Changes in Walleye Fecundity and Egg Size Before, During, and After Rehabilitation of the Red Lakes Fishery

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The Red Lakes in northern Minnesota experienced a major Walleye *Sander vitreus* fishery crash in the late 20th century, but has since recovered to record abundances and supports a major commercial and recreational fishery. Fecundity is an integral aspect of recruitment that can contribute greatly to the understanding of fishery population dynamics. To elucidate the effects of varying Walleye densities and exploitation rates on fecundity and egg size in years 1989 (overexploited fishery), 2004 (recovering fishery), and 2017 (recovered fishery), we analyzed linear models that related fecundity or egg size to morphological features for these three sampling periods. Walleyes were collected spring 2004 (n=30) and 2017 (n=30) in the Tamarac River. Fecundity data from 1989 were provided by Bushong (1990). Fecundity was higher in 2004 and 1989 than in 2017. Egg size was significantly greater in 2017 than in 1989. Considerable distinctions in Walleye size at spawn existed between all sampling years. Variance in fecundity as well as egg and fish size between fishery status scenarios is likely attributable to varying exploitation rates and related Walleye densities; these two factors were shown to be good predictor variables. Models incorporating fishery status were developed and for certain management applications, these models could provide a higher degree of selectivity and estimation accuracy for fishery managers.

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Introduction

The Red Lakes, located in Northern Minnesota, supports a large commercial and recreational fishery of Walleye *Sander vitreus*. Since the reopening of the fishery in 2006, the Red Lakes have demonstrated to be a valuable commercial and recreational resource for the region. The Red Lakes Walleye fishery started to show signs of overfishing in the early 1970's (Pereira 1992) and finally collapsed in the late 1990's due to continued overexploitation (RLFTC 2006), but following a harvest moratorium and intensive stocking efforts from 1997-2006, the Red Lakes are now considered a recovered fishery with high abundances of Walleye (Brown and Kennedy 2016) and a sustainable exploitation rate of 7.3% in 2017. Since the cessation of stocking in 2006, the Walleye population has been sustained entirely by natural reproduction. The Tamarac River is the largest tributary to Upper Red Lake (Groshens 2000) and is thought to be the most important tributary in the Red Lakes for migrating Walleyes utilizing lotic spawning areas.

The dynamic history of the Red Lakes Walleye fishery provides a unique opportunity to investigate anthropogenic influences on the fishery over time; doing so could lead to more effective future management practices. Of particular influence when considering the management of fish populations is recruitment (Ricker 1975), of which fecundity is an integral aspect (Koslow 1992). Fecundity does not provide an estimate of reproductive success, but rather serves as a measurable quality of reproductive effort (Moyle and Cech 2004). This is typically expressed as the number of eggs within a female prior to the next spawning season.

Measurements of fecundity are important because they can be useful in calculations of egg and fry survival, which can be used in estimations of recruitment (Wright and Shoesmith 1988). Therefore, to better manage Walleye fisheries, it would be helpful to understand how dramatically varying exploitation rates over the past 30 years in the Red Lakes have influenced Walleye fecundity characteristics.

To our knowledge, fecundity data of Red Lakes Walleyes has been collected twice in the past; once in 1989 when the fishery was in an overfished state with an exploitation rate of 41% (Bushong 1990), and once in 2004 during the recovery phase and an exploitation rate of zero. Walleye fecundity has been shown to increase in response to exploitation (Baccante and Reid 1988; Muth and Ickes 1993). Consequently, current Walleye fecundity data is needed to assess trends over time due to changes in Walleye abundance and exploitation rates.

The objectives of this study are to 1) determine the effects of three different fishery statuses (over exploited, recovering, and recovered) on Walleye fecundity and egg diameter in the Red Lakes and 2) to develop models that allow for the estimation of fecundity and egg size based on the status of a fishery. Completion of these objectives will elucidate the effects of varying Walleye exploitation rates on fecundity and egg diameter and allow for selective and more accurate estimates by fishery managers.

Methods

Study Site

Walleye sampling took place in the Tamarac River (48° 9'N latitude, 94°30'W longitude), a 34.9 km river which flows into the east side of Upper Red Lake. The Tamarac River drainage mainly consists of wetlands (65%), with forests covering the remaining area (Groshens 2000).

