Notes

Comparisons of Walleye Fecundity Before, During, and After Rehabilitation of the Red Lakes Fishery

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Abstract

The Red Lakes, Minnesota supported a substantial Walleye *Sander vitreus* fishery from the early to mid-20th century but experienced a major crash in the late 1990s. The population has since rebounded after a successful interagency recovery program and now supports valuable commercial and recreational fisheries. The variation in population densities associated with the collapse and subsequent recovery in the Red Lakes Walleye population provides a rare opportunity to study potential changes in relative fecundity (eggs/kg of body mass) under varying rates of exploitation: overexploited (1989 data), recovering (2004 data), and recovered (2017 data). We collected female Walleye in spring of 1989 ($n = 30$) from the Blackduck and Tamarac rivers and in spring of 2004 ($n = 30$) and 2017 ($n = 30$) from the Tamarac River. Results indicate that relative fecundity was significantly lower in 2017 (50,768, SD = 10,266) than in 1989 (58,216, SD = 6,211) and 2004 (61,964, SD = 7,472). We hypothesize that differences in relative fecundity among fishery states were due to differences in Walleye population abundances caused by varying exploitation rates in the years leading up to fecundity estimates.

Keywords: Walleye; fecundity; exploitation

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Introduction

Throughout much of the species' range, Walleye *Sander vitreus* support mixed recreational, commercial, and subsistence fisheries that are both economically and culturally important (Schmalz et al. 2011). Historically, numerous fisheries collapsed because of combinations of overexploitation, invasive species, and ecosystem change (Spencer et al. 2002; Garner et al. 2013; Blackwell et al. 2019; Cahill et al. 2022). Recovery efforts have been largely successful in many cases (Muth and Wolfert 1986; Hatch et al. 1987), and current management strategies typically involve harvest quotas allocated to different user groups to prevent future population collapses (STC 2007; Hansen et al. 2015). In Minnesota's large inland lakes, annual survey data collected through the Large Lake Monitoring Program (Wingate and Schupp 1985) are used as inputs to generate adult Walleye population estimates, which are then used to set harvest quotas for each system (MNDNR 1997, 2022; Radomski 2003).

The Red Lakes, Minnesota support valuable commercial and recreational fisheries for Walleye. Jurisdiction of the lakes is split between the Red Lake Band of Chippewa (Band) and the State of Minnesota (State), approximately 80% and 20% of the surface area of the Red Lakes, respectively. A commercial fishery was established in 1917 on the Red Lakes in response to economic conditions and high meat prices during World War I (Van Oosten and Deason 1957). The commercial Walleye catch declined sharply and became highly variable beginning in the early 1970s (Pereira et al. 1992), and ultimately collapsed in the late 1990s because of continued overexploitation (RLFTC 2015). An ambitious interagency effort commenced to recover the Red Lakes Walleye population. Commercial fishing was closed in 1997, and recreational harvest was restricted by both the State and the Band in 1998. In 1999, a moratorium on all Walleye fishing was imposed for the entire Red Lakes (Barnard et al. 2019). Recovery-level stocking events occurred in 1999 (approximately 41 million), 2001 (32 million), and 2003 (33 million) using Walleye fry produced from eggs obtained from a Lake Vermilion tributary (Logsdon 2006), where the population was genetically similar to that of the Red Lakes (Minnesota Department of Natural Resources [MNDNR], unpublished data). Recovery efforts were successful, and in response to an increasing Walleye population in the Red Lakes, the Walleye fishing moratorium was lifted in 2006. The Red Lakes Walleye fishery is now fully recovered, with a population sustained solely by natural recruitment and abundance estimates of nearly 6 million age-2 and older Walleye (Brown and Kennedy 2020).

