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[Management Brief]

Density Dependence of Walleye Maturity and Fecundity in Big Crooked Lake, Wisconsin, 1997–2003

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Abstract.—Density is an important factor regulating age at maturity and fecundity of fish populations, so we evaluated the effect of the population density of adult walleyes *Sander vitreus* on age at 50% maturity and length-specific fecundity in Big Crooked Lake, Wisconsin, during 1997–2003. Abundance of adult walleyes from mark–recapture surveys ranged from 2,046 fish (3 per acre) to 4,901 fish (7 per acre). Age at 50% maturity ranged from 3.89 to 4.88 years, length of walleye sampled for fecundity ranged from 13.0 to 24.7 in, and average fecundity of a 17-in walleye ranged from 41,061 to 53,009 eggs. Age at 50% maturity increased significantly as adult walleye population density increased, whereas average fecundity of a 17-in walleye did not change significantly with density. We conclude that age at 50% maturity could be used as an indicator of population density and exploitation stress and thus could be used to set desired levels of harvest.

Population density is an important factor regulating recruitment, growth, and mortality of fishes (Spangler et al. 1977; Muth and Wolfert 1986; Fox and Flowers 1990; Myers 2002), including walleye *Sander vitreus*. Population density may affect the growth rate of fishes, which may then affect age at maturity and fecundity (Spangler et al. 1977; Baccante and Reid 1988; Muth and Ickes 1993; Trippel 1995). Density of fish populations can be regulated by biological factors such as prey abundance, cannibalism, and competition; abiotic factors such as temperature and nutrients; or human-caused factors such as exploitation (Spangler et al. 1977; Muth and Wolfert 1986; Baccante and Reid 1988; Trippel 1995).

Age at maturity is related to density for some fish species, because as population density decreases, growth increases and age at maturity decreases (Spangler et al. 1977). For example, age at maturity was density dependent for Atlantic cod *Gadus morhua* in the Atlantic Ocean (Trippel 1995) and Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico (Carlson and Baremore 2003). Similarly, in Lake Erie, when the walleye population was heavily exploited and density was low, age at maturity decreased, and when exploitation declined and density increased, age at maturity increased (Muth and Wolfert 1986). Age at maturity was also related to exploitation of northern pike *Esox lucius* in Murray Lake, Houghton Lake, and Lac Vieux Desert in Michigan (Diana 1983).

Fecundity is sometimes related to density, because as population density decreases, growth increases and fecundity may increase (Colby and Nepszy 1981). For example, fecundity was density dependent for cisco *Coregonus artedi* in Lake Superior (Bowen et al. 1991) and for orange roughy *Hoplostethus atlanticus* in Australian waters of the Pacific Ocean (Koslow et al. 1995). Fecundity may be regulated by exploitation, because walleye fecundity increased after controlled exploitation began in two Canadian lakes (Baccante and Reid 1988). Fecundity also responded to exploitation of lake trout *Salvelinus namaycush* (Healey 1978).

Our objective was to determine whether the age at maturity and fecundity of walleyes was related to population density in Big Crooked Lake in Vilas County, Wisconsin, during 1997–2003. We then sought to evaluate the use of age at maturity and

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fecundity as indicators of abundance. Our study at Big Crooked Lake is part of a larger study to evaluate effects of increased exploitation. A 35% exploitation rate was instituted on the walleye population in Big Crooked Lake by purposefully removing 35% of the adult population each year. Population abundance was estimated in spring of each year, and the number of fish harvested throughout the year was recorded through a creel census. In the next spring, if 35% of the adult walleye population had not been harvested in the previous year, more fish were removed until 65% of the adult walleye population remained. Therefore, an induced decline in the adult walleye density in Big Crooked Lake allowed us to test whether maturity and fecundity could be used as indicators of population density.

Methods

Big Crooked Lake, located in Vilas County, Wisconsin, on the property of Dairymen's, Inc., is a private, soft-water, drainage lake of approximately 682 acres (Serns 1978; Short 2001; Hansen et al. 2004). The shoreline of the lake is 5.03 mi and includes two islands. Big Crooked Lake is an oligotrophic lake with a maximum depth of 38 ft. Total alkalinity was approximately 14 mg/L, conductivity was approximately 39 μS/cm at 25°C, and pH was 7.2 (Hansen et al. 2004). Total nitrogen was 0.69 mg/L and total phosphorus was 0.03 mg/L during turnover (Serns 1978). The lake is mostly undeveloped except for a few cabins located on the northern shore. Substrate consists mostly of sand, gravel, and rock. Fish species prominent in the catch include walleyes, muskellunge *Esox masquinongy*, northern pike, smallmouth bass *Micropterus dolomieu*, yellow perch *Perca flavescens*, rock bass *Ambloplites rupestris*, mimic shiners *Notropis volucellus*, and white suckers *Catostomus commersonii*.

