

Mille Lacs Lake Walleye Blue Ribbon Panel Data Review and Recommendations for Future Data Collection and Management

FINAL REPORT

Submitted to

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December 2014

Panel charge and general approach

Early in 2014, the Minnesota Department of Natural Resources (herein DNR) convened this panel to conduct an independent review of the Mille Lacs Lake (herein Mille Lacs) walleye (*Sander vitreus*) fishery. Mille Lacs is a large (54,000 ha) lake in central Minnesota that is popular among walleye anglers and also supports tribal subsistence walleye fisheries. The recent decline in the quality of these fisheries prompted the DNR to impose strict harvest regulations (Table 1), seek out explanations for the decline, and develop solutions. As part of this effort, this panel was tasked with examining the available data, evaluating past harvest policies, identifying those factors that are likely to have contributed most to the decline, and recommending future data collection, research, and management.

The 5-member panel consisted of fishery researchers from Michigan, Minnesota, New York, and Ontario and therefore operated primarily through conference calls and email. The DNR organized the first conference call in March 2014 to outline the panel's responsibilities and provide background information and data. The panel then operated independently of the DNR except to enquire about existing data, request additional data, or informally report on progress. We generally worked as a group to formulate hypotheses to explain the current fishery status, and then evaluated these hypotheses independently or in pairs according to our areas of expertise. We convened approximately once a month to report on progress, discuss results and/or data needs, and plan next steps. This report is a detailed account of our findings and recommendations.

Description of available data

Our findings and recommendations are based on time series of raw and processed data describing 1) walleye population characteristics, 2) potential predators, competitors, and prey, 3) invasive species, 4) zooplankton, and 5) water quality (Table 2). Most of these time series included years when the walleye population was regarded as "healthy" (i.e., 1999 or earlier). Exceptions are time series of invasive species, which began after initial detection of invaders, and zooplankton, forage fish, diets/consumption, and some age-0 and age-1 walleye data, all of which began in 2005 or 2006. Because Mille Lacs cormorant diet data are unavailable, we used data from Leech Lake, MN, as a proxy.

Formulation of hypotheses to explain the current fishery status

We started by agreeing that the decline in Mille Lacs walleye began around 2000 (Figure 1), which corresponded to a period of considerable change for both the walleye fishery and the lake itself. Significant changes to the walleye fishery included the establishment of a joint (recreational and tribal) walleye fishery in 1998, the introduction of harvestable slot limits to the recreational fishery in 1999, and a switch to protected slot limits in 2003 (Table 1). However, these changes in the fishery occurred against a backdrop of lake changes related to water quality, trophic ecology, and invasive species. For example, mean annual temperature in northern Minnesota has increased ~1.5°C since 1980 (Jacobson et al. 2008) and water clarity has increased 1.5-fold since the mid-1990s. Potential walleye competitors and predators [double-crested cormorants (*Phalacrocorax auritus*), northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*)] in Mille Lacs have increased since the mid- to late-1990s, while important walleye prey [e.g., lake cisco (*Coregonus artedii*)] have decreased. Invasive zebra mussels (*Dreissena polymorpha*) and spiny water fleas (*Bythotrephes longimanus*) were first detected in 2005 and 2009, respectively, and zooplankton biomass has been low since 2012.

Four working hypotheses guided our review. These hypotheses were that the declines in Mille Lacs walleye were caused by 1) too few spawners, possibly as a result of overharvest, 2) low egg production and/or survival to first fall, 3) low survival from first to second fall, and 4) low survival from age-1 to fishable ages. Each hypothesis focused on an important component of the walleye life cycle (with some accommodations for data availability) and was likely to result from one or more factors. For example, low survival from first to second fall could be due to starvation or predation. For each hypothesis, we also considered sub-hypotheses. In the previous example (low survival from first to second fall), these hypotheses might be that survival is low due to predation by double-crested cormorants, other fishes, or cannibalistic walleye. We adopted this 'systems approach' as an efficient way to i) identify the part (or parts) of the life cycle that are likely contributing to the decline of Mille Lacs walleye, ii) narrow the list of underlying mechanisms that are ultimately responsible for the decline, and iii) facilitate the formulation of monitoring and research recommendations to the DNR. Narrowing the list is important because walleye abundance results from a complex web of direct, indirect, and interacting mechanisms that can be difficult to untangle without prior information.

Evaluation of hypotheses

In this section, we evaluate hypotheses and sub-hypotheses for identifying the part(s) of the life cycle that is (are) likely contributing to the decline of Mille Lacs walleye. Beside each header is a weighting (in parentheses) that summarizes that hypothesis (or sub-hypothesis) as having a high, medium or low probability of being important.

1. Too few spawners, possibly as a result of overharvest (Low)

There are many examples of fish stocks being so overfished that the remaining population was insufficient to produce strong subsequent year classes (e.g., Healey et al. 1978, Reid and Momot 1985, Walters and Maguire 1996, Hansen 1999). Here, we evaluate the hypothesis that the decline in the Mille Lacs walleye fishery represents such a case, and that this decline in spawning adults resulted from excessive fishing.

We found no evidence that either low spawner abundance or high fishing levels were responsible for the decline in Mille Lacs walleye. For limited spawning stock abundance to be the primary cause for the decline, larger individuals (potential spawners) would need to have declined before a series of weak year classes evolved. In addition, the spawning stock would likely need to have declined to levels where compensatory increases in recruits produced per unit of spawning stock had become minimal and for which any past records of similarly low abundances would have also suggested low recruitment levels. As part of this overarching hypothesis, we considered the following sub-hypotheses:

1.1 Adult biomass became too low to allow strong year classes (Low): Based on results of both a statistical catch-at-age (SCAA) model (Figure 1) and gill net assessments (Figure 2), there is no evidence that adult biomass reached particularly low levels prior to the substantial decline in year class strength. For example, Figure 2 shows both that the occasional very strong year classes seen during the 1970s and 1980s were not seen during the 1990s, but this change occurred 15 years before the decline in the biomass of walleye 356 mm (14") or longer. The moderate year classes produced in the later 1980s and early 1990s were sufficient to maintain biomass of harvestable fish 356 mm (Figures 1 and 2). In addition, during the period when recruitment declined, substantial numbers of age-0 walleye were observed in the fall, which suggest that

spawning stock limitation is not the critical issue. We discuss this pattern in more detail in Hypothesis 2.

1.2. Skewed sex ratio (Low): Based on results of both SCAA and gillnet assessments, there is no evidence that the decline in the Mille Lacs walleye population was due to a skewed sex ratio in the adult population. Skewed sex ratios can limit offspring production, even when adult abundance is high (Waterhouse et al. 2014). Skewed sex ratios can result from harvesting when males and females are separated (e.g., differential migration to or behavior on the spawning grounds; Schneider et al. 2007, Pritt et al. 2013) or from length-based regulations that target one sex more than the other (Fenberg and Roy 2007). The estimated M:F ratio of adult walleye in Mille Lacs has varied consistently between 1.5 and 5.0 over the period 1987-2014 with the exception of two unusually high ratios in 1990 and 1991 (Figure 3). Although it appears that lower ratios were more common after 1995, we suspect that the observed ratios were not skewed sufficiently to explain the decline in recruitment. Further, if skewed sex ratios were a factor limiting offspring production, then we would have predicted low age-0 abundances starting in the mid-1990s and there is no evidence for this (see Hypothesis 2). It should be noted that adult males appear to be more common than adult females because male walleye mature approximately 2 years younger than female walleye and because abundance is higher at younger ages.

1.3. Not enough older or larger adults (Low). We evaluated this sub-hypothesis because there is increasing evidence in walleye (Venturelli et al. 2010) and other fishes (Hixon et al. 2014) that older adults are important to the health of a population, even if younger adults are abundant. However, we found no evidence of a sustained decline in the relative abundance of older or larger adults or the average age of adults. The proportions of adults in gill net assessments that were age 10 or older show no evidence of a sustained decline for the period 1987-2014 (Figure 4). There was some decline in the mid-1990s, but this was followed by a substantial increase that likely reflects both a decline in recruitment to the sampling gear and the protection of older and larger walleye from fishing in later years (see Hypothesis 1.5 below). Data from more recent years show an expanded age composition within the age-10+ category, although this may partially reflect improved aging practices. Given also that walleye growth rates have been stable since about 1990 (Figure 5), we find no evidence that the decline in Mille Lacs walleye is due to a scarcity of old or larger adults.

1.4. Overfishing leading to a decline in spawner abundance (Low). Spawner-per-recruit (SPR) analysis is a method to evaluate mortality rates based on a common standard, regardless of which age-classes are selected for. SPR analysis basically compares the life-time reproductive output of a fish that is captured in the fishery to the life-time reproductive output that is expected for that fish in the absence of fishing. Given that growth and maturity schedules have been fairly constant in Mille Lacs, variation in SPR essentially summarizes the level of fishing mortality. A higher SPR value corresponds to a lower fishing mortality rate. Such methods are widely used in evaluating sustainable fishing rates.

Based on spawner-per-recruit (SPR) analysis by both sexes (SPR was calculated by combining state recreational and tribal fishing mortality), we found that the fishing and total mortality rates experienced by Mille Lacs walleye were not excessive on average or for extended periods of time (Figure 6a). Based on results from other fisheries (see literature review in Bence

et al. 2014), the estimated mortality rates for Mille Lacs walleye, while not especially conservative, should be sustainable unless some other factor is limiting the production of new recruits into the fishery. The SPR values were calculated annually so as to describe long term consequences of sustaining that year's mortality rate indefinitely. The SPR time series does show that the fishing strategy used during 2010 through the start of the 2013 season, which focused on young fish, produced lower SPR values, especially for males. Cohort-based SPR values were also calculated and follow the impact of fishing on individual cohorts over time. These tended to be less variable and reflect actual long-term fishing on a year class, but could only be calculated through the 1997 year class (later year classes were not complete) (Figure 6b). Nevertheless, the 1997 year class was important in the fishery as the recent collapse began, and did not suffer especially high mortality. The positive trends in Figure 6b suggest that the fishing pressure on the later year classes became more conservative.

We also conducted an alternative analysis that calculated a safe fishing mortality rate (F_{safe}). This analysis used Mille Lacs walleye regulations (Table 1), local temperatures, and the expected change in walleye growth following a severe population decline to derive annual estimates of the maximum rate of fishing mortality that a typical walleye population can sustain. F_{safe} is half of this rate and is therefore risk-averse (Lester et al. 2014). In general, actual fishing mortality rates (estimated via SCAA) have been substantially below F_{safe} (Figure 7). What this figure shows, similar to the SPR analysis, is that a typical walleye population should not have collapsed in the face of the fishing rates (and regulations) that occurred on Mille Lacs. This argues that obviously inappropriate levels of fishing were not the root cause of the decline observed in Figure 1. Of course, this decline likely would have been less severe if fishing mortality rates were lower, but to manage in this way would have required advanced knowledge of a recruitment decline (Hypotheses 3 and 4). In addition, the apparently lower levels of recruits to the fishery may indeed call for lower levels of fishing on this population than are typically sustainable on walleye populations.

2. Low egg production and/or survival to first fall (Low)

We found no evidence that the decline in Mille Lacs walleye was due to low egg production or survival to the first fall of life. We were unable to evaluate egg production directly, but note that walleye egg production generally increases with the biomass of adult females, and that the biomass of adult females in Mille Lacs appears to be sufficient to produce strong year classes (Hypothesis 1). Because year-class strength can also depend on fertilization rates, egg quality, hatching success, and the location and timing of spawning, we examined the joint effect of these processes using indices of age-0 walleye abundance in fall. Fall is the earliest period that age-0 abundance indices are available; therefore, we effectively evaluated the hypothesis that the inability of Mille Lacs walleye to produce very strong year classes since 1988 (Figure 2) is due to egg production and/or summer survival.

None of the age-0 abundance indices showed a declining trend in recent years (Figure 8). On the contrary, both the trawl and gill net data (which data back to the 1970s) indicate that some of the highest fall abundances of age-0 walleye have occurred within the last decade. The time series for electrofishing is shorter (since 1991), but also indicates high production of age-0 walleye in the last decade. Therefore, we conclude that Mille Lacs walleye continue to be capable of producing strong age-0 year classes despite declines in adult abundances.

