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#### **ARTICLE**

# Impacts of Aging Error on Walleye Management in the Winnebago System

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#### Abstract

The age data used to manage Walleye Sander vitreus fisheries are not always accurate, as otoliths typically provide more accurate age estimates for larger, older Walleyes than dorsal spines. We assessed the impacts that the aging error associated with the use of dorsal spines has on the estimated age distribution, growth and mortality rates, and yield per recruit for Walleyes in the Winnebago system, Wisconsin. Age distributions derived from otolith age estimates more accurately portrayed variable recruitment than those derived from dorsal spine age estimates. The mean estimates of instantaneous total annual mortality developed from sex-specific catch curves were greater when dorsal spine age estimates were used (0.515 for males, 0.493 for females) than when otolith age estimates were (0.349 for males, 0.396 for females), with most of the differences being observed in natural mortality estimates. The von Bertalanffy growth models were not significantly different, but the yield-per-recruit models (which rely heavily on von Bertalanffy model parameters) incorporating spine age data produced average yield estimates 50-70% lower than the models developed from otolith ages. The yield-per-recruit models derived from spine-determined ages also resulted in lower recommendations as to the age and size of fish for maximum yield at all exploitation levels than the models developed from otolith age data. The mean dorsal spine and otolith age estimates were similar for male Walleyes <457 mm and female Walleyes <508 mm, but for larger fish otoliths yielded significantly older ages than spines. Given the economic and social impacts of the Winnebago system Walleye fishery, we recommend exclusive use of otoliths to obtain the most accurate estimates of fish age, growth, mortality, and yield. In populations in which the sacrifice of large quantities of fish is not acceptable, we recommend using spines to estimate the ages of smaller fish (males <457 mm, females <508 mm) and otoliths to estimate the ages of fish larger than these critical lengths.

Aging error associated with underestimating the ages of older fish reduces the accuracy of estimated rates of growth, mortality, and recruitment (Bradford 1991; Mertz and Myers 1997). These three rates have the greatest impact on the dynamics of a fish stock and are used extensively in population dynamics models, including catch-at-age models and cohort analyses, which are becoming more commonly used in fisheries management and research (Ricker 1975; Beverton 1987; Maceina et al. 1998). Model results are only as accurate as the data that are input into them, underlining the critical importance of collecting accurate age data for producing reliable and meaningful results (Mertz and Myers 1997).

Walleyes Sander vitreus are one of the most popular and actively managed recreational and commercial freshwater game fish species in North America, and extensive research has been conducted to determine the relationships between Walleye age estimates derived from various structures, including scales, spines, fin rays, vertebrae, cleithra, and otoliths. The majority of these studies have concluded that Walleye age estimates from otoliths are the most precise and likely the most accurate, while age estimates from nonlethal structures (scales, spines, and fin rays) typically agree with otolith age estimates for fish up to a certain age and size but underestimate the ages of larger, older fish relative to otolith ages (Campbell and

Babaluk 1979; Erickson 1979, 1983; Kocovsky and Carline 2000).

If fisheries managers could identify the critical size at which nonlethal structures begin to underestimate fish ages for Walleyes, a sampling protocol could be developed using nonlethal structures to accurately estimate the ages of smaller fish and otoliths to accurately assign ages to larger fish. For example, Kocovsky and Carline (2000) recommended the use of scales to age Walleyes <500 mm in Pymatuning Sanctuary, Pennsylvania, while otoliths were used to more accurately estimate the ages of Walleyes >500 mm. To date, no study published in the peer-reviewed literature has identified these critical lengths for Walleye age estimates derived from dorsal spines and otoliths.

The Winnebago system Walleye fishery is nationally recognized, and accurate age data are required to estimate and track mortality rates for the effective management of the fishery. Age estimates from known-age Walleyes collected from the Winnebago System showed that dorsal spines underestimated the age of Walleyes age 7 and older, while age estimates from otoliths were accurate for Walleyes up to at least age 10, with strong corroboratory evidence that these age estimates were accurate for all ages of Walleyes (Wisconsin Department of Natural Resources [WDNR], unpublished data). Due to the size of the Winnebago System (the largest inland lake in Wisconsin) its high Walleye abundance, the sacrifice of Walleyes for age estimation is tolerated by the educated and engaged general public. However, there are other populations within the state for whom the sacrifice of large numbers of fish for age estimation is not possible or acceptable. Our objectives were (1) to determine the impact that the aging error inherent in dorsal spine age assignments has on estimates of age distribution, somatic growth rates, mortality, and yield per recruit and (2) to design a sampling protocol for collecting age structures that would provide relatively accurate age estimates for Walleyes while minimizing the number of fish that would have to be euthanized.

