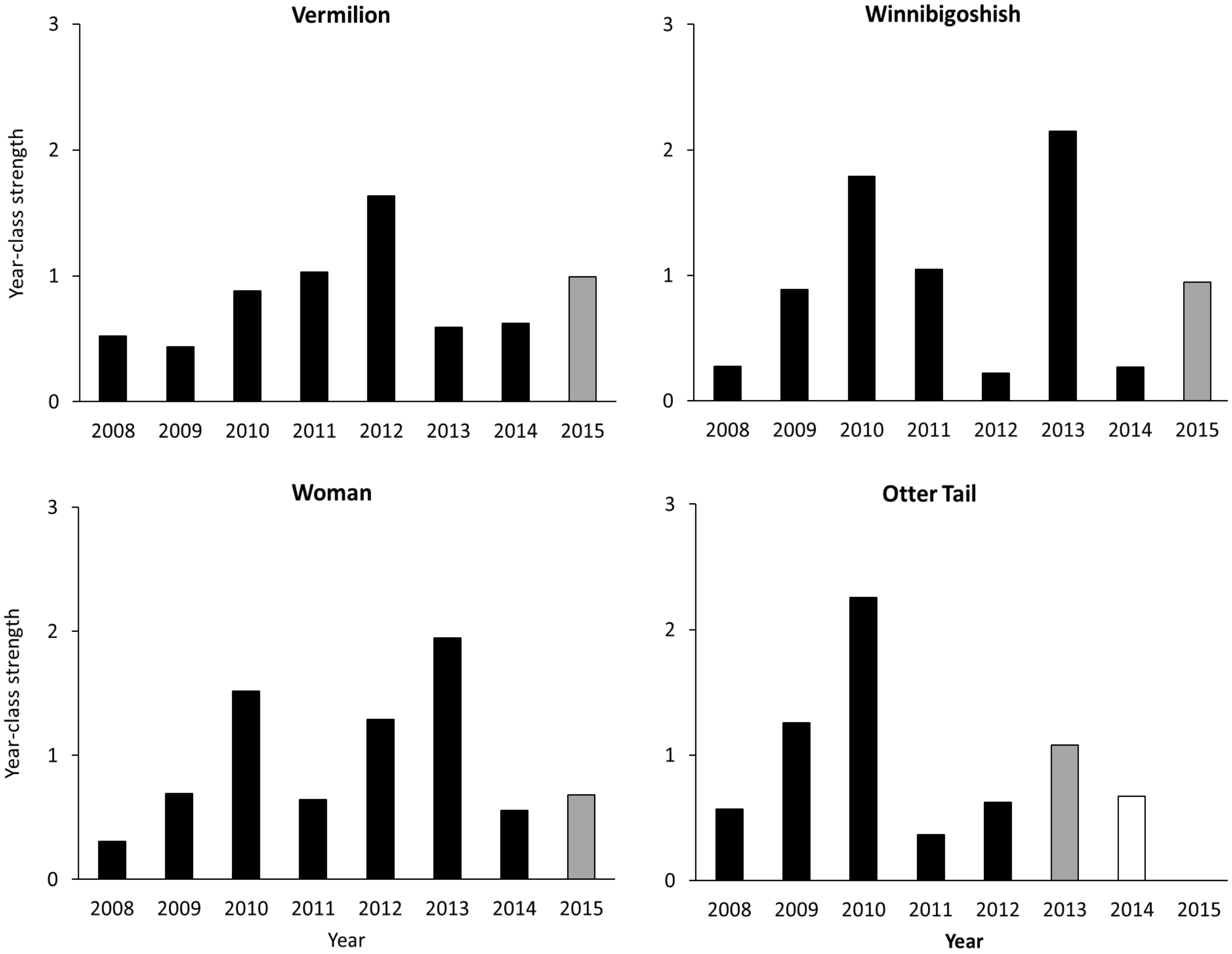

FIGURE 8. Relative strength of the experimentally stocked year-classes in the study lakes based on the availability of gill net data. Values represented by black bars were calculated with gill net CPE of ages 1-3, values represented by gray bars with ages 1-2, and the value represented by a white bar with only age 1.

Standardizing the year-class strength index to control for lake effects and allow combining the data to investigate relationships with the total fry densities (sans outliers) resulted in an increase in the overall range of year-class strength values (Figure 9). The resulting AIC scores from the analysis indicated the greatest support for the Ricker model by at least 9 points over the three other typical recruitment response models (linear, Beverton- Holt, and Ricker) and 8 points over the null model (Table 12).

The plot of the relationship between total fry density and year-class strength from the GAM model was also curvilinear (Figure 9) but the p-value was only 0.249. Inclusion of total Walleye biomass, growing degree days, and Yellow Perch CPE in the Ricker model failed to reduce the AIC score below the base model (Table 13).