3. Low survival from first to second fall (High)

We found that the survival of age-0 walleye from first to second fall has been relatively low (and declining) since ~2000, and that this may be due to cannibalism by larger walleye in both winter and summer and, more recently, predation by northern pike (winter and summer) and double-crested cormorants (summer only). We used data from fall trawl, gill netting, and electrofishing surveys to calculate the relative survival of age-0 walleye from the first to second fall of life as the ratio age-1 catch-per-unit effort (CPUE) in year $t+1$ to age-0 CPUE in year t . We used fall survey data as a starting point for evaluating age-0 survival because our evaluation of Hypothesis 2 established that Mille Lacs walleye are capable of producing strong age-0 year classes that persist through summer. Ratios based on survey data only provide relative survival estimates because it is not clear how age-0 and age-1 walleye differ in terms of their vulnerability to the gear, or how consistent this vulnerability is over time.

Our evaluation of fall survey data found that the relative survival of age-0 walleye has been highly variable over time, but relatively low (and declining) since ~2000 (Figure 9). Two (gill net and trawl surveys) out of the three survey methods also suggest that age-0 survival has been consistently low since 2005. Given strong evidence that Mille Lacs walleye can still produce strong year classes that persist through summer (Hypothesis 2) and strong evidence the fishery has not experienced a large recruitment event since 1988 (Figure 2), we conclude that low offspring survival between first and second fall is very likely contributing to the decline of walleye in Mille Lacs. Below, we evaluate sub-hypotheses related to low overwinter survival and low summer survival. We evaluate these time periods separately because the potential sources of mortality differ.

3.1 Low overwinter survival (High): The first winter of life is a critical period for walleye survival; smaller individuals can experience relatively low winter survival either because energy reserves are insufficient or because of higher vulnerability to predation or cannibalism (Chevalier 1973, Forney 1974, 1976; but see Pratt and Fox 2002). We evaluated three hypotheses related to over-winter survival.

3.1.1 Age-0 walleye too small (Inconclusive): We found inconclusive evidence that overwinter survival was low for small, age-0 walleye. A 2000-2007 spring electrofishing survey of age-1 walleye conducted by the Great Lakes Indian Fish and Wildlife Commission provided the best opportunity for assessing whether age-0 survival was related to size. We generated length-frequency histograms to compare the lengths of age-1 walleye in the spring of each year to the lengths of age-0 walleye that were captured the previous fall in DNR trawl, gill net, and electrofishing surveys. When comparing length-frequency histograms based only on electrofishing data, we found no evidence of size truncation between periods (Figure 10). However, when we included age-0 data from fall trawl and gill net surveys, there was some evidence that overwinter survival was low for smaller individuals (Figure 11). Specifically, spring age-1 walleye tend to be larger than fall age-0 walleye in most years, which suggests that smaller individuals were experiencing higher mortalities than larger conspecifics. Alternatively, this difference could result from intervening growth or an electrofishing bias for larger individuals. Unfortunately, both winter growth rates in Mille Lacs and the fate of the smaller individuals collected by fall trawling and gill netting are unknown. Given also that we have no baseline estimate of age-0 winter survival against which to compare, we find that the evidence for low overwinter survival among small, age-0 walleye is inconclusive.

3.1.2 Low energy reserves heading into winter (Low): Weight data did not support the hypothesis that age-0 walleye have low energy reserves heading into winter. The absence of weight data in spring prevented us from testing the hypothesis that overwinter survival was low for small, age-0 walleye by comparing spring weights to fall weights. Therefore, to investigate this sub-hypothesis, we examined available data to assess whether there have been recent changes in commonly used indices of condition (i.e., weight at age, Fulton's condition factor). We calculated mean weight and Fulton's condition factor for age-0 walleye captured in fall trawl, gill net, and electrofishing surveys for the period 1994-2013. Although both mean weight and Fulton's condition factor varied annually and among years and gear types, there was no evidence of a decline in recent years (Figure 12). We also analyzed age-0 walleye by size groups [95.25-184.15 mm (3.75-7.25") in 12.70 mm (0.5") increments] and found no evidence of a decline in condition in any of the groups. Fulton's condition factor for all size groups was consistently ~0.8, which is comparable to age-0 walleye condition factors reported elsewhere (Colby et al. 1979, Pratt and Fox 2002). Although we did not have pre-1994 fall age-0 weight data, results from 1994-2013 relative to the literature do not support the hypothesis that low energy reserves in fall have been resulting in low over-winter survival.

3.1.3 Predation and/or cannibalism (High): We found that walleye cannibalism and perhaps predation by northern pike could be responsible for low overwinter survival of age-0 walleye in Mille Lacs. Possible predators include walleye and northern pike. Although burbot (*Lota lota*) and smallmouth bass will also prey on age-0 walleye, gill net data suggest that burbot abundance has been very low since ~2000, and smallmouth bass are unlikely to feed in winter (Keast 1968, Armour 1993). Both walleye and northern pike are large enough to consume age-0 walleye during their first winter. The relative importance of these two predators can be evaluated by using a bioenergetics model to estimate how much walleye an average predator must have consumed given how much it grew, the kinds of things that it tends to eat (walleye and other fishes, invertebrates), and water temperature. Predator abundance, mortality, sex ratio, and reproduction are then used to scale up from the average individual to the population. These estimates were completed by DNR. Although we have not reviewed the calculations that went into these estimates, they suggest that consumption by walleye has been much greater than consumption by northern pike (Figure 13). The only exception is 2014 (more consumption by northern pike). We attribute these differences in consumption to walleye being more abundant (but increasingly less so) than northern pike (Figure 14). Overall, these results suggest that cannibalism might be responsible for low overwinter survival of age-0 walleye in Mille Lacs, and that predation by northern pike might be important in the future if northern pike abundance continues to increase. Cannibalism by walleye has long been known as an important regulator of age-0 walleye survival (Chevalier 1973, Forney 1980), and may have increased in response to a decrease in the abundance of alternative prey. However, because i) estimates of walleye consumed were not broken down by age-class, and ii) winter diets are unknown, we can only speculate as to the extent to which cannibalism is occurring in the first winter of life and, if so, has increased in recent years.

3.2 Low summer survival (High): We found that cannibalism and perhaps predation by northern pike and double-crested cormorants could be responsible for low summer survival of age-1 walleye in Mille Lacs. Other predators of age-1 walleye in summer are smallmouth bass and northern pike. Bioenergetics estimates (see Hypothesis 3.1.3) suggest that consumption by walleye since 2005 has been much greater than consumption by northern pike or smallmouth bass (Figure 13); although consumption by northern pike exceeded consumption by walleye in 2014.

Our ability to evaluate cormorant predation was limited by a lack of diet data for Mille Lacs. Cormorants re-colonized Mille Lacs in 1998 and currently number 400-500 nesting pairs (Figure 14). To put these numbers into perspective, we estimated the number of adult feeding days on Mille Lacs as the number of nesting pairs times 2 times 180 (the length of the adult feeding period in days) plus the number of chicks times 0.75 (to account for lower daily consumption rates by chicks) times 60 (the length of time in days that adults feed chicks). Data were from Ford (2013). Our rough calculation resulted in an estimated 3.33 adult cormorant feeding days per ha, which is less than a third of the feeding days at which walleye-related cormorant management has occurred on other lakes, but approaching the feeding days at which effects of cormorants on walleye have been detected (Rudstam et al. 2004, Schultz et al. 2013). Of course, the feeding days at which cormorants begin to impact walleye depends on the lake in question. Cormorants (and northern pike and smallmouth bass) prefer yellow perch, lake cisco, and shiners (family Cyprinidae) over immature walleye (Madenjian et al. 2002, DeBruyne et al. 2013, Schultz et al. 2013). Therefore, the impact of cormorants on walleye depends, in part, on the extent to which these species are available to buffer predation on walleye (DeBruyne et al. 2013). Assessing the availability of preferred cormorant prey in Mille Lacs is difficult because of short time series and multiple gear types. However, it appears that yellow perch catch rates have been above average since ~2001, but that lake cisco have declined in the same period. If cormorants in Mille Lacs prefer lake cisco over walleye but walleye over yellow perch, then the recent decline of cisco might be facilitating cormorant predation on age-1 walleye in summer.

4. Low survival from age-1 to fishable ages (High)

We found that the survival of age-1, -2, and -3 walleye has been declining since ~2000 (especially for age-1 and age-2 walleye), and that this decline is potentially due to cannibalism by larger walleye and, more recently, predation by northern and cormorants. To test the hypothesis that the decline of Mille Lacs walleye is due to low survival from age-1 to fishable ages, we used gill net assessment data to calculate the relative survival of walleye at age-1, -2, and -3 years of age. We calculated relative survival by dividing the CPUE of a given age in year $t+1$ by the CPUE of that cohort in year t . These data show a decline in the survival of all pre-recruit age classes over time (Figure 15). However, the severity of this decline tends to decrease with age. In other words, it appears that the decline in age-1 survival has been greater than the decline in age-2 survival, etc. Two hypotheses to explain declining survival are increased food limitation (essentially starvation) and increased predation.

4.1 Food limitation (Low): We conducted two analyses of fall gill net assessment data but found no evidence that Mille Lacs walleye are food-limited. For the first analysis, we calculated the average Fulton's condition factor by age (1-3) in each year for the period 1986-2013 (sexes combined). Condition was variable but did not appear to decrease (or increase) over time (Figure 16). Because starvation might manifest as decreased length-at-age rather than decreased weight

relative to length (i.e., condition), we also examined mean immature and lifetime growth patterns over time. We found that both immature and lifetime growth of Mille Lacs walleye has remained consistent since ~1990 (Figure 5). This result is somewhat surprising given the decline of lake cisco in Mille Lacs. Walleye typically grow more slowly in the absence of lake cisco (Kaufman et al. 2009), but growth in Mille Lacs may be offset by the concurrent increase in small yellow perch. Yellow perch have dominated walleye diets since 2006 (diets in 2005 were dominated by unidentified fish), but earlier diet data are unavailable to determine if this pattern is typical. Alternatively, reduced growth due to limited (or sub-optimal) forage could be offset by increased growth due to the increase in food availability that is usually associated with population declines (Venturelli et al. 2009).

4.2 Predation and/or cannibalism (High): We found that cannibalism and perhaps predation by northern pike and double-crested cormorants could be responsible for the low survival of age 1-3 walleye in Mille Lacs. The tendency for the decline in survival to decrease with age class (Figure 15) is interesting because it could result from walleye growing out of a predator window. Bioenergetics estimates of consumption (see Hypothesis 3.1.3) by the DNR suggest that consumption of juvenile walleye by larger walleye since 2005 has been much greater than consumption by northern pike or smallmouth bass (Figure 13). However, consumption by northern pike exceeded consumption by walleye in 2014, probably because walleye biomass is decreasing while northern pike biomass is increasing (Figure 14). Rough estimates of adult feeding hours combined with the literature (see Hypothesis 3.2) suggest that recent predation by cormorants may have also been sufficient to impact the survival of walleye to fishable ages.

Discussion of underlying mechanisms

Our review of the available data suggests that the decline of Mille Lacs walleye, which began around 2000 and may have accelerated around 2010, is a result of decreased survival from the first winter (age-0 fish) to approximately the third fall (age-2 fish). This decline in survival may be due to an increase in walleye cannibalism and, with increasing numbers in recent years, perhaps predation by northern pike, smallmouth bass, and cormorants. In this section, we discuss possible explanations for why walleye cannibalism would have increased in Mille Lacs. We stress that these explanations are speculative because data are generally lacking, multiple factors are probably in play, and natural variability is high.

The potential increase in cannibalism may be due to a combination of many (large) adult walleye and few lake cisco. Although walleye are known yellow perch predators (Forney 1980, Lantry et al. 2008), lake cisco can be an important food item for large walleye (Kaufman et al. 2009). If walleye in Mille Lacs once preyed heavily on lake cisco (diet data are unavailable to test this hypothesis) but cisco are no longer available, then walleye may have resorted to cannibalism (despite increased abundance of yellow perch). Cannibalism has long been known as an important regulator of early walleye survival, and walleye year class strength in Oneida Lake depends on the presence of prey species buffering cannibalism (Chevalier 1973, Forney 1980, Hall and Rudstam 1999). Population regulation through cannibalism is an interesting phenomenon that is present in some fish species and can lead to cycles in fish populations, especially when fishing rates are low (Lantry and Stewart 2000, Claessen et al. 2000). These cycles occur because cannibalism limits recruitment and ultimately erodes adult abundance; however, fewer adults leads to less cannibalism, higher recruitment, and an eventual increase in adult abundance.