## **METHODS**

Study area.—The Winnebago system is a large, shallow, eutrophic ecosystem in east-central Wisconsin composed of Lake Winnebago and three smaller lakes (Butte des Morts, Winneconne, and Poygan) that collectively comprise 668 km² of surface water. The upper Fox River and the Wolf River (along with their major tributaries) flow into the lakes, draining a 15,540-km² watershed. The floodplain of the lower 60 km of the upper Fox River and the lower 200 km of the Wolf River upstream of the lakes contain an extensive network of old channels, oxbows, and bottomland forest and marsh which in most years carry spring floodwaters over wet meadows, providing spawning habitat for Walleyes. Walleyes are abundant in the Winnebago system and are the primary focus of a high-profile, year-round recreational fishery that has an annual regional economic impact of \$234 million (Cook and Neiswender 2007).

Fish collection.—Adult Walleyes were collected during April spawning assessments (2009–2011) on the upper Fox and Wolf rivers via electrofishing using a standard Wisconsin-style boom shocker with pulsed DC (25% duty cycle, 50 pulses per second, conductivities of 330-370 µS/cm, typically producing an electrical field of 100 V at 5 A or less). In addition to electrofishing, fyke nets (19-mm bar mesh) were set in spawning marshes during the 2011 spawning assessments. Sex and reproductive stage (ripe for males; green (hard), ripe, or spent for females) were determined for all captured fish based on extrusion of gametes. The TL of all fish was measured to the nearest 0.1 in, and the first 50 fish at each spawning location were weighed to the nearest 0.02 lb (length and weight measurements were recorded in English units and later converted to metric units). Random samples of adult male Walleyes were euthanized to obtain a representative age sample for each 12.7-mm size-class (8-16 fish per class, with greater sampling of larger size-classes to account for the greater age variability at greater lengths). Age assignments from otoliths and dorsal spines were independently used to estimate the age, somatic growth, mortality, and yield per recruit of adult male Walleyes. Estimates of these population characteristics were compared to assess the impacts of underestimating fish age with dorsal spines on the management of male Walleyes in the Winnebago system. All Walleyes that were not euthanized for otolith collection were marked with Floy anchor tags (FD-94) using a Floy Mark II tagging gun (Floy Tag and Manufacturing, Inc.) equipped with a 33-mm needle. Tags were inserted at an acute angle into the base of the left posterior dorsal fin, similar to the methods described by Guy et al. (1996). Special care was taken to ensure that tags were inserted behind pterygiophores and then properly seated by gently tugging on the tag. Each tag contained a unique number sequence and the address of the Wisconsin DNR in Oshkosh. Tag returns from angler-harvested Walleyes were used to estimate annual exploitation rates (u) of adult Walleyes (1993–2011) using the equation

$$u = (N_C/0.5)/(N_T) \cdot 100,$$

where  $N_C$  is the number of tagged fish reported by anglers as harvested,  $N_T$  is the total number of fish tagged during spawning assessments conducted that spring, and 0.5 represents the 50% tag return rate by anglers (a standard value used as part of the Winnebago Walleye management program that has been vetted over time, 1989–2011; WDNR, unpublished data).

The Winnebago system hosts over 65 Walleye tournaments annually, which provide an opportunity to collect otoliths and dorsal spines from mortalities of fish >381 mm (most Winnebago system Walleye tournaments impose a 381-mm size limit). Two tournaments were monitored in June 2009, while three tournaments were monitored in June 2010. After weighin, Walleyes were deemed releasable or unreleasable by WDNR personnel and all unreleasable fish were measured and weighed as previously described. Sex and maturity were also determined

for all unreleasable fish based on color, shape, and development of the gonads. Dorsal spines and otoliths were removed from a random sample of female Walleye mortalities as previously described. As with those for male Walleyes, these age estimates were used to compare the age, growth, mortality, and yield per recruit of female Walleyes and to assess the impacts of aging error on the management of female Walleyes in the Winnebago system.