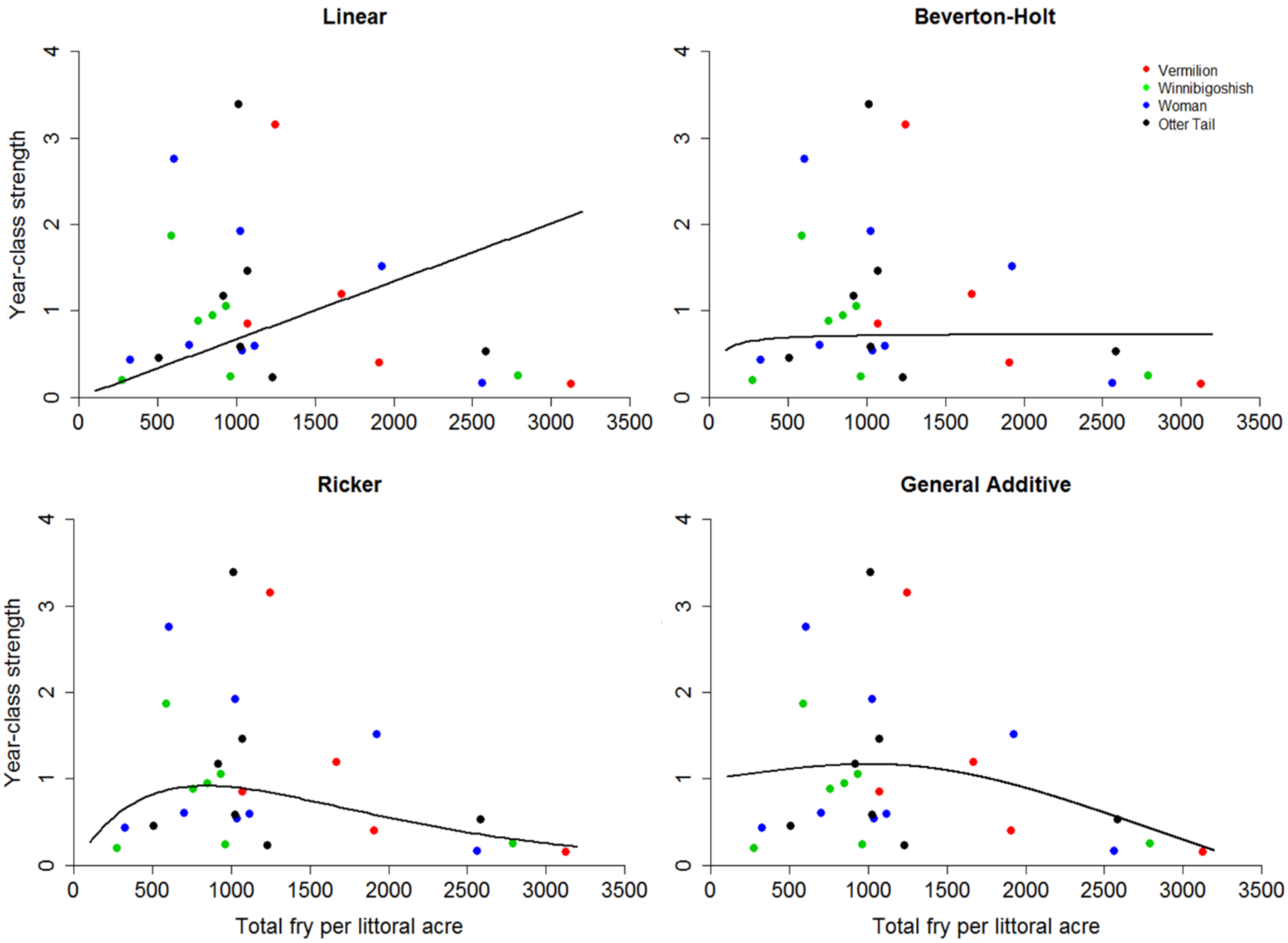

FIGURE 9. Relationship between total fry density and year-class strength standardized and combined across all study lakes. Trend lines represent linear, Beverton-Holt, Ricker, or General Additive model fits as indicated on each panel. Outlier values for Lakes Vermilion and Winnibigoshish in 2013 were omitted.

TABLE 12. Model selection criteria for linear, Ricker, and Beverton-Holt models predicting year-class strength from total fry density across all four study lakes. Presented are degrees of freedom (df), AIC, Akaike difference (Δ; the difference between each model and the model with the lowest AIC).

Models	df	AIC	Δ
Null	2	73.8	7.8
Linear	2	88.2	22.2
Beverton-Holt	3	75.7	9.7
Ricker	3	66.0	0

TABLE 13. Effects of additional explanatory variables on the AIC scores of the Ricker model predicting year-class strength from total fry density (here using records for which Perch CPE is available). Presented are degrees of freedom (df), AIC, and Akaike difference (Δ; the difference between each model and the model with the lowest AIC).

Additional explanatory variables	df	AIC	Δ
None (base model)	3	60.1	0
Walleye biomass	4	61.2	1.1
GDD	4	61.7	1.6
Perch CPE	4	61.2	1.1
Walleye biomass, GDD	5	62.7	2.6
Walleye biomass, Perch CPE	5	60.1	0
GDD, Perch CPE	5	62.6	2.5
Walleye biomass, GDD, Perch CPE	6	62.7	2.6

DISCUSSION

The results of this study indicate that the current put-back policy results in substantially more fry stocked than would be necessary to compensate for the additional fry that would have hatched in absence of the egg-take operations. Although the wild hatch rates observed in the study lakes were quite variable, they were substantially lower than the 10% value (Johnson 1961) that is the basis of the long-standing put-back policy/practice. This study also revealed that stocked Walleyes can comprise a substantial proportion of the year-classes in the egg-source lakes, and that the high densities associated with stocking were sometimes related to reductions in growth and survival that may affect recruitment and subsequent year-class strength.

The reproductive biology of Walleyes is such that high variability in hatch rates could be expected. Walleyes are highly fecund fish that broadcast their eggs over a variety of substrates in rivers, lakes, and tributary streams (Scott and Crossman 1973; McElman 1983; Bozek et al. 2011a). Since Walleyes forego the nest preparation and parental care provided by other species, their eggs can be particularly vulnerable to interannual variability in environmental conditions. Changes in water levels and stream flows (Johnson 1961; Chevalier 1977) can alter the availability of habitat suitable to protect eggs from sources of mortality such as anoxia (Colby and Smith 1967; Auer and Auer 1990) or predation by Yellow Perch (*Perca flavescens*) and Spottail Shiners (*Notropis hudsonius*; Wolfert et al.

1975; Corbett and Powles 1986). Differences in the severity and timing of storm events can also affect how many eggs become displaced from otherwise suitable incubation habitat (Johnson 1961; Roseman et al. 2001). In addition, water temperature can play a role in hatching success. Although Walleye eggs are reported to be highly resilient to changes in water temperatures (Koonce et al. 1977; Schneider et al. 2002), extended periods of low temperature increase the incubation period and hence the duration of vulnerability to other potential sources of mortality (Busch et al. 1975). The relative abundance of predators may also differ between years and lakes, as could the age structure of the spawning stock. Hatch rate and survival of offspring have been reported to increase with the age of the spawning females (Johnston et al. 2007; Venturelli et al. 2010). In addition, Walleyes are known to home to areas where they have previously spawned (Smith et al. 1952; Crowe 1962; Olson and Scidmore 1962). As a schooling species, the older and more experienced walleyes are thought to be important to spawning success by guiding younger Walleyes to suitable spawning grounds (Olson et al. 1978; Bozek, et al. 2011b; Logsdon et al. 2016).