The increase in predation in recent years may be due to a combination of increased water clarity since ~2000 and increased relative abundance of older walleye. We found that age-0 relative survival decreased with increasing water clarity (Figure 17). This relationship was weaker for age-1 relative survival and effectively absent for age-2 relative survival (Figure 18). Increased water clarity has been linked to increased feeding efficiency of northern pike (Craig and Babaluk 1989), and may increase the feeding efficiency of smallmouth bass (Ryan et al. 1999, Vanderploeg et al. 2002). The effect of increased water clarity on the feeding efficiency of double-crested cormorants is less certain; turbidity has been found to have little to no effect on predation efficiency in other cormorant species (Grémillet et al. 2012). The effect of increased water clarity on walleye is also uncertain. Although walleye feeding efficiency is expected to decline (Lester et al. 2004), the effect on survival early in life depends on the relative impact on adults and early life stages. If adult walleye feed less efficiently then increases water clarity will result in a decline in cannibalism. However, if young walleye feed less efficiently then lower growth rates may make them more susceptible to cannibalism and predation. Increased plant cover as a result of increased water clarity could also increase northern pike (and smallmouth bass) habitat and predation efficiency (but decrease cormorant and walleye feeding efficiency). Northern pike (and smallmouth bass) thermal habitat has probably also increased as a result of warming since ~1980.

The decline in Mille Lacs walleye may also be due to changes in the environment of Mille Lacs, which limits the production of strong year classes for reasons other than predation (see Hypothesis 4.1). Nutrient inputs into Mille Lacs have likely declined as a result of the 1970s Clean Water Act. The recent establishment of zebra mussels and spiny water fleas (2011 and 2010, respectively) could also be altering nutrient and energy pathways. For example, zooplankton biomass following the establishment of spiny water flea has reached a record low in Mille Lacs, especially in late summer and fall. Low zooplankton biomass does not appear to be affecting age-0 walleye condition or survival to fall (Figure 8) (perhaps because they switch from zooplankton to prey fish earlier in summer). In principle, changes in water clarity, temperature, and the fish community could impact the biomass of prey fish that is available to older walleye (including adults). For example, increased water temperatures are probably responsible for the decline in lake cisco (Jacobson et al. 2008), which are an important forage fish for adult walleye (Kaufman et al. 2009). Increased water clarity can also lead to decreased walleye abundance and productivity via a reduction in walleye feeding habitat (Lester et al. 2004). While environmental changes might ultimately reduce the individual growth of adult walleye through the mechanisms described above, current data suggest that the size at age of walleye in Mille Lacs has not declined (Figure 5).

Recommendations for data collection and research

Based on our findings, we have the following recommendations for data collection and research. We present these recommendations in no particular order. We leave it up to the DNR to assess whether it is feasible or even possible to implement a recommendation, and to rank recommendations according to management or budget priorities.

Identify and monitor key indicators. We recognize that it is impossible to anticipate data needs or monitor every aspect of a system. The data that were available to us were sufficient to identify cannibalism, predation, and system changes as the likely causes of the Mille Lacs decline. To evaluate these drivers in more detail and project forward, we recommend

identifying and monitoring key indicators related to early survival, predator abundance, diet (and consumption), invasive species, and water quality. The DNR already began monitoring some of these variables around 2005 (Table 2). More variables should be added and – given the importance of Mille Lacs walleye to state and local economies – efforts to monitor these variables should be buffered against budget pressures.

Characterize pre-2005 walleye diets. This information can be used to determine the importance of lake cisco and small walleye to larger walleye, and to estimate consumption. Diet samples were not collected prior to 2005, but it may be possible to characterize diets via stable isotope analysis of archival tissue samples (e.g., scales). If tissue samples are unavailable to characterize the base of the food web, it is unclear how to define the base of the food web, estimated variance is high, or there is particular interest in trophic position, then we recommend compound-specific isotope analysis (Chikaraishi et al. 2009, Steffan et al. 2013). This form of isotope analysis does not require samples from the base of the food web, and results in very precise estimates of trophic position. Stable isotope analysis in general should provide insight into whether diets changed markedly coincident with the decline in young walleye survival, as might be expected if cannibalism is a major mechanism for the decline in survival.

Sample/analyze walleye, northern pike, and smallmouth bass diets in both summer and winter. Seasonal diet data/analyses will help to resolve which predator is consuming which size class of immature walleye in which season.

Estimate the current and future impact of cormorants on walleye. Our back-of-the-envelope calculation suggests that cormorants may be impacting walleye. However, a focused study involving diet data and bioenergetics estimates is needed to rigorously evaluate this hypothesis. We also recommend projecting impacts based on a combination of estimated equilibrium cormorant abundance (e.g., as determined by total suitable nesting habitat) and migrant cormorant abundance.

Determine why young walleye survival is low despite high yellow perch abundance. The pattern is somewhat unexpected because the high abundance of age-0 and age-1 yellow perch might be expected to buffer young walleye from cannibalism and other predation. Yellow perch are often a preferred prey item of walleye, especially when soft-rayed fishes are unavailable (Madenjian et al. 1996, Fitzgerald et al. 2009), and have dominated walleye diets in years for which data are available (2005-2013). Assuming that the cannibalism hypothesis is correct, we recommend work to evaluate this apparent contradiction. Diet samples and bioenergetics modeling over a range of walleye sizes are obvious places to start. However, habitat changes could also be important, such as increased vegetative cover for yellow perch or a light-mediated separation of walleye and yellow perch habitat.

Determine the extent to which body length is contributing to low survival in the first winter of life. Although we found some evidence that the overwinter survival of age-0 walleye was lowest for the smallest individuals (Hypothesis 3.1.1), we could not rule out gear bias or winter growth. We recommend sampling with all three gear types in spring and fall, and using (or collecting) scales or otoliths to assess winter growth.

Estimate age-specific natural mortality rates. Total mortality is generally well estimated via statistical catch-at-age modeling, although allocation to fishing can depend upon assumed natural mortality rates. Our analyses of SPR and safe harvest rely on natural mortality being roughly constant over time and close to assumed values. This assumption could potentially be evaluated through an appropriately designed multi-year tagging study. Current tagging studies on the Mille Lacs walleye population have generally been conducted for estimating population abundance.

Evaluate how changes to the stock-recruitment relationship, consistent with changes in early-life walleye survival, influence sustainable fishing. Our findings of reduced survival between summer of age-0 and age-2 suggests that the stock-recruitment relationship may be non-stationary and that recruits to the fishery produced per spawner are atypically low for a walleye fishery such as Mille Lacs. This is a complex topic because the influence of changes in recruitment will depend upon the mechanism. Typically, stock-recruitment relationships for walleye populations are modeled using a Ricker function that has total recruitment being a domed-shape function of spawning stock size. The dome and decrease in recruitment at higher stock sizes is a result of cannibalism. Cannibalism would operate through the density-dependent parameter of the function (i.e., how fast survival declines as stock size increases), whereas one might view changes in survival due to other predators as operating via the density independent parameter (essentially the recruits produced per spawner at low spawning stock). Starvation might operate in either fashion, being density dependent if the young walleye are actually depleting their food supply. The reason why the mechanisms matter is that if the decrease in survival of young walleye is due to density-dependent factors, this would argue that per capita fishing mortality rates can remain similar to those of the past, whereas if the decline in survival is density independent, then sustainable fishing mortality rates will have declined along with the expected future harvests (see Bence et al. 2014 for further discussion).

Evaluate gear biases over time. Throughout this review, we have assumed that observed or estimated changes resulted from a perturbation rather than a change in sampling bias(es). All sampling is biased but still allows for comparisons of relative differences provided that the bias does not change. We recommend testing this ‘constant bias’ assumption whenever a change is plausible. For example, if increased water clarity is causing age-1 walleye to move offshore (i.e., away from the sampling gear) in spring, then this will create the appearance of decreased survival during the first winter of life.

Recommendations for fisheries management

We conclude that recreational and subsistence fishing mortality is unlikely to be the direct cause of the decline of Mille Lacs walleye. However, we also note that the fixed exploitation policy of 24% of fish over 356 mm that was established when state and tribal co-management was put in place does not necessarily provide for a conservative level of fishing or prevent substantial year-to-year fluctuations in the actual impact of fishing. Furthermore, our analyses treat Mille Lacs walleye as being "typical", but the high mortality of young walleye may have led to an atypical stock-recruitment relationship. Thus, the harvest policy should be revisited.

Our SPR analysis suggests that the same level of fishing produced markedly different population level impacts in different years (Figure 6a). Similarly, the maximal level of fishing for F_{safe} varied substantially over years, due both to changes in regulations and environmental conditions. Additional work is needed to determine appropriate fishing levels for the Mille Lacs walleye population. The F_{safe} analysis suggests higher rates of fishing relative to the SPR analysis, but the two analyses make different assumptions regarding natural mortality rates, historical fishing mortality schedules, life history compensation, etc.

Both the SPR and F_{safe} analyses show that it is critical to recognize that the impact of a given harvest policy depends, not just on harvest relative to population size, but also on the size and age of fish that are harvested. In the year immediately prior to the implementation of emergency regulations, the targeting of smaller fish led to some declines in the abundance of male fish. While we do not think that the level of decline seen so far would have an important impact on recruitment, it does emphasize that size/age and sex of fish being harvested matters.

Both SPR and F_{safe} can be used to summarize the overall impact of a given level of fishing or regulation. We suggest taking this impact into account when setting intended harvest levels or regulations, and that there should be some incentive to each party (state and tribes) to fish in a way that produces desired population impacts. For example, the target yield (or, alternatively, the allowed mix of regulations) for each party could be set assuming that the entire fishery was prosecuted by them, so as to achieve a desired maximum impact on the population. That party's allocation would then be set as a share of that amount, so that fishing practices that allowed more yield for the same level of impact would provide a party with higher levels of yield.

In the future, we believe there is a need to move away from a constant- F or constant exploitation rate policy like that is technically in place. The reality is that agencies believe that the prudent approach is to reduce fishing rates when stock sizes decline. We agree this approach is precautionary and prudent. While we did not see any evidence that fishing mortality rates had increased to a higher average coincident with the decline in walleye abundance, nor that sustained high levels of fishing had driven stock size down and thus caused the initial recruitment failure, fishing is one of the only drivers of walleye abundance that we can manage. If fishing levels were not reduced due to recent emergency regulations, it is possible that spawning stocks could decline to levels from which they might not easily recover. Ideally, harvest strategies should be planned and agreed to in advance. This provides more predictability to the fishery, and is particularly important if higher cannibalism rates are the new normal. However, if other evidence suggests a permanent reduction in the steepness of the stock-recruitment relationship (i.e., a density-independent change), new harvest policies should be designed and implemented accordingly.

The future character of walleye fisheries on Mille Lacs may also depend on how other species are managed. For example, small northern pike will consume more walleye than an equivalent biomass of large northern pike. If predation by northern pike is significant, then managing for a trophy pike fishery should minimize impacts on walleye. Similarly, walleye may benefit from cormorant management but only if cormorants are an important source of walleye mortality (Shultz et al. 2013, DeBruyne 2014). Smallmouth bass management strategies should also be evaluated provided that there is evidence (or the potential) for impacts on walleye.

Finally, we do not recommend walleye stocking in Mille Lacs. Stocking supplements natural reproduction and can therefore be an important part of a walleye recovery effort (e.g., Red Lakes walleye; Logsdon 2006). However, natural reproduction in Mille Lacs is already very

high. The problem appears to be lower survival from the first winter to approximately the third fall. Stocked fish will suffer the same fate and, assuming that low survival is due to cannibalism and/or predation, could exacerbate the problem by sustaining predator populations. Stocking larger (i.e., age-3) fish is infeasible for such a large lake, and is most likely to result in a large-scale, put-grow-and-take fishery. Stocking 100,000 age-1 spring walleye did not help in Oneida Lake (VanDeValk et al. 2007).