Fish age estimation from calcified structures.—The second or third dorsal spine was removed as close to the skin interface as possible with surgical nail nippers, placed in a sample envelope, and allowed to air dry for a minimum of 2 weeks. Excess dry tissue was removed before cutting 0.30–0.50-mm sections with a Buehler Isomet low-speed saw using glycerol as a blade lubricant. Sections were aged (without knowledge of sex and size) using a Meiji microscope under 25–45× magnification and dark field transmitted light. To maintain consistency between past and present aging techniques and criteria for annuli enumeration, all age estimates were made by the same reader who has aged all Walleye spines collected from the Winnebago system since 1989.

Otoliths were extracted and placed in perforated vials to minimize breakage and air dry for a minimum of 30 d. Otoliths were then embedded in Epo-Quick two-part epoxy for a minimum of 24 h before 0.30–0.40-mm sections were cut using a South Bay Technology low-speed diamond wheel saw (Model 650) with water as a blade lubricant. Cross sections were aged by a reader with 4 years of experience aging otoliths. Age was estimated without knowledge of sex and size under 25–56× magnification with an Olympus SZX7 stereomicroscope and bright field transmitted light. Isopropyl alcohol (50%) was used to help clear sections, but no polishing was done.

Data analysis.—Due to sexually dimorphic growth, data from male and female Walleyes were analyzed independently. Male length and age data from April spawning assessments and female length and age data from June tournament monitoring were incorporated into sex-specific age-length keys to assign ages to all adult Walleyes that were sampled during April spawning assessments (Robson and Chapman 1961). Due to the high-profile nature of the spring fishery and the high value placed on adult female Walleyes by the public, we were unable to euthanize adequate sample sizes of mature female Walleyes during April spawning assessments. Therefore, we used age structures removed from female Walleyes sampled within length-classes during June tournament monitoring and incorporated these age data into age-length keys to assign ages to adult female Walleyes captured during April spawning assessments. The age assignments derived from structure- and sex-specific age-length keys were used to estimate both the age distributions of the spawning stock and the mean length at age of fish within the sample, as outlined by Bettoli and Miranda (2001). Mean length at age data from individual spawning assessments (2009-2011) were averaged to establish a mean length at each age-class for adult male and female Walleyes sampled during the 3-year period.

Mean lengths at age 1 and age 2 were derived from empirical data collected during night electrofishing surveys conducted on Lake Winnebago in October 2008–2010. The von Bertalanffy growth model (von Bertalanffy 1938),

$$L_t = L_{\infty} \cdot (1 - e^{-K(t-t0)}),$$

where  $L_t$  is the length at time t,  $L_{\infty}$  is the asymptotic length (model parameter), K is Brody's growth coefficient (model parameter), and  $t_0$  is the time of zero length or fertilization (model parameter), was fit to mean length-at-age data to estimate  $L_{\infty}$ , K, and  $t_0$  for male and female Walleyes (a total of four growth models were constructed, one based on otolith age estimates and one on dorsal spine age estimates for each sex). Asymptotic 95% confidence intervals were estimated for the three model parameters using the PROC NLIN procedure available in SAS. Likelihood ratio tests were used to determine whether the von Bertalanffy growth models for male and female Walleyes were significantly different ( $P \le 0.05$ ) and whether the growth models derived from otolith age estimates were significantly different from those derived from dorsal spine age estimates.

The parameters from the von Bertalanffy models for male and female Walleyes derived from spine and otolith age data were used to develop four yield-per-recruit (YPR) models of the form

$$Y_t/N_0 = F \cdot e^{-M \cdot (t_r - t_0)} \cdot W_{\infty} \cdot (1/Z - (3e^{-K \cdot (t_r - t_0)}/Z + K) + (3e^{-2K \cdot (t_r - t_0)}/Z + 2K) - (e^{-3K \cdot (t_r - t_0)}/Z + 3K),$$