Sample Collection

Thirty Walleyes were sampled just prior to spawning in early April of 2017 using Fyke nets (frame 0.9 x 1.5 m; bar mesh 2.5 cm). Nets were placed at five randomly selected locations ranging from near the mouth to approximately 10.5 km upriver. Two nets were set at each location; one on either side of the river. The nets were set facing downriver with the lead set at an angle from shore to facilitate the capture of fish moving upstream. Walleye collection took place over two consecutive days.

For a Walleye to be sampled, it was required to be in a pre-spawn state; any fish that appeared to be partially spawned out or completely spent were avoided. To help ensure representative sampling, ten size classes in a range of 360 – 609 mm were established based on the female size distribution present in the spawn. Immediately after removal from Fyke nets, fish were weighed (to the nearest 0.1 g) and fork lengths measured (to the nearest 1 mm). Fish were then individually placed in labeled plastic bags and put on ice.

Fish were temporarily frozen for up to two days until dissection in the lab. After thawing at room temperature, ovaries were carefully dissected from each fish and weighed as a whole (to the nearest 0.01 g). Fecundity was estimated by removing a 1 g subsample from the anterior, middle, and posterior regions of the ovary and then multiplying the average number of eggs per gram of the three ovarian subsamples by the total weight of the ovary. From each subsection, diameters were measured from five random eggs (to the nearest 0.025 mm) with a Vernier dial caliper (Mitutoyo 500) underneath a stereoscopic microscope (Olympus SZ51).

Fish were aged using sagittal otoliths, employing the heat and crack method outlined by Hu and Todd (1981). Three people independently aged each fish with an agreed age being assigned. If an agreed age could not be met, the fish’s age was not used in analyses.

2004 Sampling Methods

Methods performed in 2004 were the same to that of the present study except for the following discrepancies. Thirty Walleyes were sampled via electrofishing in April of 2004 with a Smith-Root SR18 electrofishing boat in the Tamarac River on sites with preferred Walleye spawning substrate that were later confirmed and mapped by Graham et al. (2017).

Ten size classes in a range of 470 – 699 mm were established based on the female size distribution present in the spawn. Total lengths were measured and later converted to fork lengths employing the weight – length regression equation from 2017 data.

Extracted ovaries were preserved in a 10% formalin solution for approximately two months before further processing. No egg diameter measurements were taken.

Data Analysis

Estimated absolute fecundity (total eggs per female) was calculated as: $F = E*O$, where F is the total number of estimated eggs, E is the average number of eggs per gram of ovary from the three subsections, and O is ovary weight in grams. Relative fecundity (the number of eggs per unit of weight) was calculated as: $RF=F/M$, where RF is the relative fecundity, F is the total number of estimated eggs per female, and M is the mass of the fish in kilograms.

To analyze trends between years and establish linear regression equations, fecundity and egg size were plotted against fish weight, length, and age for 1989, 2004, and 2017 sampling years (egg size linear regressions only included data from 1989 and 2017; 2004 egg size diameter measurements were not taken).

To determine if sampling year could help predict fecundity or egg size, Akaike Information Criterion (AIC) scores were used to select the model (from a suite of five; Table 1) with the variables that best predicted fecundity or egg diameter (Akaike 1998). A threshold of two units was required for a model to be considered better supported. If two models were similarly supported, then the simpler of the two was chosen.

Table 1. Linear models relating fecundity (F) or egg diameter to fish weight (WW_g), fork length (FL_mm), age, and fishery status. Best supported models were selected using AIC and Δ AIC scores.