Much of the discrepancy between the wild hatch rates observed during this study and those reported for Lake Winnibigoshish by Johnson (1961) is likely due to differences in how the rates were estimated. We calculated hatch rates for this study by dividing the wild fry estimates by the estimates of total egg production (minus eggs removed for hatchery incubation). Thus, our wild hatch rate estimates were actually a combined measurement of egg deposition, fertilization, and hatch rate. Johnson (1961), in contrast, calculated hatch rates from direct observations, every 2 to 4 days, of eggs already deposited until "eye-up" (the stage of development when the eyes first become visible). Johnson (1961) first calculated reduction in total egg abundance by dividing the estimated density of eggs observed at eye-up by the density observed shortly after deposition for each sample site. He then accounted for the dead eggs in the later sample by multiplying the proportion of eggs remaining at eye-up by the proportion of eggs in the sample that were alive. Thus, Johnson's (1961) wild hatch rates were actually a measure of survival from a time thought to be shortly after egg deposition until eye-up. Johnson (1961) justified the use of survival until eye-up as a measure of hatch rate by citing Schrader and Schrader's (1922) observation that most of the egg mortality in hatcheries occurs during the first four days post-fertilization and slows substantially during the rest of incubation. Heidinger et al. (1997) and Latif et al. (1999) also reported high initial egg mortality followed by high survival during incubation in hatcheries.

Egg mortality patterns in the wild, however, may differ substantially from those in the hatchery because the eggs are susceptible to environmental perturbations and predation during the entire incubation period (Busch et al. 1975). The data presented by Johnson (1961) provided evidence of continued mortality until his last observation at eye-up. Consequently, Johnson (1961) would likely have estimated lower overall hatch rates had he been able to observe the eggs until they actually hatched; a period of time that can be substantially longer than that to eye-up. For example, McElman and Balon (1979) reported that when incubated at 15^{o}C, eye pigmentation was visible at 76 thermal units (TU; summed mean daily temperatures above 0^{o}C) but hatching did not occur until 135 TU. Thompson (1996) reported longer incubation periods at lower temperatures and noted that at 11^{o}C, eye-up occurred at 114 TU but hatching was not completed until 266 TU at the Pike River Hatchery, Minnesota.

The timing of first inspection could also affect hatch rates calculated from direct observation of eggs deposited in the wild. Eggs become more buoyant after they die (Thompson 1996; Summerfelt et al. 2011). Consequently, unfertilized eggs or eggs that die during the high-mortality periods of the first few days after deposition could more likely be displaced from the spawning location by water currents than live eggs. Eggs displaced prior to first inspection of the spawning locations would result in an underestimate of initial deposition and subsequent overestimate of hatch rates. Johnson (1961) provided indirect evidence that initial underestimation of unfertilized and dead eggs may have occurred by reporting in-lake fertilization rates (96-100%) much higher than those commonly achieved artificially under controlled conditions (65-85%; Thompson 1996;

Moore 2003). Johnson (1961) also reported that spawning occurred across at least seven days at one of the sample sites. Barton and Barry (2011) reported that protracted spawning is common within Walleye populations and that it can take one to two weeks for all females to deposit their eggs. Any eggs deposited at the sample sites after the initial egg abundance estimates in Johnson's (1961) study would not have been accounted for and would also have resulted in overestimation of hatch rates. It is also important to note that Johnson's (1961) study was not designed to measure overall hatch rates in the population but rather to compare relative success among different types of habitat.

Given the difficulties in estimating wild hatch rates from direct observation and that eggs are collected for hatchery use by forcibly expelling the eggs directly from the females, we reasoned that dividing wild fry abundance by total egg production gave us a better indication of how the eggs removed for hatchery incubation would have hatched in the wild if the parents were left unmolested. Our method was similar to that used by Forney (1976) to estimate survival from egg to fry on Lake Oneida except that he calculated abundance of fry at approximately 10 days post-hatch (dph) by examining catch rates obtained with a Miller sampler. Because Lake Oneida is typically stocked with unmarked fry, Forney (1976) was restricted to making meaningful survival estimates during the unstocked years of 1969, 1971, and 1973. The resulting estimates for Lake Oneida of 0.05% to 0.07% survival from egg to 10-dph were similar or lower than the 0.02% to 8.16% hatch rate (egg to newly-hatched fry survival) values observed during this study and much lower than the 0.6% to 36% hatch rate (deposited egg to eye-up) values reported by Johnson (1961) for Lake Winnibigoshish. Other hatch rate estimates obtained using the same procedures as the current study ranged from 0.02% to 0.60% for Red Lake, Minnesota (Logsdon 2006); 0.13% for Cass Lake, Minnesota (Kennedy 2011); 0.19% to 0.40% for Fish Lake Reservoir, Minnesota (Wilfond 2017); 0.73% for Lake Itasca, Minnesota, (G. Barnard, MNDNR, personal communication); 0.10% to 0.89% for Leech Lake, Minnesota (D. Schultz, personal communication); and 0.30% for Lake Plantagenet, Minnesota (G. Barnard, personal communication).

In contrast to wild hatch rates, the hatch rates of Walleye eggs artificially fertilized and incubated in MNDNR hatcheries typically range from 50% to 88% (N. Vanderbosch, MNDNR personal communication). It is the higher hatch rate afforded by the controlled conditions in the incubation jars that enables the production of enough fry to stock other waters in addition to those put back into the egg-source lakes. When the put-back stocking is based on a percentage of the egg take that is much higher than the wild hatch rates (such as the 10% value), the number of fry stocked can substantially exceed the additional number of fry that would have been present in the lakes if they had been allowed to hatch in the wild. The magnitude of this effect on fry density within the lakes depends on the proportion of the total eggs produced by the source population that are collected for incubation in the hatchery. The higher the proportion of eggs that are taken, then the higher the proportion of fry in the lakes that are the result of stocking at the elevated put-back percentage rather than hatching at the much lower wild hatch rates. The proportion of eggs removed from a population can vary substantially among lakes and years because the numbers of eggs removed at the egg-collection sites are based on statewide stocking needs and ease of attainment rather than the number of eggs produced by the source population (N. Vanderbosch, personal communication). Consequently, the effect of the 10% put-back stocking on the source populations can vary substantially among lakes and years.