The adult walleye population was surveyed by mark–recapture in Big Crooked Lake each year during 1997–2003. Walleyes were collected for marking in fyke nets with 3.9-ft frames and 0.75-in-square mesh immediately after ice-out in April or early May. Adult walleyes were identified as fish with externally visible gametes or fish greater than or equal to 15.0 in (Beard et al. 2003); these fish were marked by removal of a fin or with monel metal jaw tags and released. The recapture sample came from a combination of a mandatory creel census, gillnetting, and electrofishing from ice-out until June. A mandatory creel census on the lake ensured that every fish was checked by a dock attendant. Gill nets were 200, 250, and 300 ft long and 6 ft high; they were set on the bottom with a soak time of 3 to 4 hours. Gill-net twine was either nylon or monofilament, and the monofilament had a twine size of 0.01 in. Gill nets ranged from 2.5 to 4.5 in stretch measure and had a hanging ratio of 0.5 (length of the supporting rope divided by the stretched length of the netting; Hayes et al. 1996). Electrofishing was from a boat-mounted 230-V AC unit with two booms and three dropper electrodes (Hansen et al. 2004). The electrofishing boat was run as close to shore as possible, around the entire shoreline and islands, at night during spring spawning. Crews consisted of one operator and two netters, and the speed of the boat was 1.4–1.6 mi/h. We assumed the recapture sample was random because all anglers were interviewed for the creel census, angling took place throughout the lake, and the entire shoreline of the lake was electrofished. Adult walleye were vulnerable to capture in all gear types. Population abundance was estimated for adult male and female walleyes with Chapman's modification of the Petersen estimator (Ricker 1975). We estimated 95% confidence intervals for mark–recapture estimates of abundance by using formulas for exact 95% confidence intervals for the binomial proportion of marked individuals in recapture samples (formulas 24.28–24.29; Zar 1999).

Age at maturity was estimated for female walleyes from angler-caught fish observed during a mandatory creel census and from gill-net-caught fish during sampling. Walleyes caught by anglers from the first Saturday in May to the third week in June were examined for maturity by a Wisconsin Department of Natural Resources employee. Gill nets were the same as those used for mark–recapture surveys. Maturity was estimated by examining the gonads. Ages of fish shorter than 20 in were estimated from scale samples; ages of longer fish were estimated from spine samples. Scale-based age estimates were compared with those for fish of known age and for fish of partial known age (Devries and Frie 1996). Fish of known age were marked with a permanent fin clip at age 0, and the fin clip given changed yearly on a 4-year cycle. Fish of partial-known age were fish that were tagged at a younger age estimated from a scale sample.

The mean age at 50% maturity (X_m) was estimated for the walleye population in each year during 1997–2003 from the nonlinear relationship between the proportion of mature females in each class, M_x, and age, X,

$$M_x = \frac{1}{1 + e^{-r(X - X_m)}},$$

where M_x is a variable that describes the proportion of mature females as a function of age X, r is a parameter that describes the degree of curvature in the relationship between maturity M_x and age X, and X_m is a parameter that describes the inflection point in the curve, the mean age at 50% maturity (Quinn and Deriso 1999). To estimate the parameters r and X_m and their asymptotic standard errors and approximate 95% confidence intervals, we used data on the proportion of mature females M_x in each age-class X for each year of sampling and a Gauss–Newton numerical search method with additive errors (Systat 2004).

Fecundity was estimated for individual fish sampled from early March to early May during 1997–2003. Fish were collected through the mandatory creel census, fyke netting, and electrofishing, as described above. Total length was measured to the nearest 0.1 in, and weight was measured to the nearest 0.01 lb. Scales were removed from each fish to estimate age as above. Ovaries were removed, wrapped in cheesecloth, and placed in a 10% formalin solution. Prior to examination, each ovary was rinsed, blotted dry, and weighed to the nearest 0.00035 oz. A cross-section of the right ovary was taken from the medial section because this section has the least-associated error (Serns 1982). Each cross-section was weighed to the nearest 0.00035 oz, and the eggs in the cross-section were counted. The number of eggs in the entire ovary was then estimated from direct proportion by weight (Serns 1982).