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Table 1. A summary of recreational fishing regulations for walleye on Mille Lac Lakes, MN (1983-2014). Regulations are given in inches with bag limits in parentheses. HS = harvestable slot and PS = protected slot. Each year of fishing is from 1 January to 31 December. Within-year regulation changes (and associated dates) are also given.

Year(s)	Length-based reg (& limit)	Within-year change 1 (& date)	Within-year change 1 (& date)	Within-year change 1 (& date)
1983, 1984	(6)			
1985-1996	1>20" (6)			
1997, 1998	15" minimum (6)			
1999	14-20" HS with 1 >26" (6)			
2000	14-18" HS with 1 >28" (6)			
2001	16-20" HS with 1 >28" (6)	16-18" HS (6) (Jun 5)	16-18" HS with 1>30" (6) (Jul 1)	14-18" HS, with 1>28" (6) (Dec 1)
2002	14-16" HS with 1 >28" (4)			
2003	17-28" PS, with 1>28" (4)			
2004-2006	20-28" PS, with 1>28 (4)	22-28" PS, with 1>28 (4) (Jul 16)	20-28" PS, with 1>28 (4) (Dec 1)	
2007	20-28" PS, with 1>28 (4)	14-16" HS, with 1>28 (4) (Jul 9)	20-28" PS, with 1>28 (4) (Dec 1)	
2008	18-28" PS, with 1>28" (4)			
2009	18-28" PS, with 1>28" (4)			
2010	18-28" PS, with 1>28" (4)	20-28" PS, with 1>28 (4) (Jul 15)	18-28" PS, with 1>28 (4) (Dec 1)	
2011	18-28" PS, with 1>28" (4)	20-28" PS, with 1>28 (4) (Jul 27)	18-28" PS, with 1>28 (4) (Dec 1)	
2012	17-28" PS, with 1>28" (4)			
2013	17-28" PS, with 1>28" (4)	18-20" HS with 1>20" (2) (May 11)		
2014	18-20" HS, with 1>28" (2)			

Table 2. A summary of data available for the Mille Lacs Walleye Blue Ribbon Panel review. All data were collected by the DNR unless otherwise indicated.

Category	Type	Years	Notes
Walleye	Biomass of mature fish by sex and age	1987-2014	Estimated from gill net assessment data using a statistical model
	Abundance and biomass by sex and age	1987-2014, 1979-2013	Estimated from gill net assessment data using a statistical model
	Mortality by sex and age	1987-2013	Estimated from gill net assessment data using a statistical model
	Growth by sex and age	1986-2013	From gill net assessment data
	Age-0 abundance in fall	1977-2013, 1991-2013, 1979-2013	Catch per unit effort in trawls, electrofishing, and gill nets
	Age-0 lengths in fall	1982-2013	Sampled using trawls, electrofishing, and gill nets
	Age-0 weights in fall	1994, 1996, 1999-2013	Sampled using trawls, electrofishing, and gill nets
	Age-0 diets in summer	2005-2013	Sampled using gill nets
	Age-1 lengths in spring	2000-2007	Sampled during Great Lakes Indian Fish and Wildlife Commission electrofishing
	Age-1 and older diets	2005-2013	Sampled using gill nets
	Consumption of age-0 walleye by walleye	2006-2013	Estimate via an energetic growth model using abundance, growth, diet, and water temperature data
Predators, competitors and prey	Abundance of age-0 walleye prey in summer	2005-2008	Catch per unit effort of appropriately sized prey fish in trawls, beach seines, and gill nets
	Abundance of age-1 walleye prey in winter	1984-2013	Catch per unit effort of appropriately sized prey fish in trawls
	Abundance of age-1 walleye prey in spring	2005-2008	Catch per unit effort of appropriately sized prey fish in trawls, beach seines, and gill nets
	Abundance of age-1 walleye prey in summer	2005-2008	Catch per unit effort of appropriately sized prey fish in trawls, beach seines, and gill nets
	Pike biomass by age	1986-2014	Estimated by the Great Lakes Indian Fish and Wildlife Commission by applying a statistical model to gill net assessment data
	Pike diet by age and length	2005, 2007, 2012, 2013	Sampled using gill nets
	Consumption of age-0 walleye	2013	Estimate via an energetic growth model using abundance,

	by pike		growth, diet, and water temperature data
	Bass abundance by age	1999-2013	Catch per unit effort in gill net assessments; estimated via mark-recapture
	Bass diet by age and length	2005, 2012, 2013	Sampled using gill nets
	Consumption of age-0 walleye by bass	2013	Estimate via an energetic growth model using abundance, growth, diet, and water temperature data
	Cormorant abundance	1997-2013	US Fish and Wildlife Service nest and chick counts on Spirit Island
	Cormorant diet by age and size	2004-2007, 2010	Data are from Leech Lake, MN
	Consumption of age-0 walleye by cormorants	2005-2007, 2010	Data are from Leech Lake, MN
Invasive species	Spiny water flea abundance	2009-2013	Mean number sampled per vertical, open-water zooplankton tow
	Zebra mussel density	2005-2013	Number per square meter
Summer water quality and zooplankton	Alkalinity	1970,1976,1980,1984-2013	Parts per million; annual average from multiple sites and dates
	Chlorophyll-a	1984-2013	Parts per billion; annual average from multiple sites and dates
	Conductivity	1993-2013	Micromhos/cm; annual average from multiple sites and dates
	Phosphorous	1970,1980,1984-2013	Parts per million; annual average from multiple sites and dates
	Secchi depth	1974, 1981-82, 1988-2013	meters; monthly and annual averages
	Total dissolved solids	1976,1980,1984,1986, 1988-2013	Parts per million; annual average from multiple sites and dates
	Temperature	2000-2013	°C; daily means for most days/months recorded by temperature loggers set at depth of 1.8 m
	pH	1970,1980,1984-86, 1988-2013	Annual average from multiple sites and dates
	Zooplankton abundance and density	2006-2014	Mean number sampled per vertical, open-water zooplankton tow

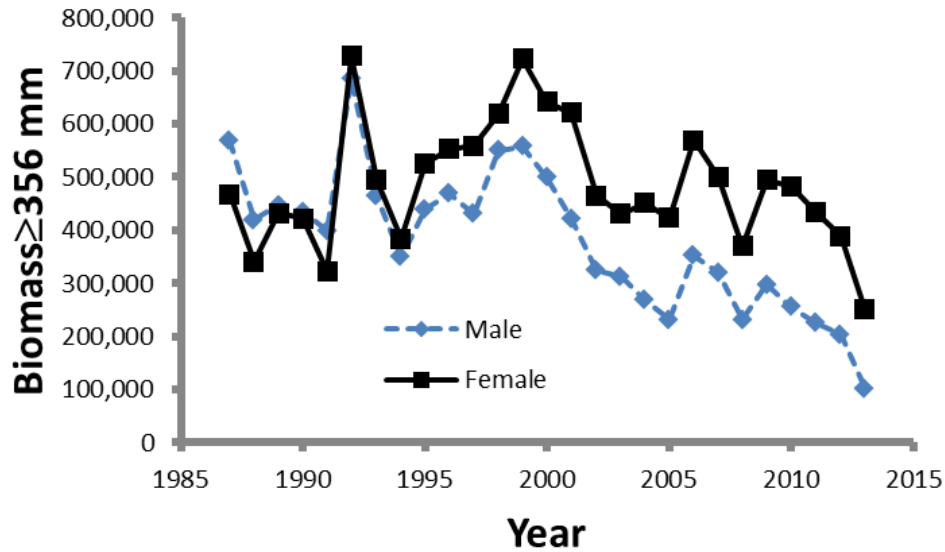


Figure 1. Estimated biomass (kg) of male and female walleye ≥ 356 mm (14") in length in Mille Lacs Lake, MN (1987-2012). Data were calculated from the base version of the SCAA model that was supplied for the Bence et al. (2014) review of the assessment model.

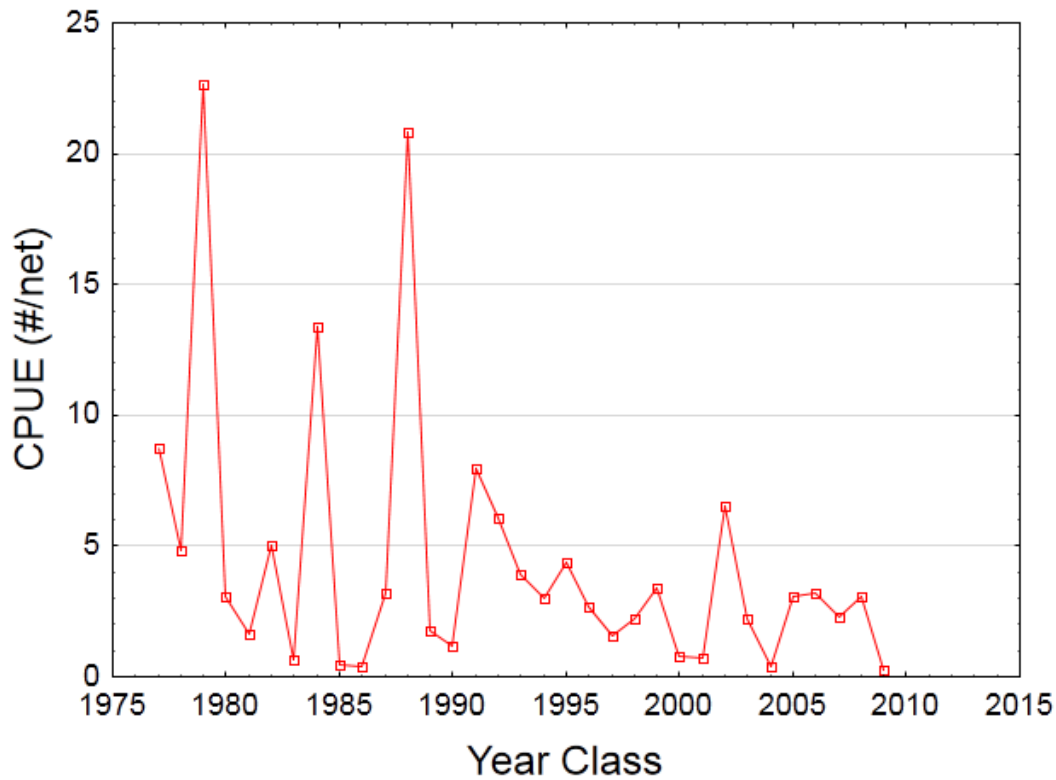


Figure 2. Recruitment of walleye to the Mille Lakes Lake, MN, recreational fishery (1977-2009). We used gill net CPUE (#/net) of 3 and 4 year-old walleye an index of recruitment because fish are fully vulnerable to angling at this age (i.e., range in mean total length $\approx 400 - 500$ mm).

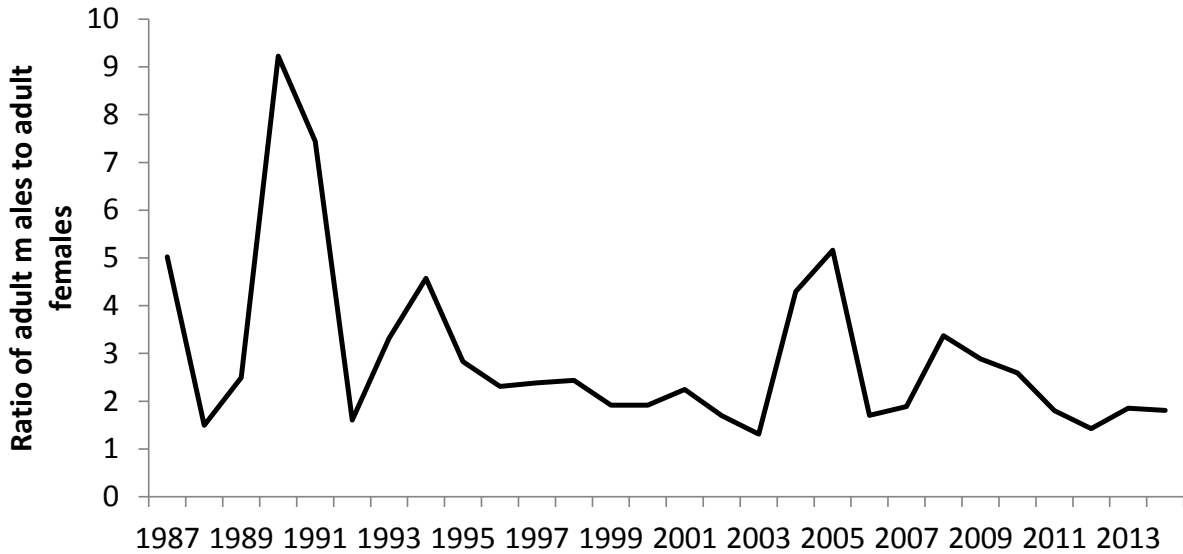


Figure 3. The ratio of adult male to adult female walleye in Mille Lacs Lake, MN (1987-2014). We calculated ratios using sex- and age-specific SCAA abundance estimates and assuming that male and female walleye mature at age-2 and -4, respectively. We based this assumption on a separate analysis of gill net assessment maturity data that showed that males and females, on average, mature at 330 and 420 mm, respectively, and that these lengths tend to correspond to ages 2 and 4, respectively (see Figure 5 below).