Although fewer than half of the put-back stockings during the current study were as high as 10% of the egg take, all of the put-back fry stockings exceeded what was predicted to have hatched naturally in absence of the egg take. If the stocking rates had been subjected to the 10% policy during this study, they would have ranged from 651 to 1,003 fry/littoral acre in Lake Vermilion, 511 to 1,309 fry/littoral acre for Lake Winnibigoshish, 754 to 2,911 fry/littoral acre in Woman Lake, and 635 to 1,134 fry/littoral acre in Otter Tail Lake. Estimates of natural reproduction during the study years would have increased the above fry densities to ranges of 1,122 to 6,536 total fry/littoral acre in Lake Vermilion, 940 to 22,758 total fry/littoral acre in Lake Winnibigoshish, 1,372 to 2,933 total fry/littoral acre in Woman Lake, and 965 to 1,831 total fry/littoral acre in Otter Tail Lake. Many of these fry densities substantially exceed the 500 to 1,000 fry/littoral acre that is typically stocked to maintain Walleye fisheries in Minnesota Lakes that lack sufficient natural reproduction (MNDNR 2017) as well as the 339 to 607 total fry/littoral acre that produced strong year-classes in Red Lake (Logsdon et al. 2016) and Leech Lake (D. Schultz, personal communication).

Recruitment of Walleyes to a fishery can be highly variable due to processes operating on life history traits during their first year of life (Rudstam et al. 2016). Environmental conditions have strong influence on life history traits, but many traits can also be density dependent (Bozek et al. 2011a). Dobie (1956) demonstrated compensatory density-dependent effects on both growth and survival of age-0 Walleyes in controlled pond experiments whereas Rudstam et al. (2016) reported that age-0 growth of Walleyes was inversely related to abundance during the demersal stage (August 1-October 1) in Oneida Lake, New York. Density-dependent responses of recruitment have also been demonstrated from both stocking (Fayram et al. 2005; Jacobson and Anderson 2007) and natural reproduction (Beard et al. 2003; Hansen et al. 2012) during studies that controlled for variability in environmental conditions by evaluating recruitment across multiple lakes and years.

Synchrony among lakes in the changes of relative size of age-0 fish during the current study indicated that growth was indeed affected by broad-scale environmental conditions such as the length or intensity of the growing season. Controlling for the annual variability in these broad- scale environmental conditions (year effects) through multiple-regression analysis, however, revealed a negative density-dependent relationship between total fry abundance and age-0 growth in both Woman and Otter Tail Lakes. Although a negative relationship was not indicated for Lake Vermilion, it could be that fry densities there were never low enough during this study for the juveniles to realize the increased growth benefits of higher per-capita forage. The ranges of total fry densities in both Woman and Otter Tail lakes included values below 600/littoral acre, whereas densities remained above 1,000/littoral acre in Lake Vermilion. Lake Winnibigoshish, in contrast, did have a very broad range of total fry densities that included both 586 and 274/littoral acre. One difference in the age-0 Walleyes between Winnibigoshish and those of both Woman and Otter Tail lakes was that those sampled from Winnibigoshish were collected at least a month earlier and consequently would not have had as much time to allow for differences in growth to manifest. We included separate intercepts and slopes for each lake in our models to account for growth differences among lakes but, in hindsight, it might have been more informative to sample the age-0 Walleyes in Winnibigoshish by fall electrofishing to assure that we captured any type of variability in growth that could have occurred in August.

It has been reported that the response of fish to changes in abundance can vary among different populations of the same species (Rose and Cowan 2000). Fish in natural systems exist in what Walters and Martell (2004) refer to as a “foraging arena” where they are subjected to a constant struggle between eating and avoiding being eaten. Both options produce risks to survival. Frequent foraging results in accelerated growth rates and a subsequent increase in body size that reduces their vulnerability to predation. However, venturing forth to forage directly exposes them to predation until such body size is achieved that exceeds the gape of potential predators (Walters and Juanes 1993).

Increased fish density can intensify the foraging/growth/predation interactions (Rose et al. 2001). These heightened interactions are particularly likely among juvenile Walleyes which do not distribute uniformly around a lake but rather aggregate in vegetative cover (Engel et al. 2000; Pratt and Fox 2001) or move together as a school between deeper water during the day and littoral shoals at night (Ryder 1977; Colby et al. 1979). Consequently, relatively moderate increases in juvenile abundance could result in meaningful increases in competition for food, localized prey depletion, and disruptions to feeding behavior even though forage remains abundant elsewhere in the lake. Growth rates can then decrease as lower local food density forces reduced consumption or subjects the fish to the metabolic inefficiencies of having to forage longer and farther for the same caloric intake (Walters and Martell 2004). Both the smaller body size due to reduced growth and the increased exposure due to expanded foraging can increase their vulnerability to predation (Pratt and Fox 2001).

If density-dependent mortality occurs early enough in life, then the reduced abundance of the cohort could free up enough per-capita forage to prevent long-term effects on the growth of survivors (Walters and Juanes 1993). Evidence of early density-dependent mortality occurred in the Red Lakes where high larval abundance corresponded with low seine catches of age-0 Walleyes in July, and the subsequent formation of year-classes that were much weaker than those from lower fry densities (Logsdon et al. 2016). Consequently, it is possible that density-dependent effects in Lakes Vermilion and Winnibigoshish were simply expressed in a different form than those of Woman and Otter Tail Lakes. Our data did indicate much lower first-year survival in Lake Vermilion during the years with the highest fry density. The lowest first-year survival estimates also occurred with the highest fry densities in Lake Winnibigoshish, but with much less contrast to years with substantially lower fry densities.