Model	AIC	Δ AIC
F = WW_g · Fishery Status	1932.07	0
F = WW_g + Fishery Status	1948.80	16.73
F = WW_g	1959.80	27.73
F = Fishery Status	2132.14	200.07
F = 1	2193.78	261.71
F = FL_mm · Fishery Status	1940.93	0
F = FL_mm + Fishery Status	1965.41	24.48
F = FL_mm	1978.40	37.47
F = Fishery Status	2132.15	191.22
F = 1	2193.78	252.85
F = Age · Fishery Status	2044.80	0
F = Age + Fishery Status	2056.13	11.33
F = Fishery Status	2109.43	64.63
F = Age	2123.95	79.15
F =1	2170.09	125.29
Egg Diameter = Fishery Status	-156.44	0
Egg Diameter = WW_g + Fishery Status	-154.52	1.92
Egg Diameter = WW_g · Fishery Status	-152.52	3.92
Egg Diameter = WW_g	-64.29	92.15
Egg Diameter = 1	-53.76	102.68
Egg Diameter = Fishery Status	-156.44	0
Egg Diameter = FL_mm + Fishery Status	-154.64	1.8
Egg Diameter = FL_mm · Fishery Status	-152.69	3.75
Egg Diameter = FL_mm	-65.66	90.78
Egg Diameter = 1	-53.76	102.68
Egg Diameter = Fishery Status	-153.01	0
Egg Diameter = Age + Fishery Status	-151.30	1.71
Egg Diameter = Age · Fishery Status	-150.60	2.41
Egg Diameter = Age	-88.24	64.77
Egg Diameter = 1	-52.29	100.72

Results

Fecundity and Egg Size

Fecundity was higher in the overexploited (1989 data) and recovering fishery scenarios (2004 data) than in the recovered fishery scenario (2017 data). In 1989, sampled fish were all relatively small but had higher fecundities compared to similarly sized fish sampled in and 2017. In 2004, sampled fish were the largest of the three years and also had higher fecundities for those larger fish than in 2017. In 2017, both small and large fish were present in the sampling but typically had lower fecundities than in 1989 (for small fish) and 2004 (for large fish), (Figures 1-3).

The median fecundity in 1989 was 36,797 (IQR = 15,337.25) eggs per fish compared to a mean of 117,213 (SD = 49,186) in 2004, and a median of 44,409 (IQR=34,028) in 2017. Walleye spawned at an earlier and more limited age range (4 – 5 years) in 1989 than in 2004 (5 – 12 years) and 2017 (6 – 13 years). Fish in 2017 had significantly larger eggs than in 1989 (Figures 4-6).

For the sake of clarity, the following direct comparisons of fecundity between years use the weight – fecundity relationship (Figure 1) regression equations and not length because fecundity was best correlated to body weight in 2017 (r^2 = 0.76 P < 0.001), 2004 (r^2 = 0.94, P < 0.001), and was the chosen relationship reported by Bushong in 1989 (r^2 = 0.81, P < 0.001). Also, other investigators have found that weight is the best and/or most appropriate physiological predictor of fecundity for Walleyes (e.g. Wolfert 1969; Muth and Ickes 1993; Henderson and Nepszy 1994).

Although 1989 had a lower median value than 2017, the 1989 weight – fecundity linear regression equation overestimates fecundity by 22.1% when applied to fish sampled in 2017. 1989 had a smaller

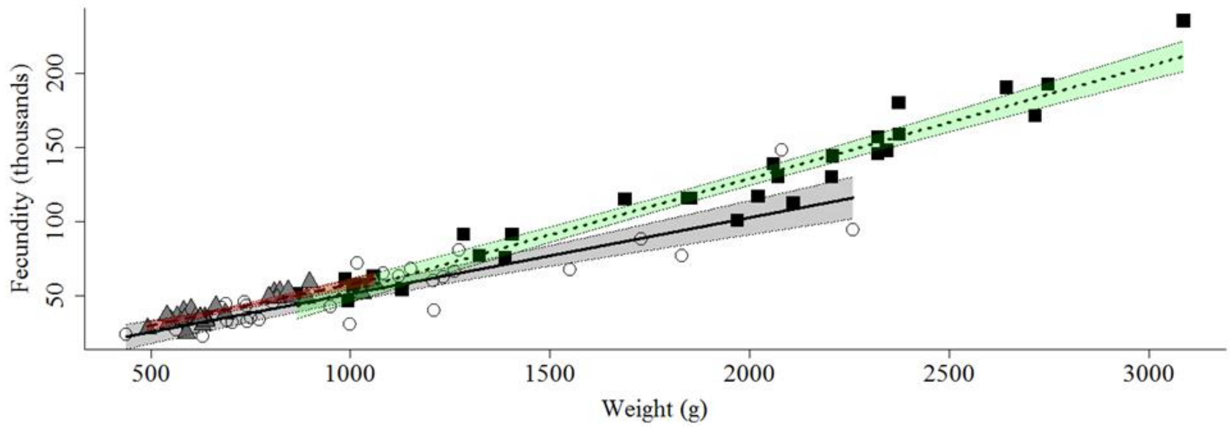

FIGURE 1. Weight – fecundity relationship, with 95% confidence intervals, for Female Red Lakes Walleyes sampled in 1989 (triangles, dashed fitted regression line (RL)), red confidence interval (CI)), 2004 (squares, dotted RL, green CI), and 2017 (circles, solid RL, grey CI).