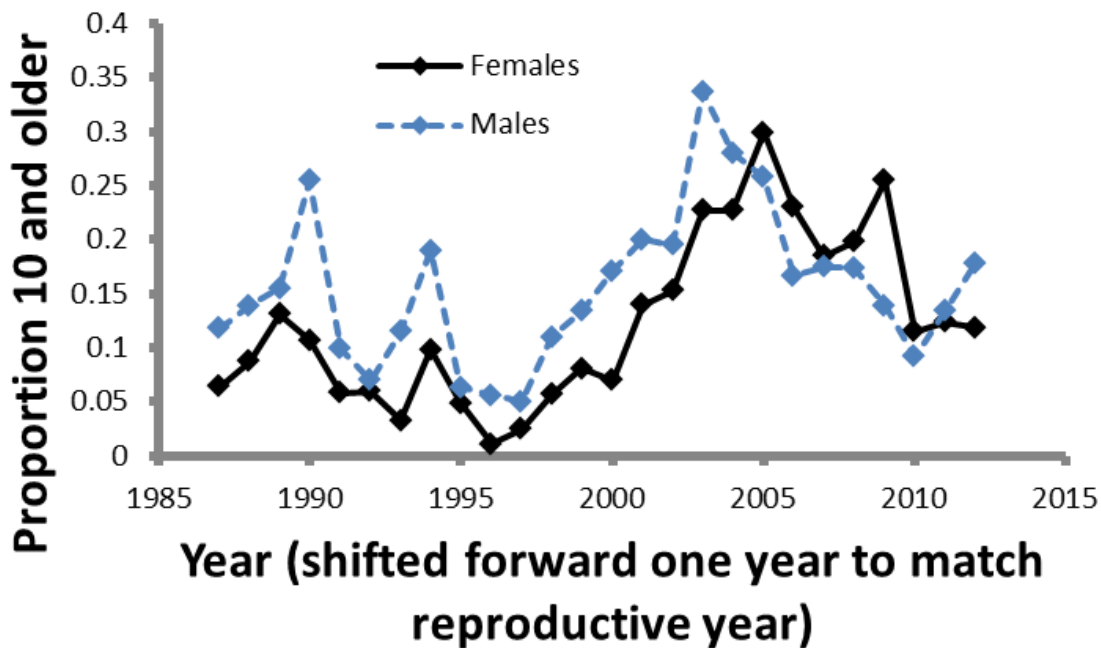


Figure 4. Proportion of walleye \geq age-10 or older in Mille Lacs Lake, MN (1987-2012) based on inshore gill-net surveys. Estimates are reported for the spawning year that they reflect (as is used in the SCAA model provided for the Bence et al. 2014 review) but were collected during the preceding year.

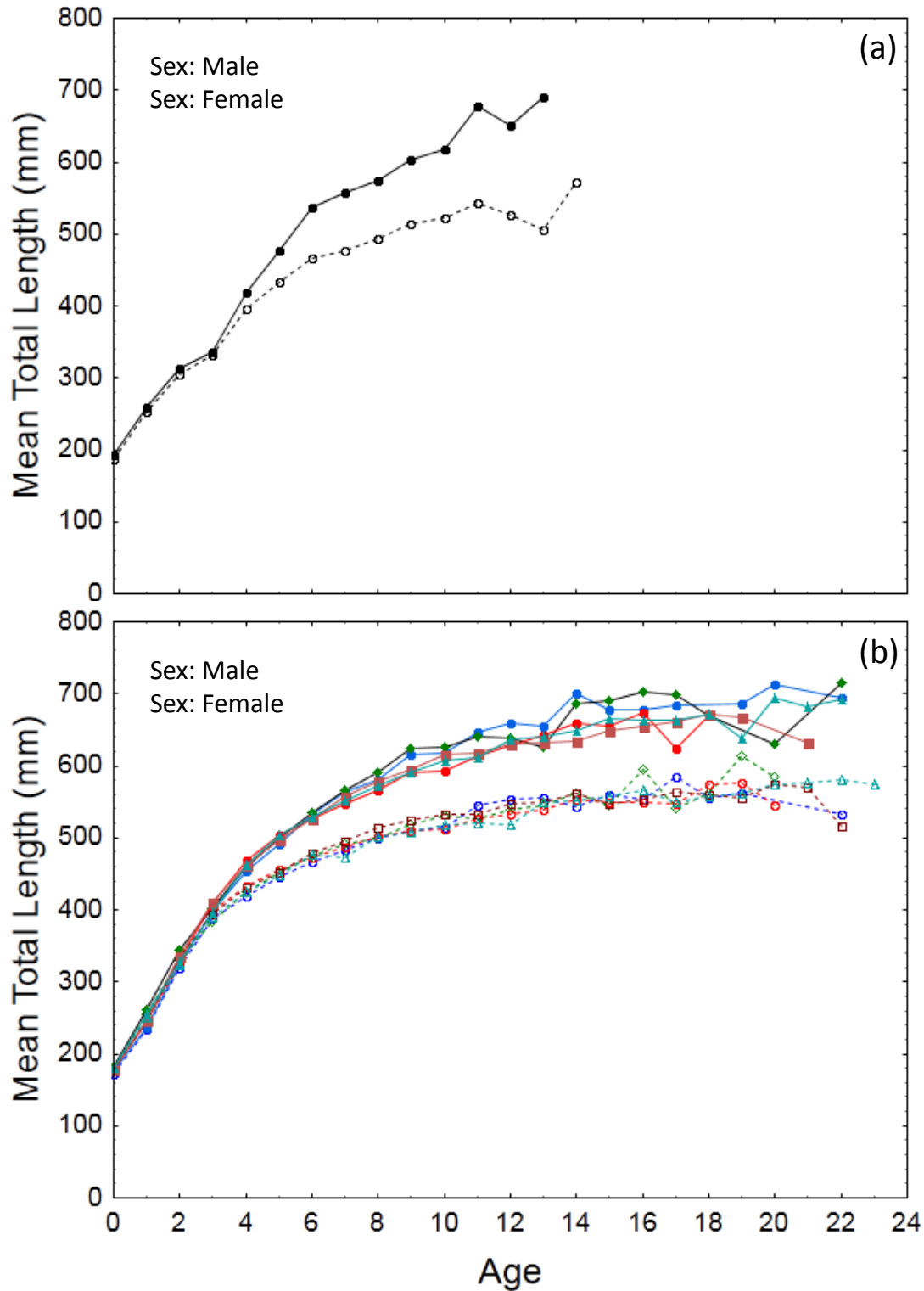


Figure 5. Mean total length versus age by sex for walleye in Mille Lacs Lake, MN. Data are partitioned into 5-year periods (1985-1989, 1990-1994, 1995-1999, etc.). The earliest period (1985-1989) is shown in (a) because we suspect large aging errors. More recent periods (b) show that growth has been remarkably constant over the last 20 years.

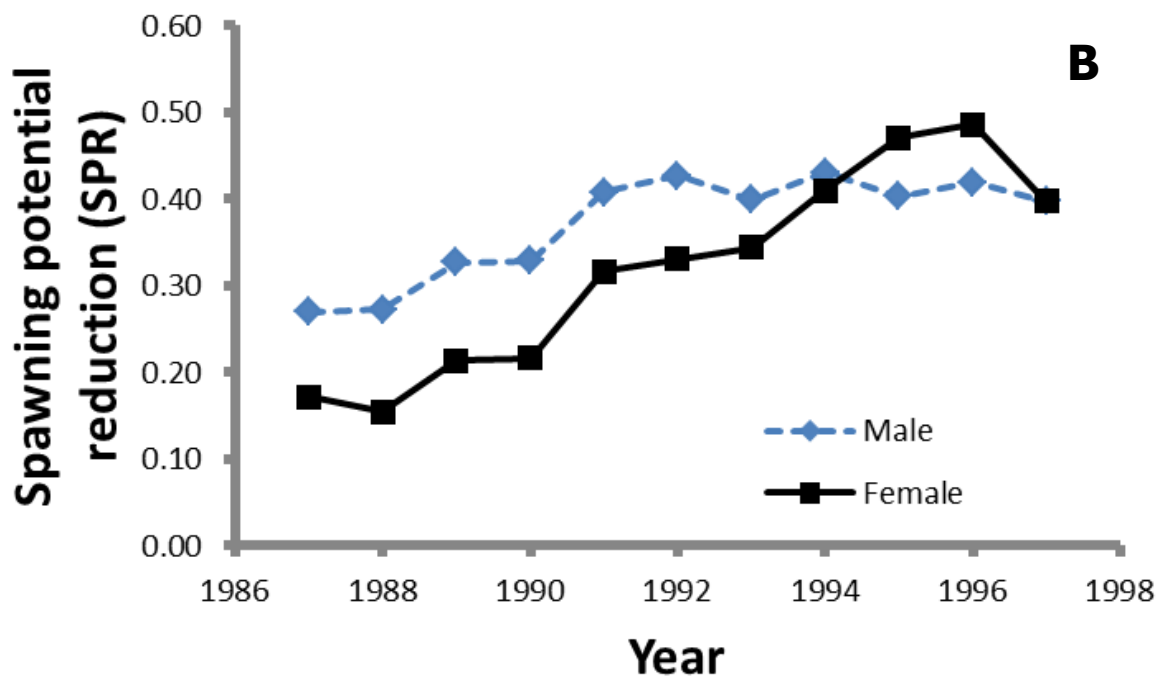
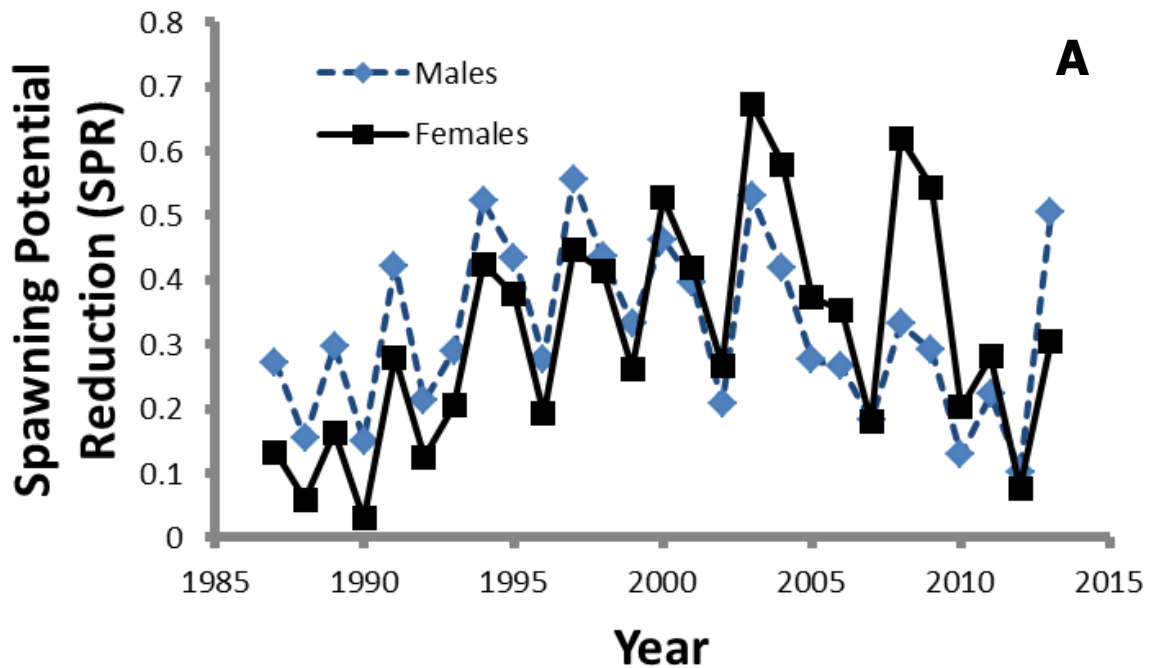


Figure 6. Sex-specific estimates of spawning potential reduction (SPR) over time (A) and on a cohort basis (B) in Mille Lacs Lake, MN. Fishery management agencies around the world use SPR as a measure of the overall level of fishing mortality and generally seek to keep values above thresholds that vary from 0.2 to 0.5. Lower, more aggressive, thresholds are applied to more productive fish stocks. SPR values average 0.32 for males and 0.31 for females.