In general, the survival estimates for all four lakes during this study indicated a somewhat weak but consistent pattern of reduced survival at higher fry densities that resulted in in a dome-shaped recruitment-response curve of the GAM model and a lower AIC score of the Ricker model than those of the Linear and Beverton-Holt models. The dome-shaped response of year-class strength to increasing fry density in the Ricker and GAM models is consistent with the form of stock-recruit relationships reported for Walleyes in Lake Erie (Madenjian et al.1996; Zhao et al. 2013) and Escanaba Lake, Wisconsin (Hansen et al. 1998). The conditions reported by Ricker (1975) to result in this type of dome-shape recruitment response include: 1) cannibalism of pre-recruits by adults, 2) density-dependent reductions in growth that lead to increased vulnerability to predation, and 3) a lag-time in the response of a predator or parasite to the abundance of pre-recruits that leads to overcompensation based on the higher initial density of the pre-recruits. Maceina and Pereira (2007) also argued that predation by a variety of species may result in a dome-shaped recruitment response if the foraging behavior or success of the predators changes with the increase of pre-recruits.

Our study differed from both the previously mentioned stocking evaluations and recruitment studies in that we had to account for both stocked and wild fry. This restricted our time series to those years in which the stocked fry were OTC-marked. Recruitment response modeling has been reported to be very challenging without long time series of highly contrasting stock sizes (Hilborn and Walters 1992). Consequently, we adapted our experimental design in an attempt to mitigate these challenges. By modeling recruitment from total fry density, we hoped to remove the effects of variability in hatch rate to allow meaningful modeling with a shorter time series of data than is typically required to predict recruitment from the parental stock. We also pooled data across lakes to help gain sample size, and manipulated stocking rates to achieve a broader range of fry densities than otherwise would have occurred. Despite our efforts, our analysis was not exempt from the ambiguity typical of recruitment response modeling (Hilborn and Walters 1992; Quinn and Deriso 1999; Rose et al. 2001). This is particularly evident in consideration of the outlier values for Lakes Winnibigoshish and Vermilion in 2013 that produced relatively moderate or strong year-classes at fry densities well beyond those in our experimental design. Much of the ambiguity in recruitment response likely occurred from sampling error (Hilborn and Walters 1992) but it is also likely that the relationship between fry density and year-class strength was somewhat obscured by environmental stochasticity (Subbey et al. 2014). We attempted to account for environmental conditions by including three additional explanatory parameters in the extended Ricker model: GDD, total Walleye biomass, and Yellow Perch CPE. Failure to reduce the resulting AIC scores beyond those of the base model indicated that these parameters had little influence on year-class strength, were site specific (Rose et al. 2001), or couldn't be detected due to sampling error. Given the short time series, fitting the extended models on an individual lake basis ran a strong risk of obtaining spurious correlations that would limit the predictive ability of the results (Hilborn and Walters 1992).

The weight of the evidence, however, did identify the occurrence of density-dependent growth and recruitment, and supported recognition of diminishing year-class benefits at higher fry densities (Beverton-Holt curve) or even a risk of suppression of year-class strength (Ricker curve) as plausible. When considered collectively, the results of this study indicate that the 10% put-back policy can be an inappropriate management strategy for lakes with egg-collection stations. If the response of recruitment to increases in fry density followed an asymptotic pattern, such as that of the Beverton-Holt model, then the higher fry densities that can result from the 10% policy would simply result in an inefficient allocation of fry. It could then be reasoned that the additional fry, while costly and beyond those needed to compensate for the egg collection, would assure that enough fry are present in the lakes to provide moderate or strong year-classes when suitable environmental and community conditions exist. However, the possibility of a compensatory response to fry density such as that denoted by the descending limb of a Ricker response curve suggests there can sometimes be an upper limit to the benefits of fry stocking, and that intermediate fry densities are both more cost effective and often more likely to result in moderate or strong year-classes. The intermediate fry densities observed during this study also include within their range the 1,000 fry/littoral acre which is the upper end of the recommended stocking quota for Minnesota waters (MNDNR 2017).

Consequently, we recommend that stocking in the egg-collection lakes no longer be based on a percentage of the egg-take (or convenience for disposing of surplus fry), but instead be conducted at levels targeted to achieve intermediate total fry densities. Likely wild fry densities could be predicted from spawner biomass estimates by applying the mean fecundity and hatch rate values from this study and accounting for the spring egg-take quota. The predicted density of wild fry for the upcoming spring could then be subtracted from 1,000 to calculate the desired annual stocking density and subsequent quota. Conceptually, this would result in stocking more fry when the reproductive potential of the lakes was low, and stocking fewer fry when the reproductive potential was high.

Unlike the Red Lakes (Logsdon et al. 2016), however, wild fry density in the four study lakes did not exhibit meaningful relationships to spawning stock biomass, even when egg removal was accounted for. The observations on the Red Lakes differed from those of the study lakes in that they occurred during a period of recovery from a severely depressed spawning stock when recruitment could have been fry limited (Logsdon et al. 2016). Because the populations in the current study lakes were at healthier levels, natural reproduction was likely to be less fry limited and more influenced by stochastic variability in environmental conditions (Subbey et al. 2014). Consequently, the total fry densities resulting from stocking quotas that are based on predicted wild fry density are likely to vary substantially at the range of spawning stock densities observed during this study. Stocking based on predicted wild fry density should, however, prevent the extremely high densities that can occur from the 10% put-back policy or the extremely low densities the can occur from a depressed spawning stock.