The mean fecundity of a 17-in walleye was estimated for each year from the linear relationship between $\log_e$(fecundity) and $\log_e$(length),

$$\log_e(\text{fecundity}) = \log_e(\alpha) + \beta \cdot \log_e(\text{length}),$$

where $\log_e$(fecundity) is a variable for the number of eggs estimated for individual female walleye sampled, $\log_e$(length) is a variable for length of individual female walleye sampled, α is a parameter for the slope of the relationship near the origin, and β is the change in the slope with length for the allometric relationship between fecundity and length. The mean fecundity of a 17-in walleye was used as an index of fecundity because 17 in was the mean length of female walleyes in the fecundity sample. The 95% confidence intervals for mean fecundity of a 17-in female walleye were estimated as the prediction interval for an estimated Y (Zar 1999).

Linear regression was used to determine whether age at maturity or fecundity or both were related to the population density of adult walleyes. First, we tested for density dependence of maturity by linear regression of the annual estimates of mean age at 50% maturity in each year, X_m, against adult walleye population density (number/acre) in each year. Adult walleye population density was also regressed against the age at 50% maturity of the next year to account for a 1-year time lag. Next, we tested for density dependence of fecundity by linear regression of the mean fecundity of a 17-in walleye against adult walleye population density (number/acre). The adult walleye population density was also regressed against the mean fecundity of a 17-in walleye of the next year to account for a 1-year time lag. We concluded that maturity and fecundity were density dependent if the slope of either line was significantly different from zero ($P \leq 0.05$); they were density independent if the slope of the line was not significantly different from zero ($P > 0.05$).

If age at maturity or fecundity was significantly related to density, we tested relationships between growth and maturity or fecundity and used inverse prediction to estimate density from either age at maturity or fecundity. First, if density was related to age at maturity or fecundity, we regressed the mean length at age 3, an index of growth in each year, against adult walleye density (number/acre) to test for density dependence of growth. Next, adult walleye population density was regressed against mean length at age 3 in the next year to account for a 1-year time lag. Next, if mean length at age 3 was significantly related to density, then mean length at age 3 was regressed against age at maturity or fecundity to determine whether variation in growth caused the variation in age at maturity or fecundity. Last, if age at maturity or fecundity was related to population density, we used inverse prediction to estimate density from either age at maturity or fecundity (Zar 1999).

Results

Population estimates, densities, age at 50% maturity, and fecundity of 17-in walleyes varied widely in Big Crooked Lake during 1997–2003 (Figure 1). Adult walleye abundance ranged from 2,046 to 4,901 walleyes, and adult walleye population density ranged from 3.00 to 7.19 adult walleyes per acre. Age at 50% maturity ranged from 3.89 to 4.88 years. The length of walleyes used in the fecundity sample ranged from 13.0 to 24.7 in and averaged 17.1 in (SD = 2.4 in). Fe-