The dynamic history of the Red Lakes Walleye fishery provides a rare opportunity to investigate exploitation-related influences on the population over time. Fecundity is an integral aspect of reproductive potential and is important when considering the management of fish populations (Ricker 1975; Koslow 1992). Although fecundity does not provide an estimate of reproductive success, it does allow managers to quantify reproductive potential (Moyle and Cech 2004) by estimating the number of eggs within a female before spawning. Fecundity estimates are useful to calculate egg and fry survival rates, which can be incorporated into stock recruitment models (Wright and Shoesmith 1988). Additionally, relative fecundity (number of eggs per unit of total fish mass) can be used to compare reproductive potential of varying size classes within populations (Kipling and Frost 1969), as well as among populations with dissimilar population characteristics (e.g., size structure; Kennedy et al. 2006). Therefore, to better manage Walleye populations, it would be helpful to understand how Walleye fecundity varies relative to changes in exploitation in the Red Lakes.

To our knowledge, fecundity data for Red Lakes Walleye have been published only once in the past, in 1989 (Bushong 1990, re-presented here with permission) when the population was in an overexploited state. Walleye fecundity has been shown to increase in response to increased exploitation (Baccante and Reid 1988) and decrease as exploitation declines (Muth and Ickes 1993); however, data available in all three exploitation states in the Red Lakes provide a rare opportunity to track fecundity through an entire crash–recovery cycle. The objective of this study was to determine the effects of three different fishery states (overexploited, recovering, and recovered) on relative fecundity of Red Lakes Walleye. We hypothesize that changes in exploitation led to density-dependent changes in relative fecundity within Red Lakes Walleye over the time periods sampled.

Study Site

The Red Lakes in northern Minnesota (Figure 1) have a total surface area of 115,038 ha, divided into two distinct basins separated by a navigable channel. Movement of tagged Walleye between the basins has been documented (Smith et al. 1952), indicating a homogeneous population. Walleye spawning occurs at shoreline sites within both basins and in several streams that flow into the Red Lakes. Two of the largest streams, the Tamarac and Blackduck rivers, have historically been used as egg sources for state and tribal hatcheries, as well as study sites for several previous studies (e.g., Smith et al. 1952; Smith and Pycha 1961; Logsdon et al. 2016, Graham et al. 2017). The Tamarac River (48°9′N, 94°30′W) is the largest tributary of Upper Red Lake (Groshens 2000) and is thought to be the most important stream in the Red Lakes for Walleye spawning migrations (Graham et al. 2017). The Blackduck River (47°53′N, 94°46′W) flows into the southeast corner of Lower Red Lake and is used as an egg source for tribal hatchery operations. Walleye for this study were collected in 1989, 2004, and 2017 in the Tamarac River and in 1989 in the Blackduck River.

Methods

1989 sampling

A University of Minnesota graduate student collected 30 female Walleye in late April near the mouth of the Blackduck and Tamarac rivers using spawning impoundment nets as described in Bushong (1990). They included only females that had not yet spawned ("green"), and they distributed sizes to include 10 fish from each of three size categories through the range of females present on the basis of fork length (<380 mm, 380–410 mm, >410 mm) to ensure representative sampling. They recorded total length (TL, nearest mm) and total mass (nearest g) for each included fish. They estimated ages independently using scales, dorsal spines, opercles, and otoliths. They assigned final ages by comparing ages from each structure and re-examining all structures. They dissected ovaries and weighed them whole to the nearest 0.01 g. They removed two subsamples (1 to 2 cm thick, 5.50 to 12.30 g) approximately one-third of the distance from each end of one randomly selected ovary per fish, and they weighed sections to the nearest 0.01 g. They preserved subsamples in Gilson's fluid (Nielsen and Johnson 1983). They counted the number of eggs in each subsample to determine the number of eggs per gram of ovarian tissue, which they then used to estimate the total number of eggs per female.

2004 sampling

Minnesota Department of Natural Resources staff collected 30 green female Walleye in April of 2004 from the