Stocking based on predicted wild fry abundance would be most responsive to population changes in Lakes Vermilion and Winnibigoshish where annual surveys allow updated egg production estimates prior to each spring. Since annual sampling is not conducted on Woman and Otter Tail Lakes, however, the stocking quotas could be based on the most current netting results and then repeated annually until the lakes are re-surveyed. Alternatively, fry stocking could be conducted at a fixed rate (as occurs in other Minnesota waters) for several survey cycles and adjusted as needed based on resulting growth, recruitment, and prey availability levels. Although natural reproduction is known to vary in Woman and Otter Tail lakes, the fixed-rate stocking option may actually result in similar or more stable total fry densities than the wild fry prediction option due to the: 1) low predictability of hatch rates, 2) the relatively low effect of changes in the egg-take on reproduction, and 3) the lower confidence in spawner biomass estimates resulting from less frequent sampling and fewer nets that reduces the ability to accurately predict wild fry production. The fixed rate stocking method may also be more acceptable to the public in waters that do not have a dedicated Large Lake Specialist to collect and disseminate the additional information on the fishery. Initial fixed stocking rates could be derived by subtracting the mean of observed wild fry densities from 1,000. This would result in a recommended starting fry-stocking density of approximately 695 fry/littoral acre in Woman Lake and 625 fry/littoral acre in Otter Tail Lake.

Our understanding of the recruitment response to fry density in these study lakes remains uncertain and incomplete. Consequently, whichever method is used to set the stocking quotas, it is important that managers proceed using an adaptive management approach consisting of: 1) a systematic stocking strategy, 2) frequent monitoring, and 3) changes in the stocking quotas based on the resulting growth, recruitment, and prey abundance in the individual lakes over time. Attention to growth rates is particularly important, as growth can be measured sooner and more precisely than year-class strength, and because invasive species will likely alter system productivity. To facilitate evaluation of the fry stocking, it is also important that surplus fry or additional life stages not be stocked in addition to the prescribed fry quotas. Managers should also consider periodic stocking blanks (years without stocking) or OTC marking of the fry to help further define natural reproduction; particularly after major changes in spawning stock abundance, egg-take quotas, fish community structure, or condition of available habitat.

ACKNOWLEDGMENTS

We thank all the individuals who provided information and assistance during this project because a study of this scope and duration could not have been conducted without the help of many. The numerous MNDNR staff from the Tower, Grand Rapids, Walker, and Fergus Falls Areas conducted the majority of the egg-collecting, hatching, OTC-treatment, stocking, and fish sampling during this study. Additional sampling assistance was provided by Steve Shroyer, Andy Carlson, Owen Baird, and Tim Brastrup. Andrew Carlson along with Dan Isermann, Matt Gunderson and students from UWSP processed the ovaries for fecundity determination. Dan Isermann and Bill Evarts assisted with OTC-mark identification. Don Pereira, Dan Isermann, and David Staples provided assistance in experimental design and data analysis. This project was funded in part by the Federal Aid in Sport Fish Restoration Program (Project F-26-R).

REFERENCES

Anderson, C. S. 1998. Partitioning total size selectivity of gill nets for Walleye (*Stizostedion vitreum*) into encounter, contact, and retention components. Canadian Journal of Fisheries and Aquatic Sciences 55:1854-1863.

Auer, M. T., and N. A. Auer. 1990. Chemical suitability of substrates for Walleye egg development in the lower Fox River, Wisconsin. Transactions of the American Fisheries Society 119:871-876.

Barton, B. A., and T. P. Barry. 2011. Reproductive and environmental biology. Pages 199-231 *in* B. A. Barton, editor. Biology, Management, and Culture of Walleye and Sauger. American Fisheries Society, Bethesda, Maryland.

Beverton, R. J. H., and C. S. Holt. 1957. On the dynamics of exploited fish populations, volume 19. Ministry of Agriculture, Fisheries, and Food, London, UK.

Beard, T. D., M. J. Hansen, and S. R. Carpenter. 2003. Development of a regional stock-recruitment model for understanding factors affecting walleye recruitment in northern Wisconsin lakes. Transactions of the American Fisheries Society 132:382 -391.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer, New York.

Bozek, M. A., D. A. Baccante, and N. P. Lester. 2011a. Walleye and Sauger life history. Pages 233-301 *in* B. A. Barton, editor. Biology, management, and culture of Walleye and Sauger. American Fisheries Society, Bethesda, Maryland.

Bozek, M. A., T. J. Haxton, and J. K. Raabe. 2011b. Walleye and Sauger habitat. Pages 133-197 *in* B. A. Barton, editor. Biology, management, and culture of Walleye and Sauger. American Fisheries Society, Bethesda, Maryland.

Brooks, R. C., R. C. Heidinger, and C. C. Kohler. 1994. Mass-marking otoliths of larval and juvenile Walleyes by immersion in oxytetracycline, calcein, or calcein blue. North American Journal of Fisheries Management 14:143-150.

Busch, W. N., R. L. Scholl, and W. L. Hartman. 1975. Environmental factors affecting the strength of Walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960-70. Journal of the Fisheries Research Board of Canada 32:1733-1743.

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.

Chevalier, J. R. 1977. Changes in Walleye (*Stizostedion vitreum vitreum*) population in Rainy Lake and factors in abundance, 1924-75. Journal of the Fisheries Research Board of Canada 34:1696-1702.

Christie, G. C., and H. A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Canadian Journal of Fisheries & Aquatic Sciences 45:301-314.

Colby, P. J., and L. L. Smith, Jr. 1967. Survival of Walleye eggs and fry on paper fiber sludge deposits in Rainy River, Minnesota. Transactions of the American Fisheries Society 96:278-296.

Colby, P. J., R. E. McNichol, and R. A. Ryder. 1979. Synopsis of biological data on Walleye. FAO Fisheries Synopsis 119, Rome.

Corbett, B. W., and P. M. Powles. 1986. Spawning and larva drift of sympatric Walleyes and White Suckers in an Ontario stream. Transactions of the American Fisheries Society 115:41-46.

Crowe, W. R. 1962. Homing behavior in Walleyes. Transactions of the American Fisheries Society 91:350-355.

Dobie, J. 1956. Walleye pond management in Minnesota. Progressive Fish-Culturist 17:51-57.

Engel, S., M. H. Hoff, and S. P. Newman. 2000. Walleye fry hatching, diet, growth, and abundance in Escanaba Lake, Wisconsin, 1985-1992. Wisconsin Department of Natural Resources, Research Report 184, Madison.