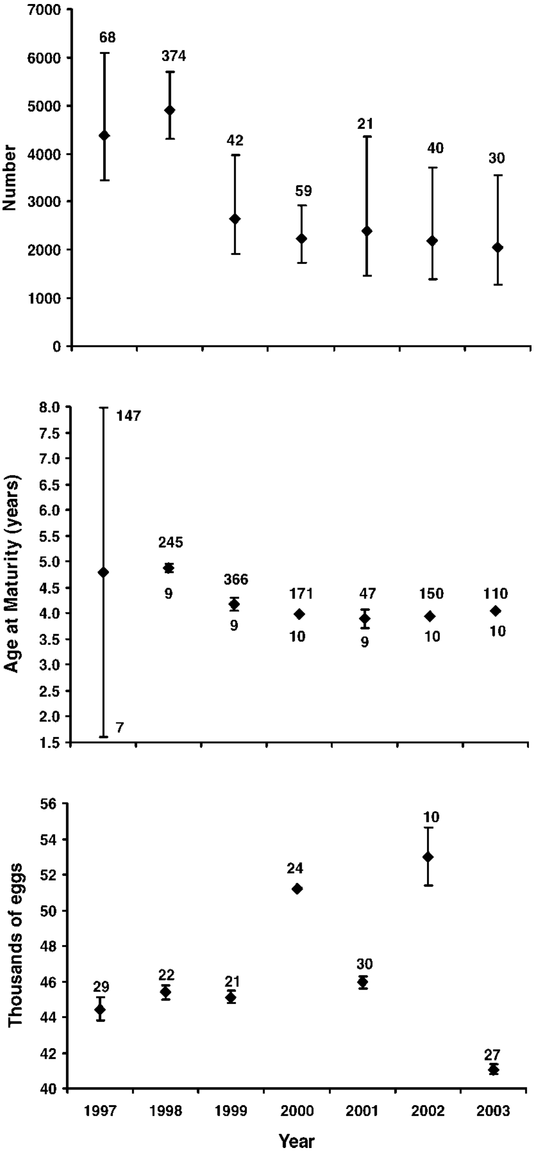

FIGURE 1.—Adult abundance (upper panel), age at 50% maturity (middle panel), and fecundity (lower panel) ± 95% confidence interval of walleyes in Big Crooked Lake, Wisconsin, during 1997–2003. Numbers above abundance estimates are the numbers of recaptures in each year, numbers above age at 50% maturity are the numbers of fish for each year, and numbers above fecundity estimates are sample sizes in each year.

cundity for a 17-in walleye ranged from 41,061 to 53,009 eggs.

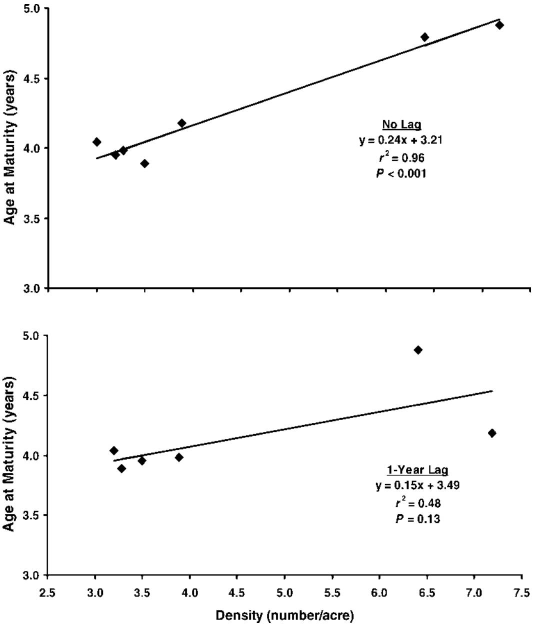

FIGURE 2.—Age at 50% maturity versus adult population density (upper panel) and age at 50% maturity versus adult population density in the previous year (lower panel) for walleyes in Big Crooked Lake, Wisconsin, during 1997–2003.

The age of walleyes at 50% maturity was positively related to adult walleye population density in Big Crooked Lake during 1997–2003 ($F_{1,5}$ = 111.08; $P < 0.001$; Figure 2). The age at 50% maturity decreased from 4.9 to 3.9 years as the walleye population density decreased from 7.19 to 3.00 walleyes per acre. Age at 50% maturity in the next year was not significantly related to adult walleye population density ($F_{1,4}$ = 3.63; $P = 0.13$; Figure 2). Population density increased from 2.1 to 7.5 walleyes per acre as age at 50% maturity increased from 3.75 to 5.0 years, based on the inverse prediction model (Figure 3). Length at age

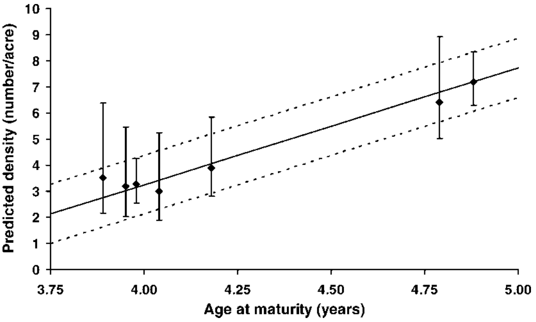

FIGURE 3.—Observed (error bars = 95% confidence interval) and predicted adult walleye population density (regression line ± 95% prediction interval) versus age at 50% maturity for walleyes in Big Crooked Lake, Wisconsin, during 1997–2003.