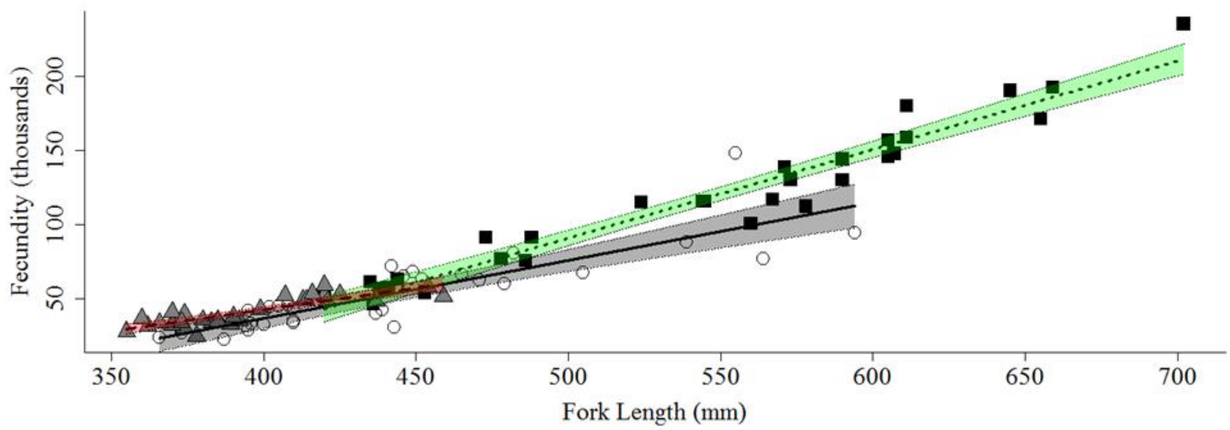

FIGURE 2. Fork length – fecundity relationship, with 95% confidence intervals, for Female Red Lakes Walleyes sampled in 1989 (triangles, dashed RL, red CI), 2004 (squares, dotted RL, green CI), and 2017 (circles, solid RL, grey CI).

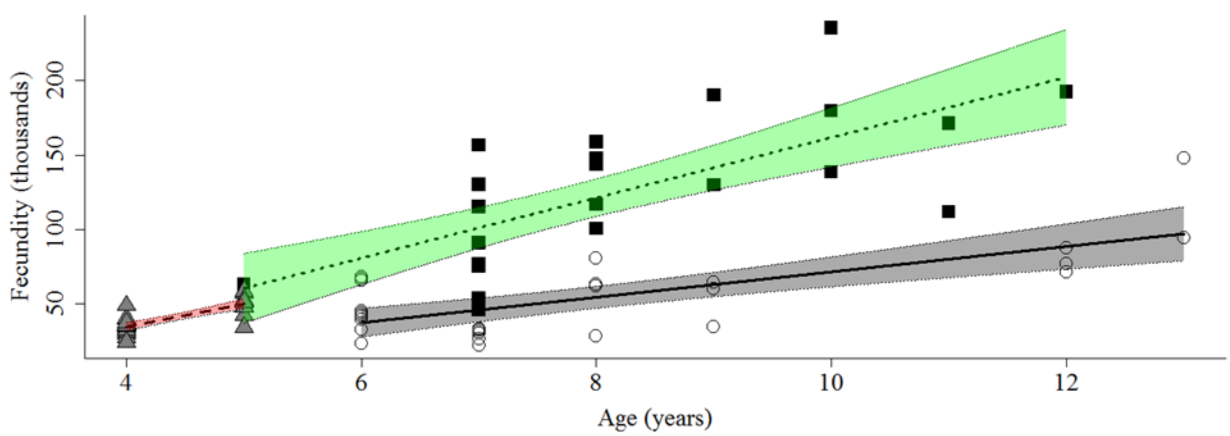

FIGURE 3. Age – fecundity relationship, with 95% confidence intervals, for Female Red Lakes Walleyes sampled in 1989 (triangles, dashed RL, red CI), 2004 (squares, dotted RL, green CI), and 2017 (circles, solid RL, grey CI).