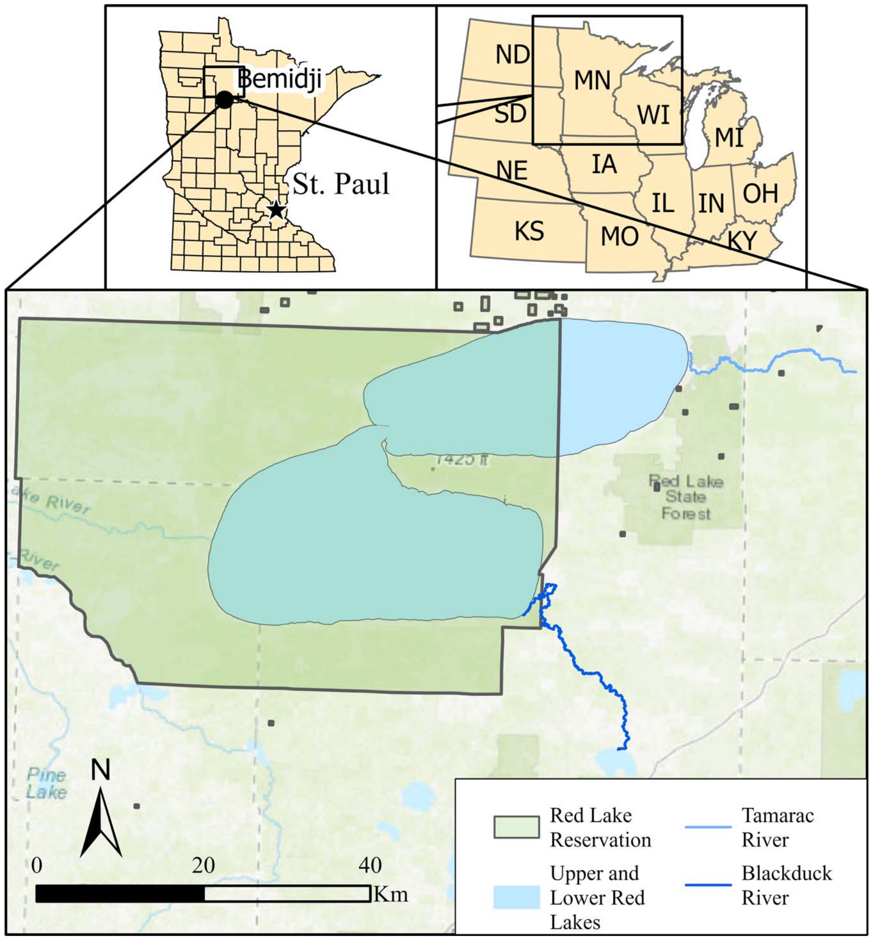

Figure 1. Map indicating the locations of the Upper and Lower Red Lakes, the Tamarac River, the Blackduck River, and the Red Lake Reservation within Minnesota. We collected female Walleye *Sander vitreus* that had not yet spawned in or near the Blackduck River (1989) and the Tamarac River (1989, 2004, 2017) and removed ovaries to estimate fecundity.

Tamarac River using a Smith–Root SR18 electrofishing boat. They included 10 fish from each of three size categories through the range of females present (<550 mm, 550–622 mm, >622 mm TL) to ensure representative sampling. They measured TL (nearest mm) and total mass (nearest g) and placed fish into individually labeled plastic bags (in case of postmortem egg expression). They put fish on ice and temporarily froze them for up to 2 d.

After thawing at room temperature, they dissected ovaries from each fish and weighed them whole (nearest 0.01 g). They estimated fecundity by removing three 1.0-g subsamples from the anterior, middle, and posterior thirds of the ovary and counting the eggs in each subsample. They then multiplied the mean of the subsample counts by the total mass of the ovary. They also removed sagittal otoliths from each fish for age estimation. They mounted otoliths following the methods of Hu and Todd (1981) and the otoliths were independently aged by three people. They assigned agreed ages to each fish.

2017 sampling

We collected 30 female Walleye from the Tamarac River over 2 consecutive days during April 2017 using Fyke nets. We selected 10 green females in each of three size categories through the range of females present (<426 mm, 426–473 mm, >473 mm TL) to ensure representative sampling. We measured fork lengths (nearest mm) and total mass (nearest g), and converted fork lengths to TL using the equation TL = fork length × 1.05 (P. Brown, Red Lake DNR, personal communication). We froze, processed, and aged the fish following the same methods as in 2004. We excluded one individual from age analysis because of the inability of readers to reach an agreed age. Likewise, we estimated fecundity following the same methods as in 2004.