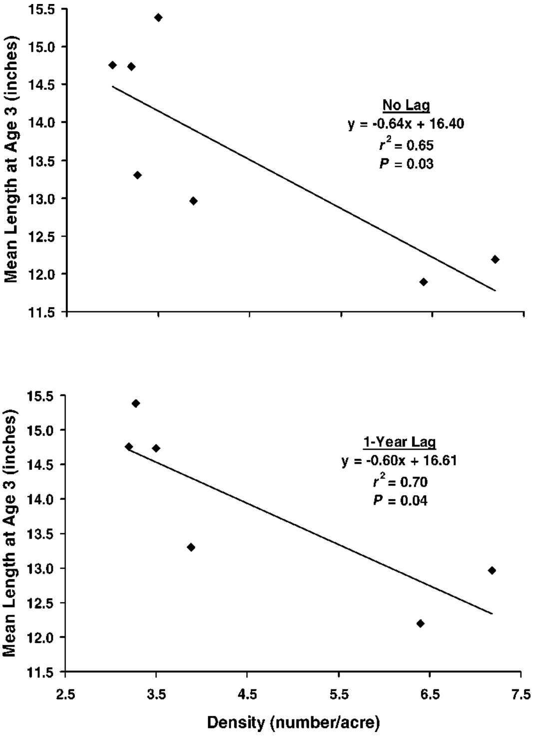

FIGURE 4.—Mean length at age 3 versus adult population density (upper panel) and mean length at age 3 versus adult population density in the previous year (lower panel) for walleyes in Big Crooked Lake, Wisconsin, during 1997–2003.

3, an index of growth, was significantly related to adult walleye population density ($F_{1,5}$ = 9.20; P = 0.03; Figure 4) and to age at 50% maturity ($F_{1,5}$ = 13.81; P = 0.01; Figure 5). Similarly, length at age 3 in the next year was also significantly related to adult walleye population density ($F_{1,4}$ = 9.33, P = 0.04; Figure 4).

Fecundity of a 17-in walleye was not significantly related to adult walleye population density in Big Crooked Lake during 1997–2003 ($F_{1,5}$ = 0.39; P = 0.56; Figure 6). Fecundity varied without trend from 41,061 to 53,009 eggs as the walleye population density decreased from 7.19 to 3.00 walleyes per acre. Fecundity of a 17-in walleye in the next year was not significantly related to adult walleye population density ($F_{1,4}$ = 0.17; P = 0.70; Figure 6).

Discussion

We found that age at maturity decreased as walleye population density decreased in Big Crooked Lake, which is similar to the findings of other studies. Trippel (1995) and Carlson and Baremore (2003) found that a decrease in age at maturity coincided with a decrease in density for Atlantic cod in the Atlantic Ocean and for Atlantic sharpnose shark in the Gulf of Mexico, respectively, which suggests that age at maturity is density dependent. Carlson and Baremore (2003) and Wolfert (1969) found that a decrease in age at maturity coincided with an increase in growth rates for Atlantic sharpnose shark in the Gulf of Mexico and for walleye in Lake Erie, respectively, which suggests that growth may be the mechanism by which age at maturity changes with density. Age at ma-

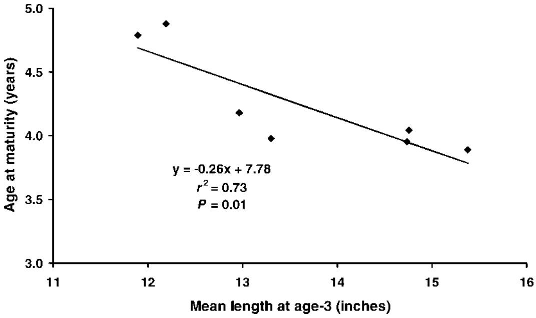

FIGURE 5.—Age at 50% maturity versus mean length at age 3 for walleyes in Big Crooked Lake, Wisconsin, during 1997–2003.