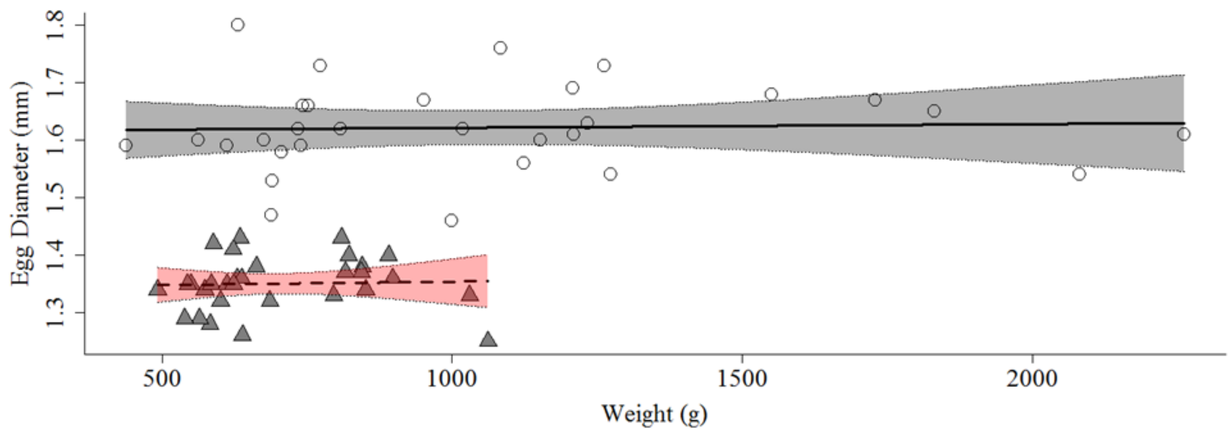

FIGURE 4. Weight - average egg diameter relationship, with 95% confidence intervals, for female Red Lakes Walleyes sampled in 1989 (triangles, dashed RL, red CI) and 2017 (circles, solid RL, grey CI).

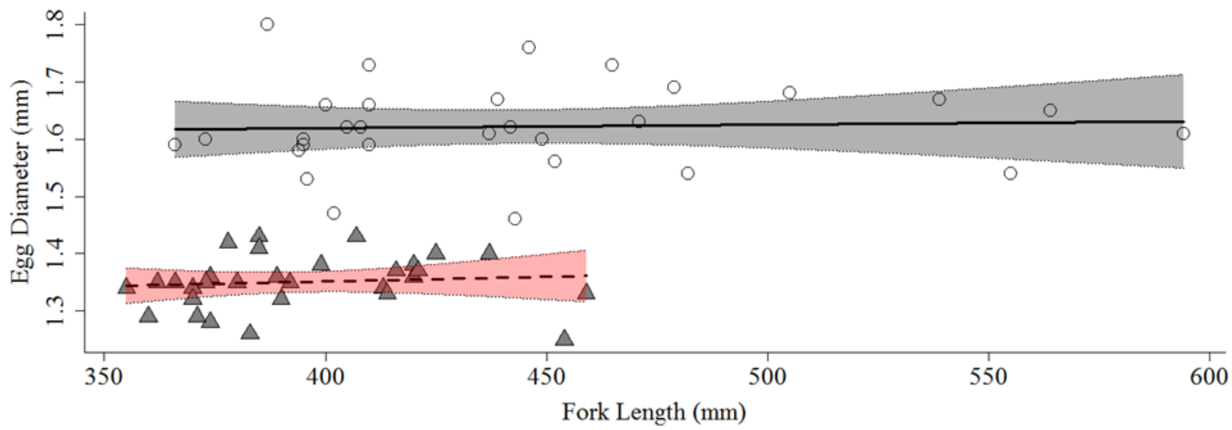

FIGURE 5. Fork length – average egg diameter relationship, with 95% confidence intervals, for female Red Lakes Walleyes sampled in 1989 (triangles, dashed RL, red CI) and 2017 (circles, solid RL, grey CI).