Data analysis

All data are available in supplementary file Data S1. Because of differences in size and age distributions of Walleye among years, we used relative fecundity (eggs/kg of body mass) for all analyses. We tested relative fecundity data for normality using the Shapiro–Wilk test (Shapiro and Wilk 1965) and for homogeneity of variances using the Bartlett test (Bartlett 1937). Because variances among years were not equal, we used a one-way analysis of means not assuming equal variances (Welch 1951) to test for significant differences in relative fecundity among years (i.e.,

Table 1. Sample size (*N*) and mean (SDs in parentheses) total length, mass, age, fecundity (estimated eggs/fish), and relative fecundity (eggs/kg) for female Walleye *Sander vitreus* from the Red Lakes in years 1989, 2004, and 2017.

Variable	1989 Overexploited	2004 Recovering	2017 Recovered
N	30	30	30
Total length (mm)	421 (29)	581 (64)	466 (62)
Mass (g)	701 (152)	1,848 (628)	1,051 (457)
Age (y)	4.4 (0.5)	7.8 (1.8)	7.9 (2.3)
Fecundity	40,793 (9,521)	117,213 (49,186)	53,491 (26,865)
Relative fecundity	58,216 (6,211)	61,964 (7,472)	50,768 (10,266)

population status). In cases of significant differences in one-way results, we used Dunnett's modified Tukey–Kramer pairwise multiple comparison as a post hoc test (Dunnett 1980). Finally, we investigated relationships between relative fecundity and TL, mass, and age using linear regression. Sampling year was included in models as an additive or interactive variable to account for changes within the population related to exploitation. Models were evaluated using Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson 2002), with the lowest score representing the model best supported by the data. All statistical analyses were performed using R 3.5.2 (R Core Team 2022).

Results

Walleye collected in 1989 were substantially smaller and younger than those collected in 2004 and 2017 (Table 1). Walleye collected in 2004 were larger than those collected in 2017, but average age was similar between the two years. Relative fecundity data were normally distributed in all years (1989: $W = 0.97$, $P = 0.42$; 2004: $W = 0.99$, $P = 0.94$; 2017: $W = 0.98$, $P = 0.76$), though variances were significantly different among years (Bartlett's *K*-squared = 7.53, $df = 2$, $P = 0.02$). Relative fecundity was significantly different among years (Figure 2, one-way test: $F_{2,56} = 11.53$, $P < 0.0001$). Dunnett's multiple comparison test indicated that mean relative fecundity was significantly lower in 2017 (50,768 eggs/kg) than in 1989 (58,216 eggs/kg; difference = −7,448, 95% confidence interval = −12,859 to −2,038) or in 2004 (61,694 eggs/kg; difference = −11,197, 95% confidence interval = −16,922 to −5,471). However, relative fecundity was not significantly different between 1989 and 2004 (difference = 3748, 95% confidence interval = −633 to 8,129). Linear regressions for all response variables were better supported by the data when sampling year was included as an additive variable (Table 2). Relative fecundity of Red Lakes Walleye among years was positively correlated with mass ($r^2 = 0.12$, $F_{1,88} = 12.11$, $P = 0.0008$) and TL ($r^2 = 0.11$, $F_{1,88} = 10.73$, $P = 0.0015$). However, age was not significantly correlated with relative fecundity ($r^2 = 0.006$, $F_{1,87} = 0.54$, $P = 0.4643$, Figure 3). However, significant correlations were largely driven by fish collected in 2004, as no within-year relationships were significant for 1989 or 2017 data (Table 3).

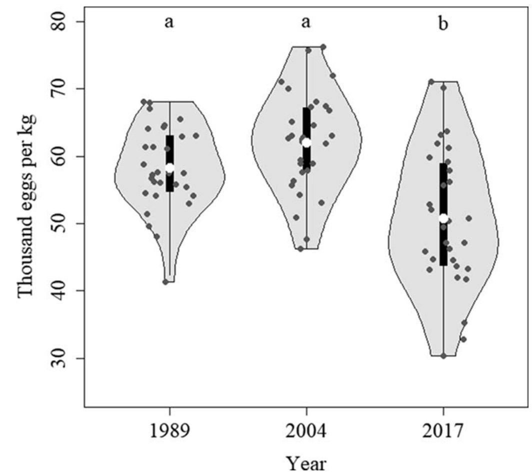

Figure 2. Violin plot of female Walleye *Sander vitreus* relative fecundity (thousand eggs/kg body mass) in 1989, 2004, and 2017 from the Red Lakes, Minnesota. Different letters indicate significant differences (one-way test, $P < 0.0001$). Gray points represent individual observations, white points represent annual means, and thick black bars represent interquartile ranges. Violin shapes represent the distribution shape of the data such that wider sections have a higher probability of representing members of the population.