Fayram, A. H., M. J. Hansen, and N. A. Nate. 2005. Determining optimal stocking rates using a stock-recruitment model: an example using Walleye in northern Wisconsin. North American Journal of Fisheries Management 25:1215-1225.

FDA (U.S. Food and Drug Administration). 2017. Aquaculture approved drugs. Available: www.fda.gov/AnimalVeterinary/DevelopmentApprovalProcess/Aquaculture/ucm132954.htm (March 2015).

Fielder, D. G. 2002. Methodology for immersion marking Walleye fry in oxytetracycline hydrochloride and its detection with fluorescence microscopy. Michigan Department of Natural Resources, Fisheries Technical Report 2002-1, Ann Arbor.

Forney, J. L. 1974. Interactions between Yellow Perch abundance, Walleye predation, and survival of alternate prey in Oneida Lake, New York. Transactions of the American Fisheries Society 103:15-24.

Forney, J. L. 1976. Year-class formation in the Walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966-73. Journal of the Fisheries Research Board of Canada 33:783-792.

Forney, J. L. 1977. Evidence of inter- and intraspecific competition as factors regulating Walleye (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. Journal of the Fisheries Research Board of Canada 34:1812-1820.

Forney, J. L. 1980. Evaluation of a management strategy for the Walleye in Oneida Lake, New York. New York Fish and Game Journal 27:105-141.

Haddon, M. 2001. Modelling and quantitative methods in fisheries. Chapman & Hall/CRC, Boca Raton, Florida.

Hansen, J. F., A. H. Fayram, and J. M. Hennessy. 2012. The relationship between age-0 Walleye density and adult year-class strength across northern Wisconsin, North American Journal of Fisheries Management 32:663-670

Hansen, G. J. A., S. R. Carpenter, J. W. Gaeta, J. M. Hennessy, and M. J. Vander Zanden. 2015. Predicting Walleye recruitment as a tool for prioritizing management actions. Canadian Journal of Fisheries and Aquatic Science 72:661-672.

Hansen, M. J., M. A. Bozek, J. R. Newby, S. P. Newman, and M. D. Staggs. 1998. Factors affecting recruitment of Walleyes in Escanaba Lake, Wisconsin, 1958–1996. North American Journal of Fisheries Management 18:764-774.

Heidinger, R. C., R. C. Brooks, D. Leitner, and I. Soderstrom. 1997. Prediction of Walleye egg and embryo survival at two stages of development. Progressive Fish-Culturist 59:64-67.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment. Chapman and Hall, London.

Johnson, F. H. 1961. Walleye egg survival during incubation on several types of bottom in Lake Winnibigoshish, Minnesota, and connecting waters. Transactions of the American Fisheries Society 90:312-32.

Johnston, T. A., M. D. Wiegand, W. C. Leggett, R. J. Pronyk, S. D. Dyal, K. E. Watchorn, S. Kollar, and J. M. Casselman. 2007. Hatching success of Walleye embryos in relation to maternal and ova characteristics. Ecology of Freshwater Fish 16:295-306.

Kennedy, A. J. 2011. Adult Walleye population abundance, spawning stock biomass, and wild fry production in Cass Lake, Minnesota, and connected waters. Minnesota Department of Natural Resources, Federal Aid in Sport Fish Restoration, Project F-29 R(P)-29, Final Report, St. Paul.

Koonce, J. F., T. B. Bagenal, R. F. Carline, K. E. F. Hokanson, and M. Nagięć. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. Journal of the Fisheries Research Board of Canada 34:1878-1889.

Kutner, M. H., C. J. Nachtsheim, J. Neter, and W. Li. 2004. Applied linear statistical models, 5th edition. McGraw-Hill/Irwin, New York.

Latif, M. A., R. A. Bodaly, T. A. Johnston, and R. J. P. Fudge. 1999. Critical stage in developing Walleye eggs. North American Journal of Aquaculture 61:34-37.

Lester, N. P., A. J. Dextrase, R. S. Kushneriuk, M. R. Rawson, and P. A. Ryan. 2004. Light and temperature: key factors affecting Walleye abundance and production. Transactions of the American Fisheries Society 133:588-605.

Li, J., Y. Cohen, D. H. Schupp, and I. R. Adelman. 1996. Effects of Walleye stocking on year-class strength. North American Journal of Fisheries Management 16:840-850.

Logsdon, D. E., B. J. Pittman, and G. C. Barnard. 2004. Oxytetracycline marking of newly hatched Walleye fry. North American Journal of Fisheries Management 24:1071–1077.

Logsdon, D. E. 2006. Contribution of fry stocking to the recovery of the Walleye population in the Red Lakes. Minnesota Department of Natural Resources, Division of Fish and Wildlife, Section of Fisheries, Investigational Report 535, St. Paul.

Logsdon, D. E., C. S. Anderson, and L. M. Miller. 2016. Contribution and performance of stocked Walleyes in the recovery of the Red Lakes, Minnesota, fishery. North American Journal of Fisheries Management 36:828-843.

Lucchesi, D. O. 2002. Evaluating the contribution of stocked Walleye fry and fingerlings to South Dakota Walleye populations through mass marking with oxytetracycline. North American Journal of Fisheries Management 2002:985-994.

Maceina, M. J., and D. L. Pereira. 2007. Recruitment. Pages 121-185 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Madenjian, C. P., J. T. Tyson, R. L. Knight, M. W. Kershner, and M. J. Hansen. 1996. First-year growth, recruitment, and maturity of Walleyes in western Lake Erie. Transactions of the American Fisheries Society 125:821-830.

Maloney, J. E., and F. H. Johnson. 1955. Life histories and inter-relationships of Walleye and Yellow Perch, especially during their first summer, in two Minnesota lakes. Transactions of the American Fisheries Society 85:191-202.

McElman, J. F., and E. K. Balon. 1979. Early ontogeny of Walleye, *Stizostedion vitreum*, with steps of saltatory development. Environmental Biology of Fishes 4:309-348.

McElman, J. F. 1983. Comparative embryonic ecomorphology and the reproductive guild classification of Walleye, *Stizostedion vitreum*, and White Sucker, *Catostomus commersoni*. Copeia 1983:246-250.