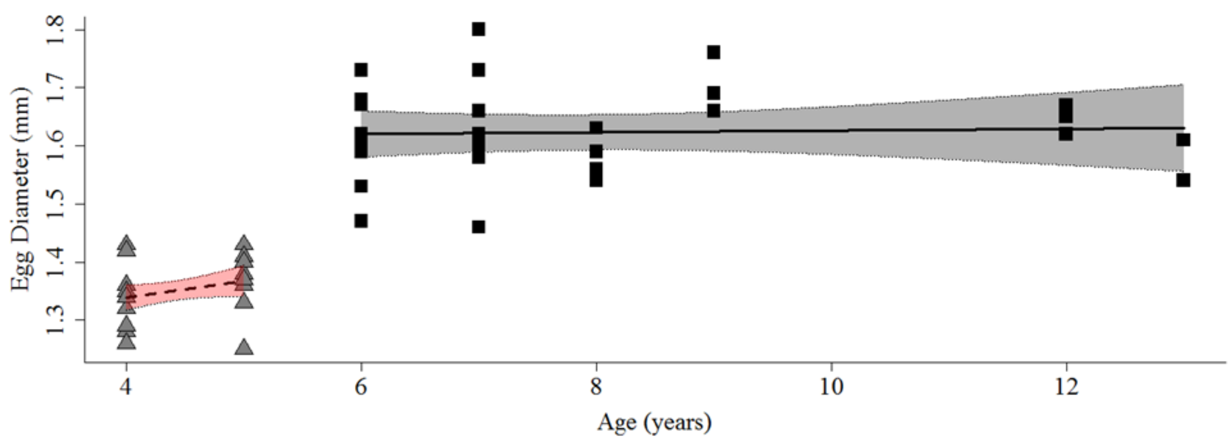

FIGURE 6. Age – average egg diameter relationship, with 95% confidence intervals, for female Red Lakes Walleyes sampled in 1989 (triangles, dashed RL, red CI) and 2017 (circles, solid RL, grey CI).

median fecundity than 2017 because only small fish were present in 1989, while both small and large fish were present in 2017. Although the two slopes (1989 and 2017) are similar, and the confidence intervals partially overlap, the 1989 regression equation predicted higher fecundities than in 2017. Similarly, the 2004 regression equation also overestimated 2017 fecundity; by 12.7%. The average fecundity in 2004 was about 62% higher than the median in 2017, but because the 2004 and 2017 regression lines intersected, the 2004 equation underestimated smaller 2017 fish, thereby bringing total over-estimation of 2017 fecundity downwards. The 2004 regression equation underestimated 1989 fecundity by 31.7% and the 1989 regression equation underestimated 2004 fecundity by 8.9%. This dual underestimation occurred because the 1989 and 2004 slopes intersected each other at the large and small ends of their size distributions, respectively, and hence shared little overlap. The fish sampled in 1989 had higher fecundities than comparably sized fish sampled in 2004, but the fish in 2004 had higher fecundities than predicted by the 1989 regression equation.

Now shifting focus to the age – fecundity relationship, the regression equation for 2017 stands apart from that of 1989 and 2004 which were much more analogous to each other than to 2017 (Figure 3). For a given age, fecundity was higher in 1989 and 2004 than in 2017. The 1989 and 2004 age – fecundity regression equations overestimate 2017 fecundity by 44.9 and 56%, respectively.

Model Development based on Fishery Status

Model selection by AIC resulted in fishery status as a significant predictor of fecundity and egg size, thereby enabling the development of estimation models which incorporate them (Table 2). Fecundity was significantly related to weight, fork length, and age in all three years, therefore fecundity estimation equations allow for the incorporation of one of these three predictor variables in conjunction with fishery status.

Egg diameter was not related to weight, fork length, or age for the two years (1989 and 2017) data were available. Thus, egg diameter estimation equations only integrate “overexploited” and “recovered” fishery statuses (Table 2).