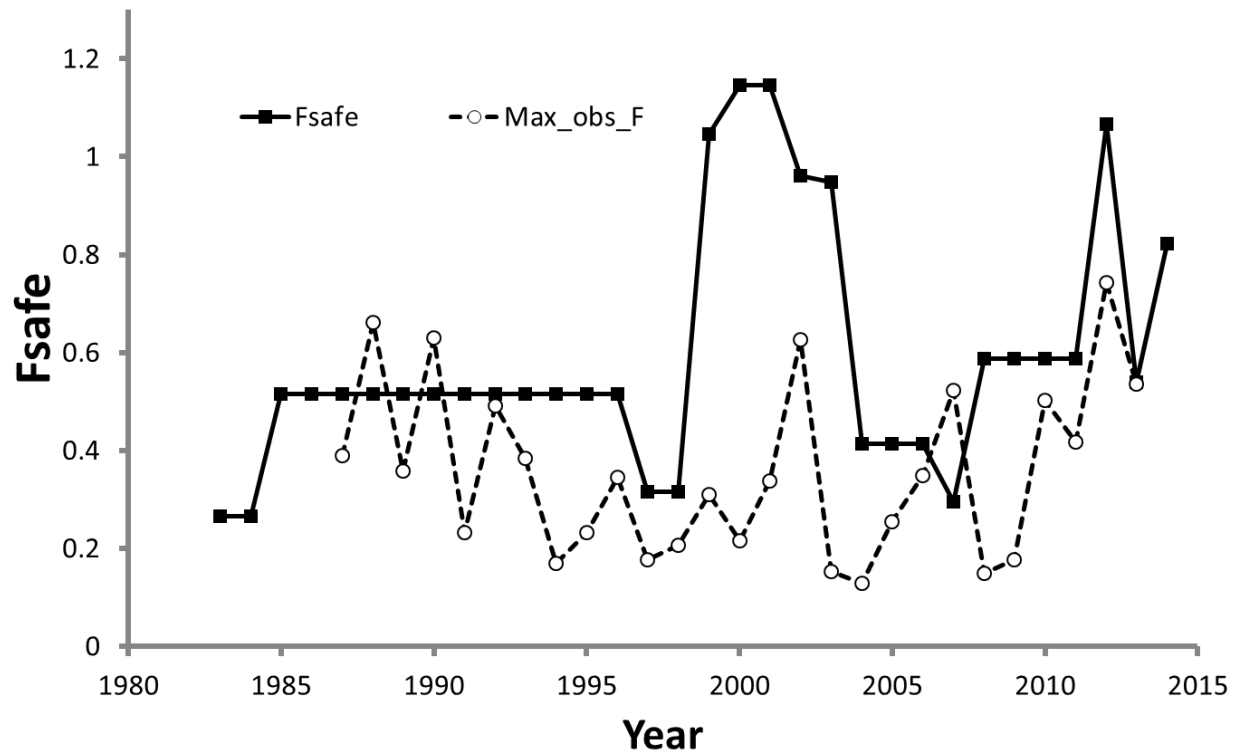


Figure 7. Annual estimates of F_{safe} (minimum value in each year given regulations in Table 1) and F (maximum value across all female walleye ages in a year) in Mille Lacs Lake, MN (1984-2014). F_{safe} was calculated according to methods outlined by Lester et al. (2014) and modified by Paul Venturelli and Natnael Hamda (unpublished). F_{safe} calculations take into account Mille Lacs water temperatures and the selectivity implied by regulations in a year. Assumptions are 2-fold growth compensation, 5% hooking mortality, and a natural mortality rate that decreases with immature size but is fixed at 0.25/yr for adults. F was based on SCAA (Bence et al. 2014). Both rates are instantaneous annual.

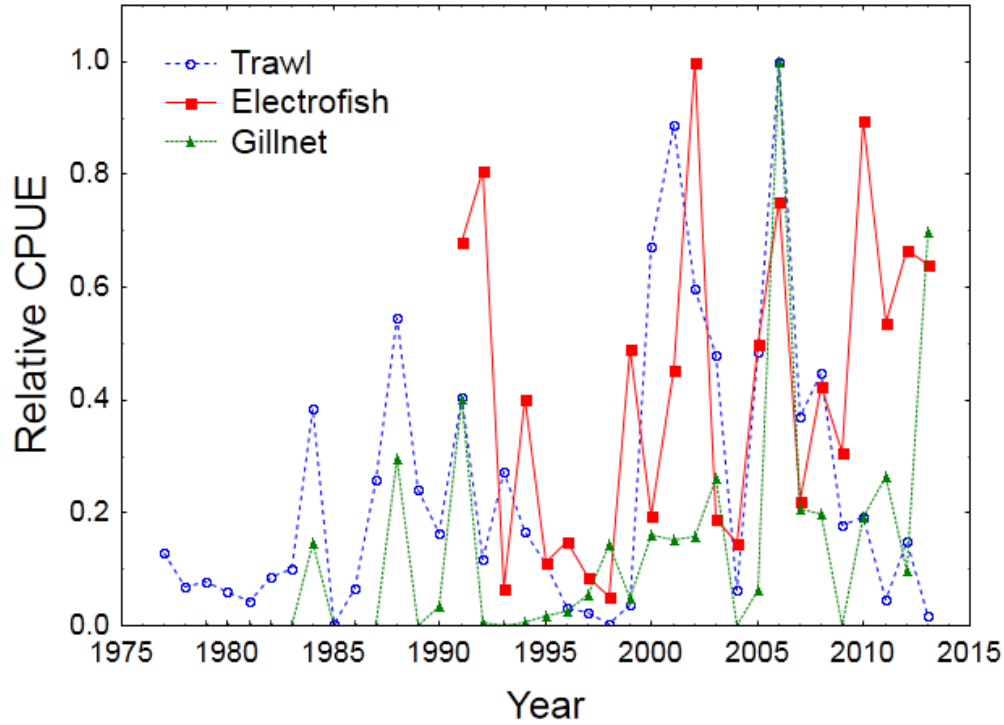


Figure 8. Variation in age-0 walleye abundance based on fall surveys (trawl, electrofish, and gill net) in Mille Lacs Lake, MN (1977-2013). The y-axis is catch-per-unit effort (CPUE) standardized so that maximum CPUE = 1 for each survey method.

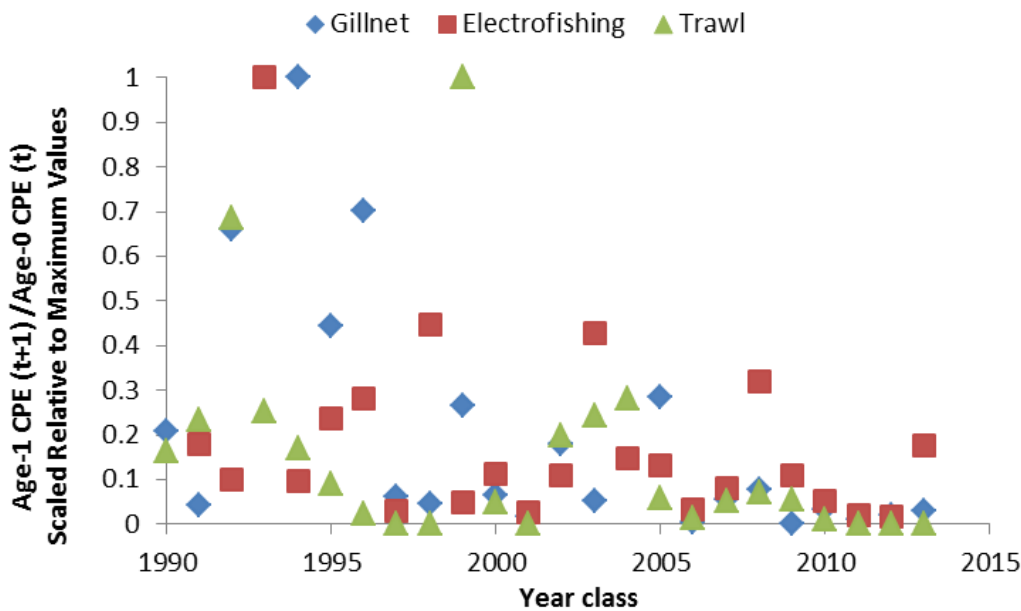


Figure 9. Relative survival of age-0 walleye in Mille Lacs Lake, MN (1990-2013), calculated by dividing age-1 CPUE at time $t+1$ by age-0 CPUE at time t for various survey gear used to assess the Mille Lacs walleye population. Relative survivals for each survey method were scaled relative to their maximum values so that scales were common to the methods.

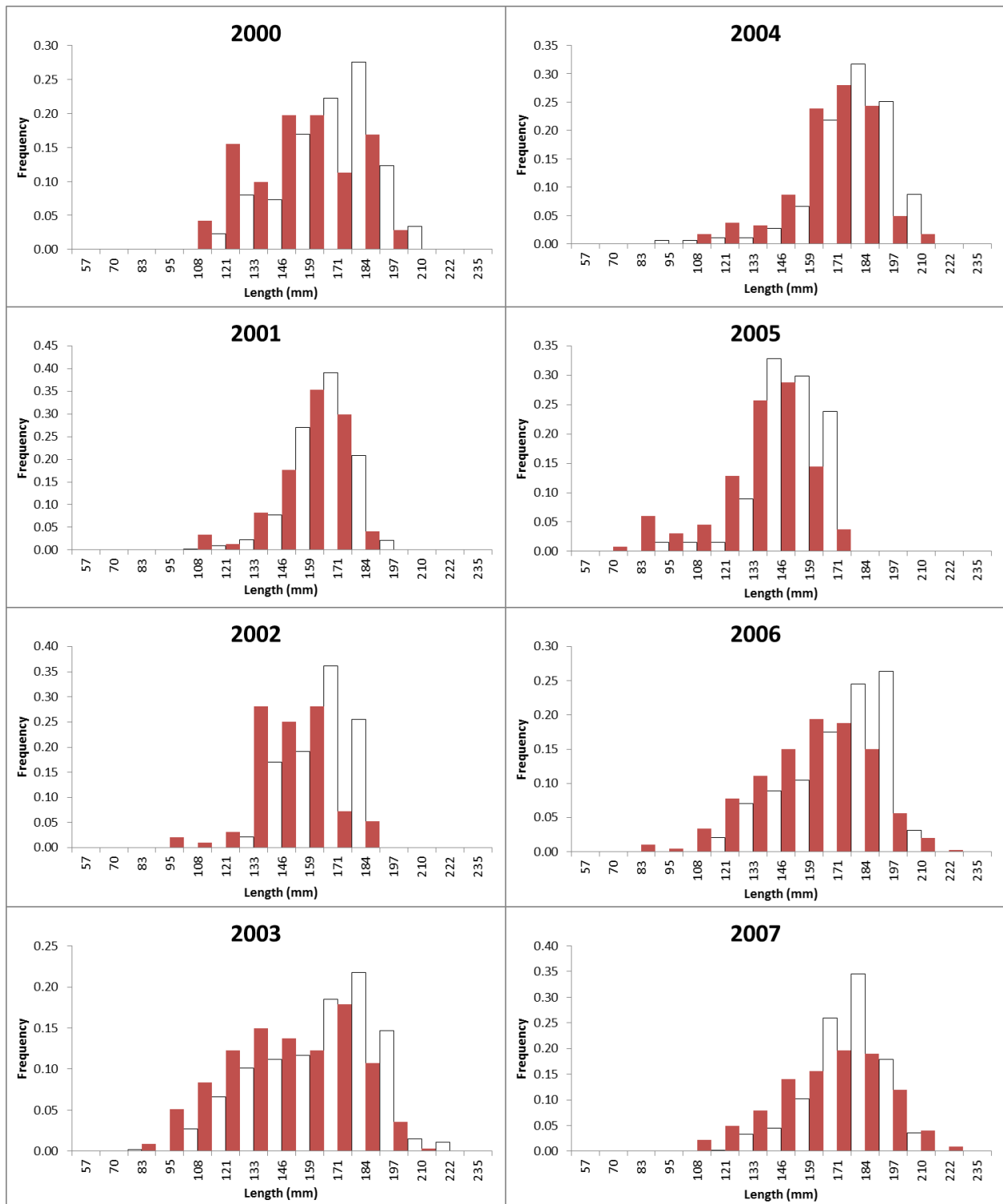


Figure 10. Fall electrofishing age-0 length frequencies (red bars; year t) in comparison to spring electrofishing age-1 length frequencies (clear bars, year $t+1$) for walleye in Mille Lacs Lake, MN (2000-2007).