Discussion

Relative fecundity of female Walleye in the Red Lakes was significantly lower after recovery of the fishery (2017) than in 1989 (overexploited fishery) and 2004 (recovering fishery). Although previous studies have observed variable fecundity rates in the absence of extreme exploitation (Bagenal 1957; Nikolskii 1965; Colby et al. 1979; Schueller et al. 2005), others indicate that Walleye fecundity is sensitive to changes in

Table 2. Candidate models relating relative fecundity (*F*) to fish mass (g), total length (mm), and age, with year included additively or interactively. Best supported models were selected using Akaike's information criterion corrected for small sample size (AICc) and ΔAIC_c scores. Models were considered better supported by the data if $\Delta AIC_c > 2$. If $\Delta AIC_c < 2$, the simplest model was considered better supported by the data. Models were developed using female Walleye *Sander vitreus* collected from the Red Lakes, Minnesota before spawning in spring of 1989, 2004, and 2017.

Model	AIC_c	ΔAIC_c
F = mass + year	634.61	0
F = mass × year	636.15	1.55
F = mass	651.01	16.40
F = 1	660.48	25.87
F = length + year	636.89	0
F = length × year	637.60	0.71
F = length	652.26	15.37
F = 1	660.48	23.58
F = age + year	628.21	0
F = age × year	632.34	4.13
F = age	655.76	27.55
F = 1	660.48	32.27

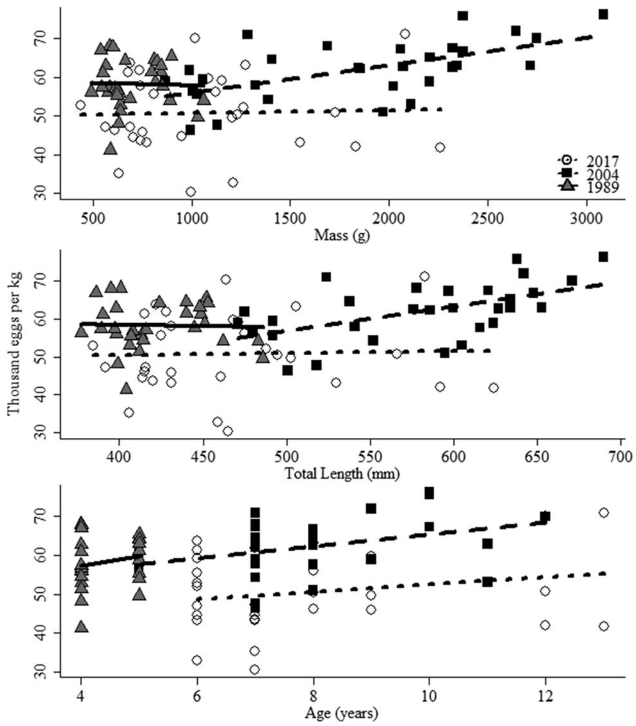

Figure 3. Linear relationships of mass, total length, and age with relative fecundity (thousand eggs/kg of body mass) for female Red Lakes Walleye *Sander vitreus* sampled in 1989 (triangles, solid line), 2004 (squares, dashed line), and 2017 (circles, dotted line). Overall relationships were significant for mass ($P < 0.001$) and total length ($P = 0.002$) but not for age ($P = 0.46$). Detailed regression statistics presented in Table 3.