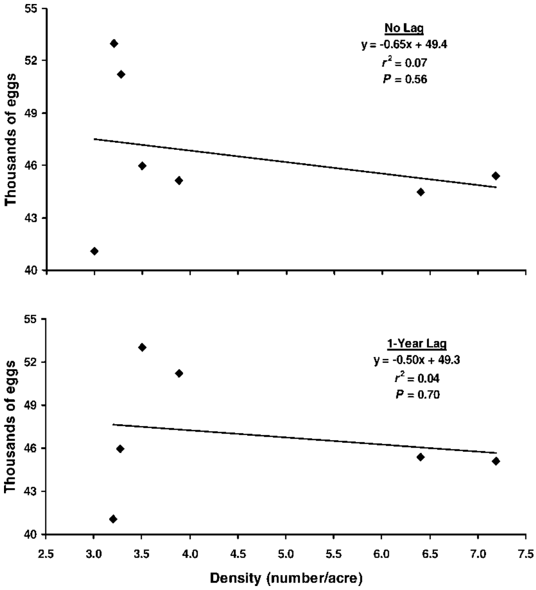

FIGURE 6.—Mean fecundity of a 17-in walleye versus adult population density (upper panel) and mean fecundity of a 17-in walleye versus adult population density in the previous year (lower panel) for walleyes in Big Crooked Lake, Wisconsin, during 1997–2003.

turity was related to exploitation for northern pike in Murray Lake, Houghton Lake, and Lac Vieux Desert in Michigan (Diana 1983) and for walleye in Lake Erie (Muth and Wolfert 1986). If age at maturity is regulated by changes in density that can be caused by exploitation, then age at maturity would be a good indicator of overexploitation. Therefore, age at maturity could be used to manage the walleye fishery in Big Crooked Lake, Wisconsin, because age at maturity is an indicator of population density. Our results are promising, but confirming the relationship over a broader range of population densities would help to define the shape of the relationship between population density and age at maturity. Because other factors also influence population density, density and age at maturity may change independently of exploitation in other systems.

We found that walleye fecundity was not significantly related to walleye population density in Big Crooked Lake, which is in contrast to findings for other studies, which found that increasing fecundity coincided with decreasing population density for ciscoes in Lake Superior (Bowen et al. 1991) and orange roughy in Australian waters of the Pacific Ocean (Koslow et al. 1995). However, average fecundity may be related to population density over a broader range of population density than we observed in our study. Alternatively, other studies have shown that fecundity was more strongly related to factors other than population density. For example, fecundity may be related to prey availability, rather than population density, as was found for brown trout *Salmo trutta* (Bagenal 1969) and rainbow trout *Oncorhynchus mykiss* (Scott 1962). Fecundity may also vary 1 year later than population density, because walleyes develop their eggs in the fall of the previous year and therefore depend on energy acquired during the preceding summer (Nikolskii 1969; Henderson and Morgan 2002). However, we found that walleye fecundity in the next year was not related to walleye population density. Fecundity may depend on the level of intraspecific and interspecific competition for prey (Baccante and Reid 1988). If density of a species declines, then intraspecific competition would decline, or if density of competing species declines, then the level of interspecific competition would decline, and in either case, a lower level of competition may result in a greater number of available prey per individual. This in turn would allow individual fish to dedicate more of their energy intake to producing eggs and would result in higher fecundity. Last, fecundity may vary because older female percids may not spawn every year (Henderson et al. 2000); moreover, walleye fecundity may be inversely related to egg size because younger fish spawn as if semelparous and older fish spawn as if iteroparous (Henderson and Nepszy 1994). Therefore, if not all older females spawn and egg size varies, population fecundity may vary over time with density. Finally, the large variation in estimates of fecundity could be due to sources of error in the cross-sectional sampling method used for estimating fecundity.

Yearly changes in age at maturity could be used to set harvest levels for Big Crooked Lake, Wisconsin, because yearly changes in age at maturity reflected yearly changes in walleye population density. To use our model for age at maturity as a predictor of population density in other lakes, our relationship between population density and age at maturity would need to be verified. Population density could be estimated by mark–recapture or another method, and age at maturity could be estimated from samples of gonads and ages obtained during creel or fishery surveys. Inverse prediction (Zar 1999) could then be used to estimate population density from age at maturity with as much precision as population density can be estimated from mark–recapture surveys, as we found. Harvest regulations could then be adjusted to achieve the desired population density. Age at maturity could also be used as an indicator of exploitation stress. If age at maturity for a population decreased, the harvest rate could be lessened to reduce exploitation stress on the population. In contrast to age at 50% maturity, fecundity is a poor indicator of density and so should not be used to index exploitation stress or to predict density without further study over a broader range of walleye population densities.

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