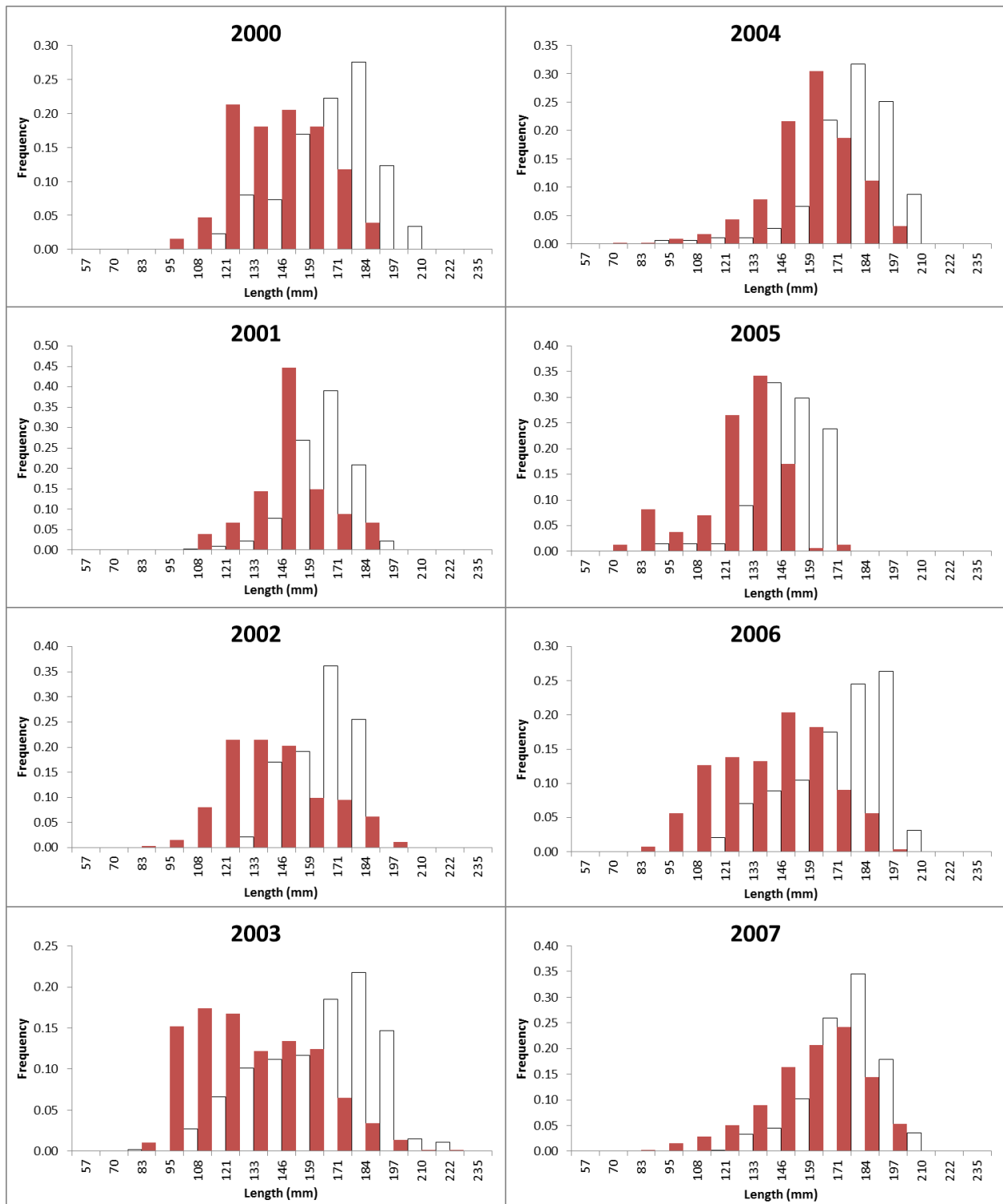


Figure 11. Fall age-0 length frequencies (red bars; year t) in comparison to spring age-1 length frequencies (clear bars, year $t+1$) for walleye in Mille Lacs Lake, MN (2000-2007). Age-0 length frequencies were from individuals collected during gill net, trawl, and electrofishing surveys. Age-1 length frequencies were from individuals collected during tribal electrofishing surveys.

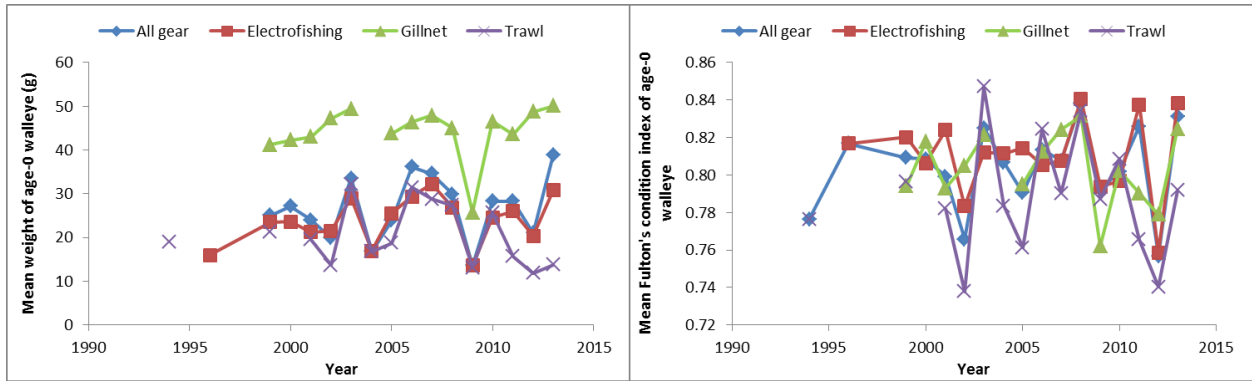


Figure 12. Time series of mean weight (left panel) and Fulton's condition factor (right panel) of age-0 Mille Lacs Lake walleye from individuals collected by electrofishing, gill net, trawl, and all survey gears combined (1994-2013).

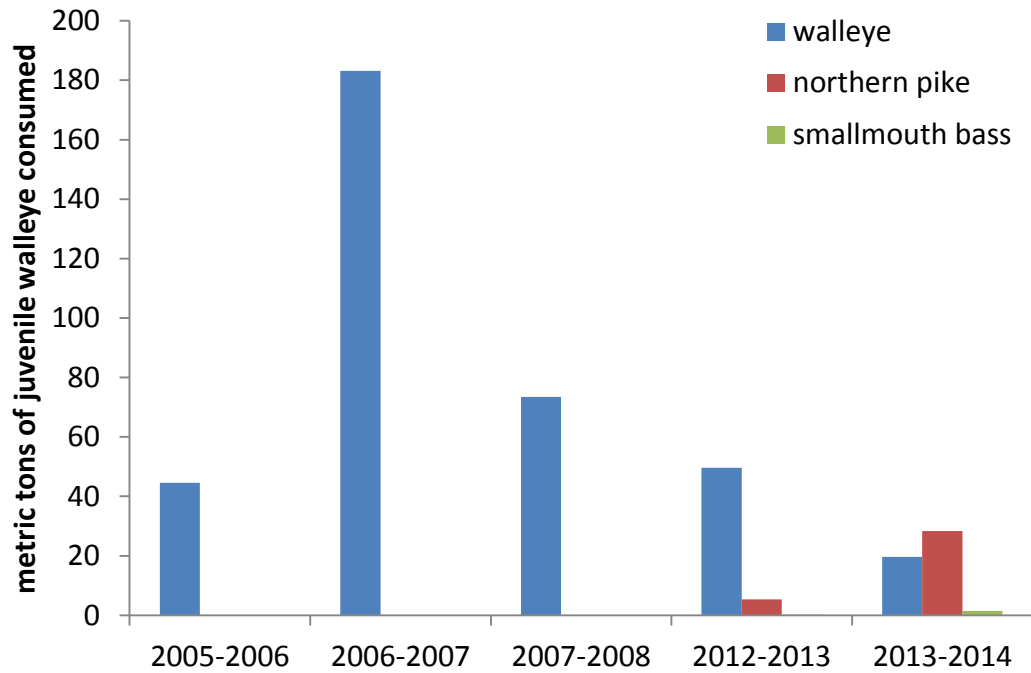


Figure 13. Consumption of juvenile walleye by walleye, northern pike, and smallmouth bass in Mille Lacs Lake, MN (2005-2014). Consumption was estimated via bioenergetics simulation by Tyler Ahrenstorff (MNDNR Fisheries Research Biologist). These simulations ran from Oct 1st of one year to September 30 of the next year.

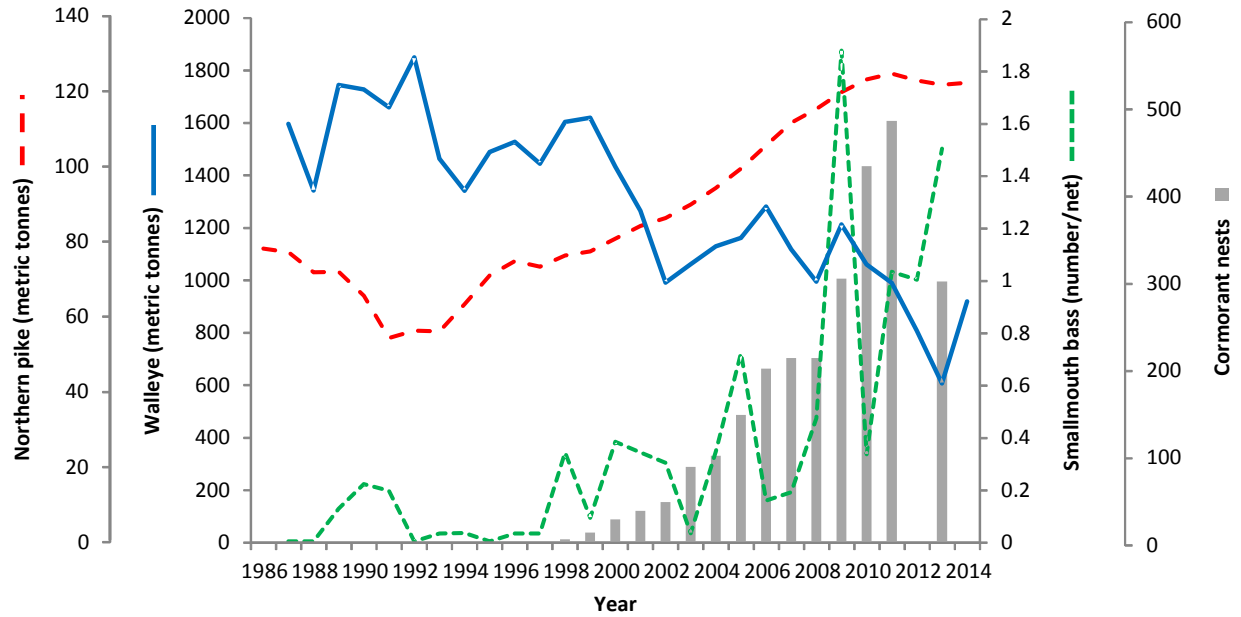


Figure 14. Change over time in the abundance of walleye (SCAA model), northern pike (surplus production model), smallmouth bass (fall gill net surveys) and cormorants (Spirit Island nest surveys) in Mille Lacs Lake, MN. We estimated cormorant nests in 2013 via a non-linear, nest-chick regression.