exploitation. Baccante and Reid (1988) found that Walleye relative fecundity increased significantly in two Ontario lakes that were experimentally exploited over a 5-y period. Under exploitation rates of 12–16%, relative fecundity of female Walleye increased by 24%, from 39,700 eggs/kg to 49,300 eggs/kg, whereas exploitation rates of 25–65% led to a 34% increase, from 41,300 eggs/kg to 55,400 eggs/kg. Additionally, Muth and Ickes (1993) found that Walleye fecundity in Lake Erie decreased by 25% after the rehabilitation of the population. Baccante and Colby (1996) reported relative fecundity for Walleye populations from 36 water bodies throughout North America. Relative fecundity ranged from 29,700 to 87,397 eggs/kg throughout the range, whereas angling exploitation rates, which were available for 15 of these water bodies, ranged from 4 to 55.6% per year. Data were presented from four Minnesota populations and relative fecundity ranged from 45,298 to 73,700 eggs/kg at exploitation rates of 11–34% per year. Our relative fecundity observations (range 50,768–61,964 eggs/kg) for Red Lakes Walleye were within the range reported for Minnesota lakes, whereas the observed 17% decrease in relative fecundity after recovery efforts (2017) is consistent with findings from Lake Erie as reported by Muth and Ickes (1993).

Relative fecundity has also been shown to increase through periods of exploitation and decrease after population recovery in Atlantic Cod *Gadus morhua* populations (Stares et al. 2007). Fecundity of other commercially harvested species, such as Lake Whitefish *Coregonus clupeaformis* and Lake Trout *Salvelinus namaycush*, was more variable in exploited than unexploited populations, and fecundity for both species generally increased as high levels of exploitation continued (Healey 1978). Although no direct correlation with exploitation is presented, an inverse relationship between relative fecundity and population density has also been shown in White Crappie *Pomoxis annularis* (Mathur and McCreight 1979), Northern Pike *Esox lucius* (Kipling and Frost 1969), and Common Carp *Cyprinus carpio* (Weber and Brown 2012). High levels of commercial and recreational harvest could have had similar effects in the Red Lakes. Over 7 million pounds of Walleye were harvested from the Red Lakes from 1982 to 1997, and actual harvest was deemed by fishery managers to have been at least twice that amount because of the magnitude of illegal harvest occurring during that period (Barnard et al. 2019). Concurrently, experimental gill-net catch per unit effort dropped from approximately 25 fish/net in 1987 to less than 1 fish/net in 1997 (Ostazeski and Spangler 2001). Before the Walleye harvest moratorium (1995–1998), annual mortality in the Red Lakes averaged 70.0%, peaking as high as 87.5% in 1994 (MNDNR, unpublished data). Throughout the closure of the fishery (1999–2005), annual mortality averaged 39.1%, and that rate has remained relatively stable since the fishery reopened (35.6%, 2006–2019; MNDNR, unpublished data). Although these mortality estimates do not directly measure exploitation on the Walleye population, they do indicate that exploitation was a major contributor to overall mortality rates before the closure, providing further evidence that high exploitation likely led to density-dependent changes in relative fecundity within Red Lakes Walleye.

Table 3. Degrees of freedom, *F* statistic, *P* value, and adjusted R^2 for linear models relating relative fecundity (*F*) to fish mass (g), total length (mm), and age of female Walleye *Sander vitreus* in 1989, 2004, and 2017 from the Red Lakes, Minnesota. Significant relationships ($P < 0.05$) indicated by an asterisk (*).

Response variable	Year	Degrees of freedom	*F* statistic	*P* value	Adjusted R^2
Mass	All	1,88	12.11	<0.001*	0.11
	1989	1,28	0.02	0.88	−0.03
	2004	1,28	15.36	<0.001*	0.33
	2017	1,28	0.03	0.86	−0.03
Total length	All	1,88	10.73	0.002*	0.10
	1989	1,28	0.03	0.87	−0.03
	2004	1,28	12.10	0.002*	0.28
	2017	1,28	0.03	0.86	−0.03
Age	All	1,87	0.54	0.46	−0.005
	1989	1,28	1.14	0.29	0.005
	2004	1,28	4.51	0.04*	0.11
	2017	1,27	1.26	0.27	0.009

Baccante and Reid (1988) experimentally exploited two Walleye populations in Canada and reported significantly higher fecundity after initiating exploitation. They concluded, much 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 and enabling them to allocate more energy toward reproductive investments. Similarly, Orange Roughy *Hoplostethus atlanticus*

(Koslow et al. 1995) and Cisco *Coregonus artedi* (Bowen et al. 1991) displayed inverse relationships between population density and fecundity. This inverse relationship likely indicates a density-dependent response to increased exploitation, thus serving as a natural compensatory mechanism to increase population size and therefore avoid local extinction (Rose et al. 1999).