where  $Y_t$  is the yield per recruit,  $N_0$  is the number of fish that recruit to the population (set to 1 to eliminate it from equation), F is the instantaneous fishing mortality (treated as a variable), M is natural mortality (treated as constant),  $t_r$  is the age of recruitment to the fishery,  $W_{\infty}$  is the weight at  $L_{\infty}$  derived from the von Bertalanffy models and weight-length models for summer male and female Walleyes from the Winnebago system in 2009–2011 (WDNR, unpublished data), and Z is total mortality (F + M). These models were run at instantaneous fishing mortality rates (F) ranging from 0 to 1.0 so as to include the mean annual exploitation estimates (u) for male and female Walleyes during 1993–2011; they were also run at ages ranging from 1 to 20 to allow evaluation of the impact of aging error on predicted yields driven by the hypothetical size limits derived using spine versus otolith length-at-age data for the range of ages of each sex observed in the fishery. The impact of spine versus otolith age data on the mean yields predicted by YPR models was evaluated for male and female Walleyes. The YPR model estimates for males age 1–10 at an F of 0.185 ( $u \approx 14.7\%$ ) and females age 1–12 at an F of 0.285 ( $u \approx 22.6\%$ ; average rates for adult male and female exploitation, 1993-2011) were averaged for both the spine and otolith age models and compared. The maximum ages selected for this analysis were the ages at which male and female Walleyes were beginning to approach their average asymptotic lengths in the Winnebago system (526 and 665 mm; WDNR, unpublished data).

Sex-specific catch curves were developed from both dorsal spine and otolith age assignments for all adult fish sampled during spring spawning assessments. The first ages represented in the catch curves were 4 for male Walleyes and 5 for female Walleyes (the ages at which >85% of male Walleyes and >95% of female Walleyes are mature; WDNR, unpublished data). A linear regression from each catch curve yielded the slope of the line of best fit through the descending limb of the catch curve, from which the rates of instantaneous total annual mortality (Z) were estimated as the negative values of the slopes of the lines of best fit. Rates of conditional total annual mortality (A) were then calculated from the equation

$$A = 1 - e^{-Z}$$
.

Rates of instantaneous fishing mortality were estimated from the mean rates of conditional total annual mortality and instantaneous annual mortality using the Baranov catch equation (Ricker 1975),

$$F = \mu(Z/A)$$
,

where  $\mu$  is the mean estimate of exploitation from angler tag returns. Instantaneous natural mortality rates (M) were estimated by subtracting the estimated values for F from those for Z.

Mean dorsal spine and otolith age estimates from 25.4-mm length-classes were calculated from adult male age data collected during April spawning assessments (2009–2011) and female age data collected during June tournament monitoring (2009–2010) to determine the lengths at which dorsal spines began to underestimate fish age relative to the ages derived from otoliths. Fisheries managers do not positively know the age of fish when they handle them during surveys; therefore, it is important to determine the length at which age estimates from otoliths and nonlethal structures deviate. Dorsal spine age estimates were considered to underestimate fish age if the mean spine age estimate was not within the 95% confidence interval around the mean otolith age estimate for that length-class.

#### **RESULTS**

Age was determined for 668 male Walleyes and 537 female Walleyes. The adult male and female stocks were dominated by fish age 10 and younger (>89% of the adult population in all years) based on age data from both dorsal spines and otoliths, but there was poor agreement between the age-class strengths estimated from the two structures (Tables 1–2; Figure 1). For example, the 2001 year-class (age-8 fish in 2009 and age-9 fish in 2010) was estimated to compose >20% of the adult stock in both 2009 and 2010 based on otolith age assignments, while that same year-class was significantly smaller in both years based on dorsal spine age estimates (Tables 1–2; Figure 1). Older age-

TABLE 1. Age composition (percent) of adult male Walleyes in the Winnebago system derived from otolith and dorsal spine age estimates, 2009–2011.