TABLE 2. Results of best supported models from AIC model analysis. Model equations allow for the estimation of fecundity (F) based on fishery status along with a fish’s wet weight in grams (WW_g), fork length in millimeters (FL_mm), or age in years (Age). Equations take into consideration one of three different fishery status scenarios: 1) an “overexploited” fishery with a high harvest rate (characterized by 1989 data), 2) a “recovering” fishery with zero harvest (characterized by 2004 data), and 3) a “recovered” fishery with sustainable harvest (characterized by 2017 data). The egg diameter estimation equation is solely based on fishery status and therefore should only be used for “overexploited” and “recovered” fishery scenarios. To select an overexploited fishery scenario, place zeros where “recovering” or “recovered” appear. To select a recovering fishery scenario, insert a 1 where “recovering” appears and zeros where “recovered” appears. To select a recovered fishery scenario, insert a 1 where “recovered” appears and a zero where “recovering” appears.

Model	Model Equation	R^2	RMSE	AIC
F = WW_g * Fishery Status	F = 1460.27 + 56.1 · (WWg) - 24,696.11 · (Recovering) + 2098.65 · (Recovered) + 19.90 (WWg) · (Recovering) + 4.58 · (WWg) · (Recovered)	0.95	10,270.6	1932.1
F = FL_mm * Fishery Status	F = -74,645.75 + 292.45 · (FL_mm) – 134,055.21· (Recovering) – 45,712.43 · (Recovered) + 306.15 · (FL_mm) · (Recovering) + 99.31 · (FL_mm) · (Recovered)	0.95	10,788.4	1940.9
F = Age* Fishery Status	F = -26,474 + 15,288 · (Age) – 14,187 · (Recovering) + 12,697 · (Recovered) + 4,952 · (Age) · (Recovering) – 6,760 · (Age) · (Recovered)	0.78	26,543.8	2044.8
Egg Diameter = Fishery Status	Egg Diameter = 1.35 + 0.27 · (Recovered)	0.83	0.06240	-156.44

Discussion

Changes in Fecundity

Female Walleye fecundity was lower in 2017 (recovered fishery) than in 2004 (recovering fishery) and 1989 (overexploited fishery) in the Red Lakes, which is similar to the findings of other studies. Muth and Ickes (1993) found that Walleye fecundity was significantly higher prior to stock rehabilitation than after. Increases of fecundity after exploitation has also been reported for Lake Whitefish *Coregonus clupeaformis* and Lake Trout *Salvelinus namaycush* (Healey 1978). Baccante and Reid (1988) experimentally exploited two lakes in Canada and reported significantly higher Walleye fecundity levels after the initialization of exploitation and concluded –much as the same as others (e.g. Serns 1982; Lester et al. 2014) – that exploitation reduces population density, thereby improving feeding conditions for the remaining fish which can then allocate more energy towards reproductive investments. This negative relationship between population density and fecundity has also been found for other species, e.g. Orange Roughy *Hoplostethus atlanticus* (Bowen et. al. 1991) and Cisco *Coregonus artedi*, (Koslow et. al. 1995). It is thought that this density dependent response to increase fecundity can serve as a natural compensatory mechanism to increase population size and avoid local extinction (Rose et al. 1999).

In the current study, these exploitation – driven changes in Walleye density seem to be the main cause for fecundity variance between the three fishery status periods. In fall of 2016 and 2003 the estimated abundances of age 3 + Walleyes was 6,583,166 and 3,815,935, respectively (MNDNR, Unpublished Data); fall abundances of the year prior to the sampling year are reported here because Walleyes develop eggs during late summer/fall preceding the spring spawn. Abundance estimates for the Red Lakes are not available for the late 1980's, but experimental gill-netting performed during this period suggest that Walleye abundances in 1988 were precariously close to the threshold of total collapse, which happened just a few years thereafter (Ostazeski and Spangler 2001). Also, significant increased growth associated with exploitation usually occurs only after large declines in population size but before the advent of population collapse; increased growth in Red Lakes Walleyes did not occur until the late 1980's (Ostazeski and Spangler 2001; Gangl and Pereira 2003). For these reasons it is therefore reasonable to assume that Walleye abundances in and around 1988 were substantially lower than in 2016 or 2003. It is likely, therefore, that fish sampled in 2017 had the lowest fecundity because of higher adult intraspecific competition than in the overexploited and recovering fishery scenarios.