Data from the current study indicate that variation in Walleye fecundity may be related to the different levels of exploitation. Adult abundance estimates for the entire Red Lakes are not available for autumn of 1988, but abundance of age-3 and older Walleye in the Red Lakes was estimated at 3,815,935 in autumn 2003 and 6,583,166 in autumn 2016 (MNDNR, unpublished data). For comparison, adult Walleye abundance estimates for the upper basin of the Red Lakes were 2,037,033 in 1988, 2,581,384 in 2003, and 2,985,576 in 2016 (MNDNR, unpublished data). These population estimates, calculated from gill-net catch per unit effort in annual surveys using selectivity models (Anderson 1998), indicate substantial changes in population levels in years leading up to fecundity estimates. Furthermore, significantly increased growth associated with exploitation often occurs only after large declines in population size but before total population collapse (Spangler et al. 1977; Schmalz et al. 2011); increased growth in Red Lakes Walleye did not occur until the late 1980s (Cyterski and Spangler 1996; Ostazeski and Spangler 2001; Gangl and Pereira 2003). For these reasons, it is reasonable to assume that Walleye abundances throughout the Red Lakes were substantially lower in 1988 than in 2003 or 2016. It is likely, therefore, that fish sampled in 2017 experienced higher adult intraspecific competition, which could explain the decrease in relative fecundity once the population recovered.

Relative fecundity of Red Lakes Walleye tended to increase with increasing length, mass, and age across years. Although the correlations were quite weak ($r^2 \leq 0.12$), the relationships between relative fecundity and both TL and mass were significant. However, within-year relationships were only significant in 2004 and correlations were inconsistent across years (Figure 2). Using a different measure of relative reproductive potential (relative clutch mass; mature ovary mass divided by total body mass), Henderson and Nepszy (1994) observed no such correlation in Lake Erie despite significant correlations between total fecundity and ovary and total body mass individually. Likewise, Serns (1982) reported significant relationships between total fecundity and length, weight, and age of Walleye in Escanaba Lake, Wisconsin, although no relative fecundity data were presented. As was the case for Lake Erie and Escanaba Lake, Walleye in the Red Lakes were subject to some level of exploitation in all years except 2004, the only instance where relative fecundity and Walleye size were significantly correlated. This suggests that changes in relative fecundity in response to extreme, high or low, exploitation rates may follow a similar pattern to changes in growth rates, which often lag behind changes in population density until densities are substantially different (Spangler et al. 1977; Schmalz et al. 2011). This result provides further evidence that changes in relative fecundity (along with other population dynamics) were likely more influenced by the recovery (i.e., increased abundance levels triggering density-dependent responses) of the Red Lakes Walleye fishery.