Age	2009		2010		2011	
	Otolith	Dorsal spines	Otolith	Dorsal spine	Otolith	Dorsal spine
0						
1						
2			0.84	0.39	4.15	1.92
3			2.85	1.52	49.31	34.97
4	27.51	14.60	9.46	7.96	4.52	19.41
5	23.31	30.63	32.40	30.37	16.47	18.20
6	7.89	12.36	11.61	20.62	13.88	13.62
7	4.95	19.70	12.43	18.99	4.80	4.65
8	25.92	12.37	3.66	12.82	1.54	3.72
9	0.00	3.02	20.94	3.47	0.32	2.04
10	0.60	1.58	0.34	1.03	3.82	0.53
11	1.72	1.55	0.00	1.39	0.05	0.60
12	0.50	2.80	2.04	0.61	0.00	0.18
13	2.81	0.37	0.52	0.57	0.39	0.06
14	0.01	1.01	1.83	0.18	0.12	0.04
15	0.38		0.01	0.07	0.43	
16	0.91		0.01		0.03	0.06
17	0.94		0.26			
18	2.55		0.15		0.05	
19			0.64			
20					0.12	

classes were detected from the otolith age estimates each year that were not detected with the dorsal spine age estimates. With otoliths the oldest males were estimated to be 18 years of age in 2009, 19 in 2010, and 20 in 2011; with dorsal spines, however, the oldest males were estimated to be 14 in 2009, 15 in 2010, and 16 in 2011.

Likelihood ratio tests detected a significant difference in the otolith-based von Bertalanffy growth model parameters between male and female Walleyes (F = 30.5; df = 3, 33; P < 0.001) (Figure 2) but were unable to detect a significant difference between otolith- and dorsal spine–based von Bertalanffy growth models for male (F = 0.35; df = 3, 33; P = 0.79) and female Walleyes (F = 0.93; df = 3, 29; P = 0.44) (Figure 3). Although no significant difference was found between the growth models derived from dorsal spine and otolith age estimates for either sex, fish were projected to attain greater asymptotic lengths when dorsal spine age estimates were used for the models (Figure 3).

Yield-per-recruit modeling showed that the average yields of Walleyes up to their asymptotic ages (age 10 [which corresponds to 526 mm] for males and age 12 [665 mm] for females) at the long-term average instantaneous fishing mortality rates (0.185 for males and 0.285 for females) were 73.0% (SD = 9.5%) less for males and 49.8% (10.8%) less for females when the models incorporated spine ages rather than otolith ages. The

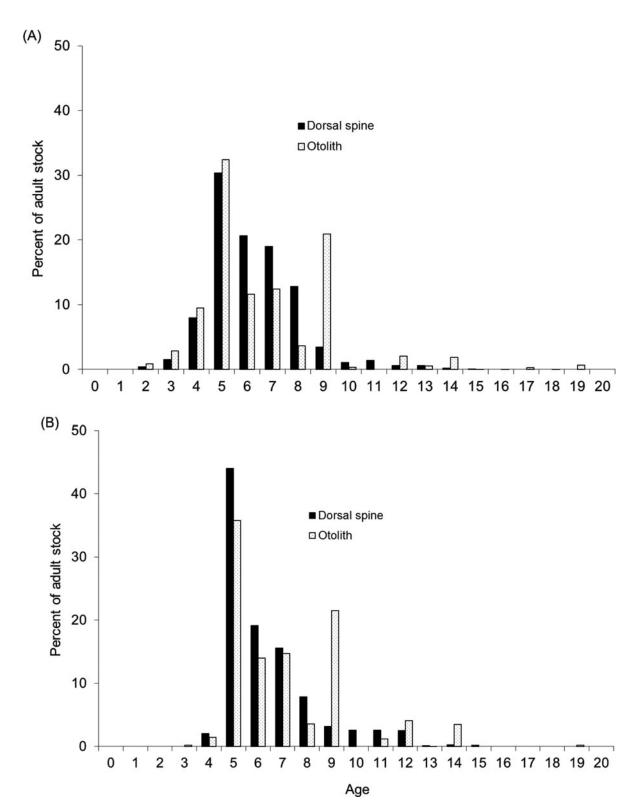


FIGURE 1. Age distributions of adult ( $\mathbf{A}$ ) male and ( $\mathbf{B}$ ) female Walleyes sampled during April 2010 spawning assessments in the Winnebago system, based on dorsal spines and otoliths.

TABLE 2. Age composition (percent) of adult female Walleyes in the Winnebago system derived from otolith and dorsal spine age estimates, 2009–2010.