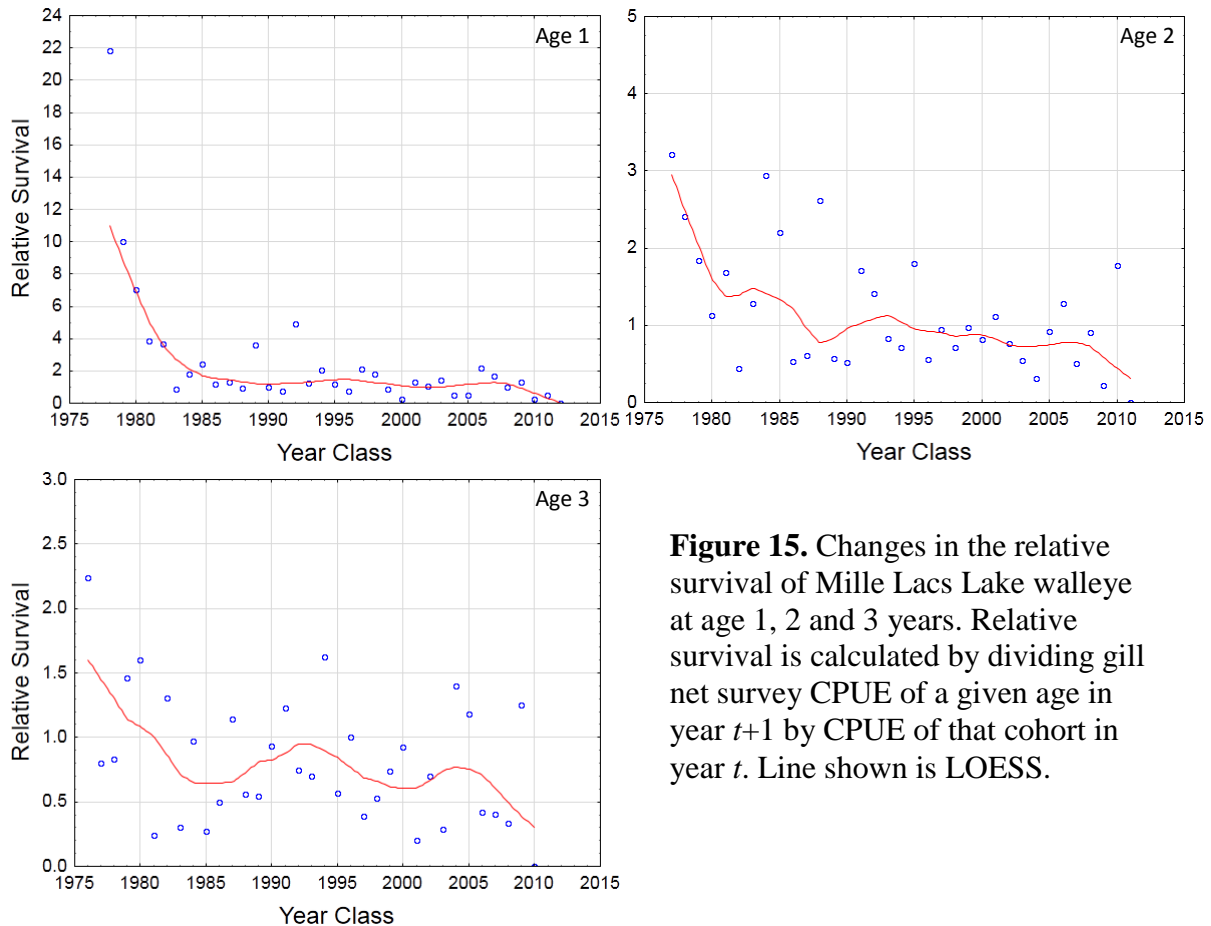


Figure 15. Changes in the relative survival of Mille Lacs Lake walleye at age 1, 2 and 3 years. Relative survival is calculated by dividing gill net survey CPUE of a given age in year $t+1$ by CPUE of that cohort in year t . Line shown is LOESS.

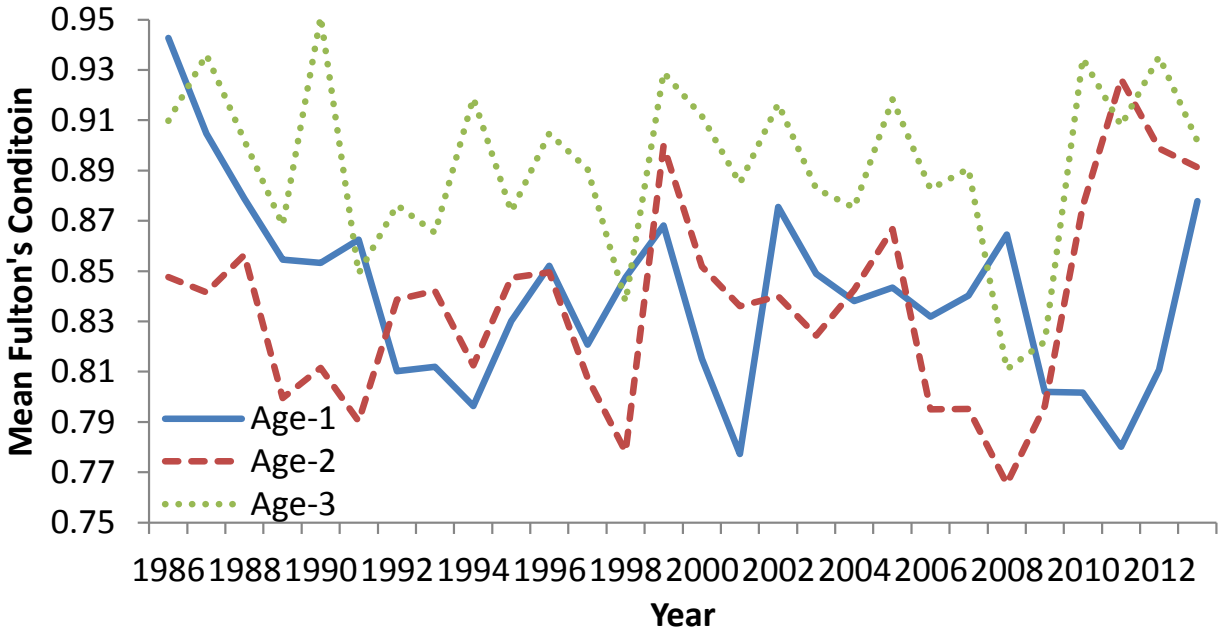


Figure 16. Mean Fulton's Condition Factor of age-1, -2, and -3 walleye (sexes combined) in Mille Lacs Lake, MN (1986-2013).

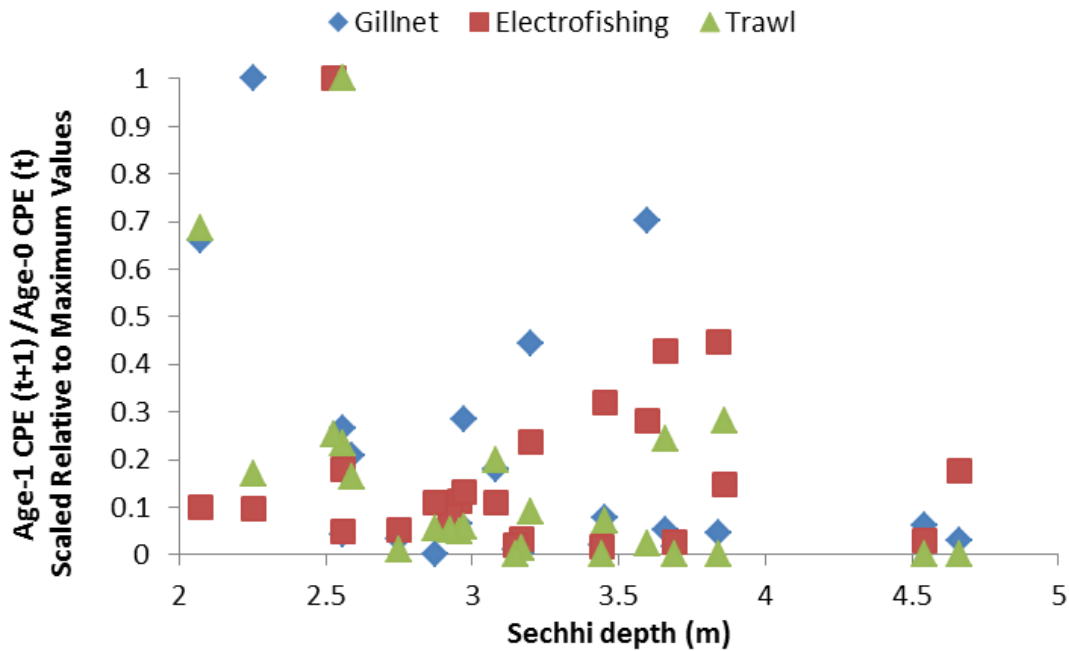


Figure 17. Relative survival of age-0 walleye calculated by dividing age-1 CPUE at time $t+1$ by age-0 CPUE at time t for various survey gear used to assess the Mille Lacs walleye population (1990-2013) in relation to average June to October Secchi depth.

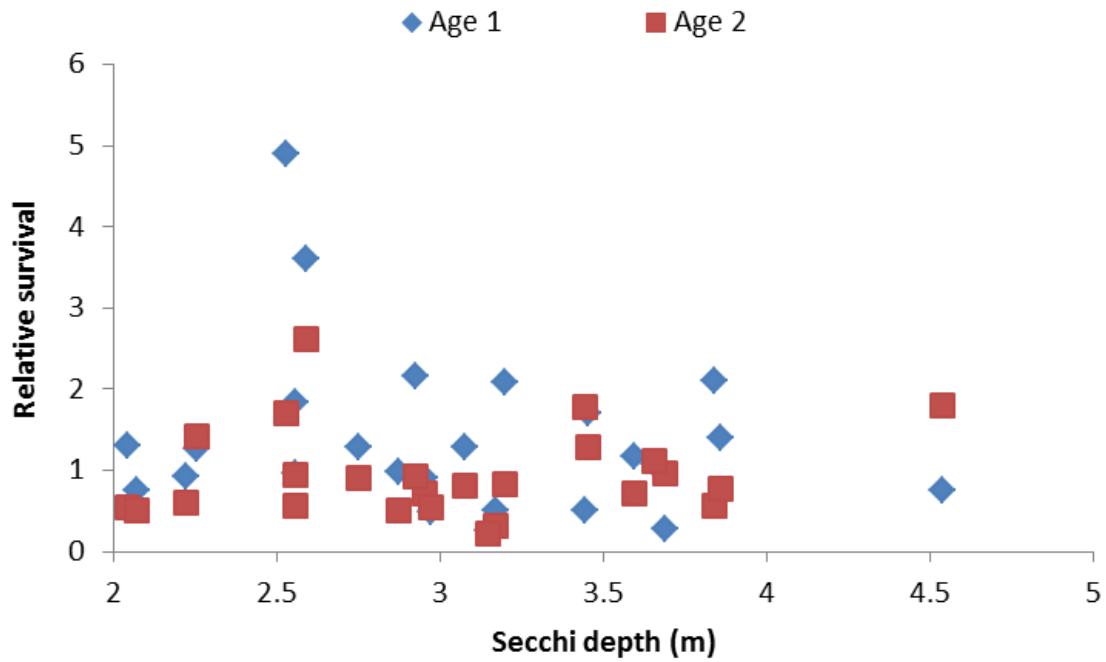


Figure 18. Relative survival of age-1 and age-2 Mille Lac Lakes walleye (calculated by dividing gill net survey age $i+1$ CPUE in year $t+1$ by age i CPUE in year t at time) in relation to average June to October Secchi depth (1990-2013).