Fecundity trends also differed between the "overexploited" and "recovering" fishery status scenarios, again likely due to a discrepancy in population density but also the age and size structure of the Walleye population at each time period. Higher exploitation commonly results in a decrease of age at maturity and increases in growth rate (Spangler et al. 1977; Gangl and Pereira 2003; Schmalz et al. 2011; Schueller et al. 2005). An exemplification of this phenomenon, fish that participated in the 1989 spawn were exclusively young fish (4 – 5 yr), but fish in 2004 had a much broader age range (5 – 12 yr). In exploited systems the largest and oldest fish are preferentially targeted (Shelton et al. 2012). This selective removal of large and old individuals is why fish were all young in the 1989 spawn. When the Red Lakes Walleye fishery was allowed to recover under a fishing moratorium, such selective pressure against large fish disappeared and the age distribution present in the spawn adjusted accordingly to include older fish. In this manner, it is probable that the 1989 weight/length – fecundity regression equations predicts higher fecundities for small fish than the 2004 regression equation because the relatively small Walleyes present in the late 1980's did not have to compete for resources with many large Walleyes, allowing them to attain more resources for growth and gonad development than similarly sized fish in 2004. A possible explanation of the 1989 regression equation's underestimate of fecundity for large fish in 2004 is that the limited and relatively homogeneous size range present in the 1989 spawn resulted in a slightly flatter slope than 2004, which had much greater size variation and thus a more positive slope.

Although evidence is strong that these changes in fecundity are a result of a density dependent, exploitation–driven response, it is possible that other factors have led to this outcome. For example, Walleye and other fishes' fecundity are quite variable and are dependent on food abundances and community structure (Nikolski 1965; Colby et al. 1979). In the current study we have maintained that changes in exploitation are the root cause of these basal modifiers of fecundity, but other unknown factors may exist. Also, these apparent changes in fecundity are based on just three different sampling events in nearly 28 years, and therefore would need to be confirmed by other similar studies.

Change in Egg Size

Walleye eggs were significantly larger in the "recovered" than the "overexploited" fishery scenario. Red Lakes Walleye egg size and fish size were not related in 2017, a finding consistent with Bushong (1990). Most research suggests that offspring from larger eggs have larger gapes, better feeding success, faster growth, greater resistance to starvation, and lower mortality rates (Reviewed by Johnston 1997). In 2017, Walleye abundance was much higher than in 1989. Therefore, it would be reasonable to assume that in the "recovered" fishery scenario, Walleye fry experience more competition for food resources just like their adult counterparts. Larger eggs would assumedly grant a better chance of survival in a system with higher intraspecific competition and lower available food sources. As an interesting side note, preliminary zooplankton abundance survey work in Lower Red Lake in 2017 has yielded unusually low counts of zooplankton (Heidi Rantala, Personal Communication). Larger eggs in 2017 could therefore be a compensatory adaption to decreased levels of zooplankton, a generally known fish larvae food source. However, further investigation is necessary to better understand this increase in egg size after recovery of the Red Lakes Walleye fishery. Such future research should focus on confirming this size difference by sampling multiple spawning as well as analyzing within-population variability of egg characteristics such as size and general egg quality.

Prediction Models Based on Fishery Status

With the development of fecundity and egg diameter estimation models, managers can be better equipped to estimate these important elements of recruitment. Being that fecundity and egg size appear to have changed between the overexploited, recovering, and recovered fishery status scenarios in the Red Lakes, accurate estimation would necessitate a model that accounts for this significant variability. Instead of depending upon generic models, managers can choose the specific fishery status scenario that most closely matches the context of their circumstances and needs. Although not universally applicable, these models allow for a degree of selectivity that is rare in the literature.

In conclusion, this study suggests that Red Lakes Walleye fecundity characteristics and egg sizes have changed over time in response to changing exploitation rates and consequent related fish density responses. Future changes in the Red Lakes Walleye population and/or exploitation rates can therefore be expected to also influence fecundity and egg size, thus having potentially significant impacts on future management decisions.

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