		2009	2010		
Age	Otoliths	Dorsal spines	Otoliths	Dorsal spines	
0					
1					
2					
3	0.65		0.19		
4	8.69	9.76	1.45	2.05	
5	21.45	23.00	35.77	44.05	
6	29.53	30.58	13.98	19.14	
7	3.51	13.38	14.67	15.56	
8	23.80	11.37	3.53	7.87	
9	1.40	1.50	21.47	3.14	
10		2.18		2.56	
11	3.61	3.28	1.13	2.56	
12	1.23	2.76	4.09	2.50	
13	3.72	1.02	0.06	0.13	
14	0.31	0.58	3.46	0.26	
15		0.20		0.19	
16	0.38	0.38			
17	0.00				
18	1.53				
19			0.19		
20					

model derived from spine age data indicated that at an annual u of 14.7% the maximum yield per recruit of male Walleyes (70 g) would be attained by implementing a 300-mm minimum size limit (msl) at age 2; by contrast, the model derived from

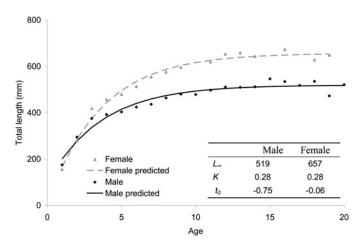
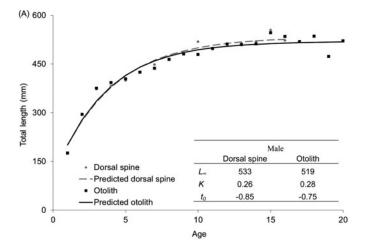


FIGURE 2. Length-at-age data derived from otolith age estimates and predicted growth from otolith-based von Bertalanffy growth models for male and female Walleyes sampled during April spawning assessments (2009–2011). The 95% confidence intervals are as follows:  $L_{\infty}=502$ –537 mm (males) and 635–678 mm (females); K=0.205–0.354 and 0.228–0.329; and  $t_0=-1.499$  to +0.007 and -0.447 to +0.335.



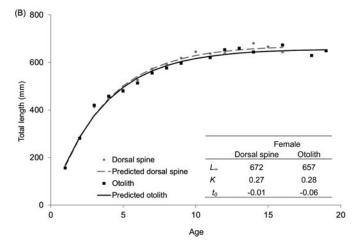


FIGURE 3. Comparison of empirical length at age and predicted growth from von Bertalanffy growth models constructed from dorsal spine and otolith age estimates for (A) male and (B) female Walleyes sampled during April spawning assessments (2009–2011). The 95% confidence intervals are as follows:  $L_{\infty}=508-559$  mm (males) and 652–692 mm (females); K=0.182-0.330 and 0.233–0.315; and  $t_0=-1.618$  to +0.075 and -0.318 to +0.291.

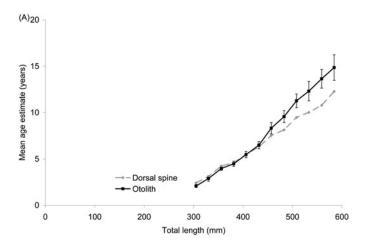
otolith age data indicated that a higher yield (183 g) would be attained with a 399-mm msl at age 3. Models run for females found similar results: the model derived from spine age data indicated that at an annual u of 22.6% the maximum yield per recruit (362 g) would be attained by implementing a 460-mm msl at age 4, while the model derived from otolith age data indicated that a higher yield (632 g) would be attained with a 500-mm msl at age 5.

The mean estimates of instantaneous total annual mortality derived from the catch curves were higher for both males and females when based on dorsal spine age estimates rather than otolith age estimates. The mean estimate for adult males was 0.515 (range = 0.388–0.639, SD = 0.126; N = 3) with dorsal spine age data and 0.349 (range = 0.249–0.411, SD = 0.087; N = 3) with otolith age data; the estimates for adult females were 0.427 in 2009 and 0.557 in 2010 (mean = 0.493) with dorsal spine age data and 0.346 in 2009 and 0.446 in 2010 (mean =

0.396) with otolith age data. Although the mean estimates of Z based on dorsal spine age estimates were consistently higher than the estimates derived from otolith-based estimates, the small sample size (N=3 for males and 2 for females) limited our ability to statistically compare spine- and otolith-age-based catch curves.