Although the data indicate that changes in Walleye fecundity are related to variations in exploitation and resulting density-dependent effects, it is possible that other factors contributed to this outcome as well. One possible explanation is that the available forage was different across years. Ritchie and Colby (1988) indicated that variation in mayfly *Hexagenia limbata* production in alternating years may have contributed to annual variation in Walleye fecundity observed by Baccante and Reid (1988). Additionally, there may be a genetic influence on the changes in fecundity in Red Lakes Walleye. Logsdon and Anderson (2018) found that Walleye fecundity varied among four Minnesota lakes, and that fecundity within each lake varied annually over a 5-y span. Their analysis included fish captured at the Pike River spawning station on Lake Vermilion, the same station that contributed eggs for fry stocking during the Red Lakes recovery from 1999 to 2003 (Logsdon et al. 2016). Mean relative fecundity estimates from Lake Vermilion ranged from 67,673 to 74,960 eggs/kg in fall gill nets, whereas average relative fecundity measured during the spawning run was 62,469 eggs/kg in 2011 (Logsdon and Anderson 2018). However, because the reported values were greater than the range observed for this study (50,768–61,694 eggs/kg), genetic factors were likely not a leading cause of changes in fecundity in Red Lakes Walleye. Finally, normal annual variation cannot be discounted as a potential cause of observed changes in relative fecundity. Logsdon and Anderson (2018) reported relative fecundity rates in four Minnesota lakes over a 5-y period. In this time frame, variation in relative fecundity within the lakes ranged from 4.8% to 21.1%, beyond the 17.7% variation observed over nearly 30 y in the Red Lakes. However, fecundity was only measured once in each Red Lake fishery status (overexploited, recovering, recovered), making comparisons of annual variation within each status impossible. That said, Walleye management in the lakes included in Logsdon and Anderson (2018) is vastly different from the Red Lakes. Walleye populations within the Red Lakes have been sustained through natural reproduction since the last recovery stocking in 2004 (Logsdon 2006; Logsdon et al. 2016), whereas lakes included in Logsdon and Anderson (2018) serve as source lakes for Walleye stocking operations throughout Minnesota and, in turn, receive annual "put-back" stockings that can lead to fry densities more than double the density observed during the Red Lakes recovery (1,606 fry/littoral ha; Logsdon et al. 2016). Potential density-dependent effects, including decreased age-0 growth and survival to age-2, were acknowledged by the authors, whereas another study observed that age-0 growth increased with distance from the stocking site in another chain of lakes serving as an egg source (Amundson 2021). Both studies also documented high contributions of stocked fish to the adult populations within the study lakes. Therefore, it is possible that annual variation in Walleye fecundity reported by Logsdon and Anderson (2018) is artificially elevated through density-dependent effects of high stocking rates, which could indicate that changes observed in the Red Lakes were influenced by exploitation and subsequent density-dependent changes to fecundity rather than annual variation.

This study suggests that Red Lakes Walleye fecundity has changed over time in response to changing fishery status, likely due to varying exploitation rates and related density-dependent responses. Future changes in the Red Lakes Walleye population and related fishery can therefore be expected to also influence fecundity, thus having potentially significant impacts on future management decisions. Furthermore, model selection techniques applied in this study provide a framework for approximating relative fecundity on the basis of exploitation rates (i.e., closed harvest, moderate exploitation, or overexploitation). As reproductive potential of female Walleye is correlated with recruitment (Serns 1982; Shaw et al. 2018), managers could have advanced notice of potentially strong or weak year classes. This information would be especially useful to resource managers using adult population estimates to set harvest quotas (MNDNR 1997, 2022; Radomski 2003; STC 2007; Hansen et al. 2015), as adaptive management strategies could be used to reduce potential population imbalances.

Supplemental Material

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Data S1. Group (year), fork length (mm), total length (mm), mass (g), fecundity (total number of eggs), age, eggs/kg of body mass, and relative fecundity (thousand eggs/kg of body mass) for female Walleye *Sander vitreus* that had not yet spawned from the Red Lakes, Minnesota. One Walleye was excluded from age analysis because of an inability of otolith readers to reach an agreed age and therefore is labeled N/A.
Available: https://doi.org/10.3996/JFWM-22-047.S1 (5 KB XLSX)

Reference S1. Brown P, Kennedy AJ. 2020. Red Lakes Walleye management program annual report to the Red Lakes Fisheries Technical Committee, 2019 sampling year. Bemidji: Minnesota Department of Natural Resources, Division of Fish and Wildlife.
Available: https://doi.org/10.3996/JFWM-22-047.S2 (1.358 MB PDF)

Reference S2. Bushong DL. 1990. Fecundity and egg quality in exploited Walleye (*Stizostedion vitreum vitreum*) populations. Master's thesis. St. Paul: University of Minnesota.
Available: https://doi.org/10.3996/JFWM-22-047.S3 (1.840 MB PDF)

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Data Availability Statement

The data set and code analyzed in this study are openly available in the repository "figshare" at https://doi.org/10.6084/m9.figshare.20449911.v3 (Glade 2022).

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