Miranda, L. E., and P. W. Bettoli. 2007. Mortality. Pages 229-277 *in* C. S. Guy, and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Minnesota Department of Natural Resources. 2017. Walleye stocking operational plan 2016-2020. Minnesota Department of Natural Resources, Committee Report, St. Paul.

Moore, A. A. 2003. Manipulation of fertilization procedures to improve hatchery Walleye egg fertility and survival. North American Journal of Aquaculture 65:56-59.

Ogle, D. H. 2016. Introductory fisheries analysis with R. CRC Press, Boca Raton, Florida.

Olson, D. E., and W. J. Scidmore. 1962. Homing behavior of spawning Walleyes. Transactions of the American Fisheries Society 91:355-361.

Olson, D. E., D. H. Schupp, and V. Macins. 1978. An hypothesis of homing behavior of Walleyes as related to observed patterns of passive and active movement. Pages 52-57 *in* R. L. Kendall, editor. Selected coolwater fishes of North America. American Fisheries Society, Special Publication 11, Bethesda, Maryland.

Piper, R. G., I. B. McElwain, L. E. Orme, J. P. McCraren, L. G. Fowler, and J. R. Leonard. 1982. Fish Hatchery Management. U.S. Fish and Wildlife Service, Washington, DC.

Pratt, C. T., and M. G. Fox. 2001. Biotic influences on habitat selections by young-of-year Walleye (Stizostedion vitreum) in the demersal stage. Canadian Journal of Fisheries and Aquatic Sciences 58:1058-1069.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin 191, Ottawa.

Robson, D. S., and H. A. Regier. 1964. Sample size in Petersen mark-recapture experiments. Transactions of the American Fisheries Society 93:215-226.

Rose, K. A., J. H. C. Jr., K. O. Winemiller, R. A. Myers, and R. Hillborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding, and prognosis. Fish and Fisheries 2:293-327.

Rose, K. A., and J. H. Cowan. 2000. Predicting fish population dynamics: compensation and the importance of site-specific considerations. Environmental Science and Policy 3:S433-S443.

Roseman, E. F., W. W. Taylor, D. B. Hayes, R. L. Knight, and R. C. Haas. 2001. Removal of Walleye eggs from reefs in western Lake Erie by a catastrophic storm. Transactions of the American Fisheries Society 130:341-346.

Rudstam, L. G., J. R. Jackson, A. J. VanDeValk, T. E. Brooking, W. W. Fetzer, B. J. Irwin, and J. L. Forney. 2016. Walleye and Yellow Perch in Oneida Lake. L. G. Rudstam, E. L. Mills, J. R. Jackson, and D. J. Stewart, editors. Oneida Lake: Long-term dynamics of a managed ecosystem and its fishery. American Fisheries Society, Bethesda, Maryland.

Ryder, R. A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult Walleyes (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 34:1481-1491.

Schneider, J. C., J. Copeland, and M. Wolgamood. 2002. Tolerance of incubating Walleye eggs to temperature fluctuations. North American Journal of Aquaculture 2002:75-78.

Schrader, F., and S. H. Schrader. 1922. Mortality in Pike-perch eggs in hatcheries. Appendix V to the Report of the U.S. Commissioner of Fisheries for 1922. Bureau of Fisheries Document No. 926.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottawa. Washington D.C.

Smith, L. L., Jr., L. W. Krefting, and R. L. Butler. 1952. Movements of marked Walleyes, *Stizostedion vitreum vitreum* (Mitchill), in the fishery of the Red Lakes, Minnesota. Transactions of the American Fisheries Society 81:179-196.

Smith, L. S. 1982. Introduction to Fish Physiology. T.F.H. Publications, Inc., Neptune, New Jersey.

Subbey, S., J. A. Devine, U. Schaarschmidt, and R. D. M. Nash. 2014. Modelling and forecasting stock–recruitment: current and future perspectives. ICES Journal of Marine Science 71:2307-2322.

Summerfelt, R. C., J. A. Johnson, and C. P. Clouse. 2011. Culture of Walleye, Sauger, and hybrid Walleye. Pages 451-570 *in* B. A. Barton, editor. Biology, management, and culture of Walleye and Sauger. American Fisheries Society, Bethesda, Maryland.

Thompson, D. 1996. Stripping, fertilizing, and incubating Walleye eggs at a Minnesota hatchery. Pages 41-44 *in* R. C. Summerfelt, editor. Walleye culture manual NCRAC Culture Series 101, North Central Regional Aquaculture Center Publications Office, Iowa State University, Ames, Iowa.

Venturelli, P. A., C. A. Murphy, B. J. Shuter, T. A. Johnston, P. J. v. C. d. Groot, P. T. Boag, J. M. Casselman, R. Montgomerie, M. D. Wiegand, and W. C. Leggett. 2010. Maternal influences on population dynamics: evidence from an exploited freshwater fish. Ecology 91:2003-2012.

Walters, C. J., and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences 50:2058-2070.

Walters, C. J., and S. J. D. Martell. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.

Wilfond, D. 2017. Fish Lake Reservoir OTC Walleye study. Minnesota Department of Natural Resources, Federal Aid in Sport Fish Restoration, Project F-29 R(P)-31, Final Report, St. Paul.

Wingate, P. J., and D. H. Schupp. 1985. Large lake sampling guide, Minnesota Department of Natural Resources, Division of Fish and Wildlife, Section of Fisheries, Special Publication 140, St. Paul.

Wolfert, D. R., W. D. N. Busch, and C. T. Baker. 1975. Predation by fish on Walleye eggs on a spawning reef in western Lake Erie, 1969-71. Ohio Journal of Science 75: 118-124.

Wood, S. 2017. Package ‘mgcv’. Available: https://cran.r-project.org/web/packages/mgcv/mgcv.pdf (March 2017).

Zhao, Y., P. M. Kocovsky, and C. P. Madenjian. 2013. Development of a stock–recruitment model and assessment of biological reference points for the Lake Erie Walleye fishery. North American Journal of Fisheries Management 956-964.