The mean annual estimates of adult exploitation based on 1993-2011 tag return data are 14.7% (range = 7.1-23.0%, SD = 0.054; N=19) for adult males and 22.6% (range = 5.4-32.9%, SD = 0.077; N=19) for adult females (WDNR, unpublished data). The estimates of instantaneous fishing mortality were very similar when using dorsal spine (0.19 for males and 0.29 for females) and otolith age estimates (0.17 for males and 0.27 for females), while the estimates of instantaneous natural mortality were higher with dorsal spines (0.32 for males and 0.20 for females) than with otoliths (0.17 for males and 0.12 for females).

The mean dorsal spine and otolith age estimates were similar for males <457 mm and females <508 mm (Figure 4).



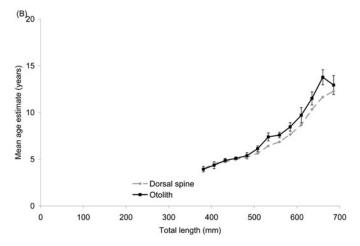


FIGURE 4. Mean age estimates derived from dorsal spines and otoliths for 25.4-mm length-classes of (A) male Walleyes sampled during April spawning assessments and (B) female Walleyes sampled during June tournament monitoring (2009–2011). The error bars represent 95% confidence intervals around the mean otolith age estimates.

However, the mean dorsal spine age estimates were significantly lower than the mean otolith age estimates for male and female Walleyes larger than these critical lengths, at which the 95% confidence intervals did not overlap (Figure 4).

#### **DISCUSSION**

The use of otoliths—and thus more accurate age data—has greatly advanced understanding of the population dynamics of the Walleye population in the Winnebago system. Otolith age estimates have allowed older year-classes of Walleyes to be observed that were not represented when using age estimates derived from nonlethal structures. Priegel (1969) reported a maximum longevity of 8 years for Walleyes in the Winnebago system using scales, whereas longevity was perceived to be 16 years with the dorsal spine age data included in this study. The use of otoliths for age estimation has shown that the Walleyes in the Winnebago system can reach at least age 20.

The detection of these older age-classes leads to estimates of instantaneous total annual mortality and natural mortality that are lower than previous estimates. The total annual mortality and natural mortality estimates derived from catch curves based on otoliths were lower than those based on dorsal spines for the male and female Walleyes sampled in every year of this study. These results are important, as fishing mortality and natural mortality are believed to be compensatory risks of death for certain species, i.e., natural mortality rates decrease as fishing mortality rates increase (Allen et al. 1998). Therefore, by overestimating natural mortality rates, managers may incorrectly perceive that harvest can be increased, which could lead to overharvest (Lai and Gunderson 1987; Rien and Beamesderfer 1994; Reeves 2003). Leaman and Nagtegaal (1987) estimated much lower instantaneous natural mortality rates, and thus substantial reductions in total allowable catch, for Yellowtail Rockfish Sebastes flavidus when using age estimates derived from sectioned otoliths (0.07) than when using otolith surface readings (0.25). Similarly, underestimating the age of snappers (*Lutjanus* spp.) caused overestimates of natural mortality rates, and the population would have been overfished if the inflated estimates of natural mortality had been applied to the snapper management program (Newman et al. 2000). The greater the aging error, the less accurate the mortality estimates are, underscoring the importance of using accurate age data to estimate mortality rates that in turn are used to make critical management decisions. Given the economic and social importance of the Walleye population in the Winnebago system, it is imperative to collect data that are as accurate as possible in order to accurately track the mortality rates of this population through time.

There are many factors that can affect mortality, such as variable recruitment, exploitation, prey abundance, and thermal regimes (Kocovsky and Carline 2001). As strong and weak year-classes move through a fishery, they affect the trajectory of the catch curves and thus the mortality estimates. Due to the inherent variability in the estimated rates of mortality within populations, it is imperative to collect accurate age data for an

extended period of time to fully understand the mortality dynamics of a fish population (Koonce et al. 1977; Kocovsky and Carline 2001). This study includes 3 years of otolith age data for males and 2 years for females, and otolith age estimates will continue to be used to track annual mortality through time to better observe how year-class strength affects mortality estimates. More years of paired age data collection (dorsal spines and otoliths) would provide more statistical power to detect differences between catch curves developed with age data from the two aging structures.

Given that year-class strength can affect the mortality estimates derived from catch curves, it is important to accurately assign fish to age-classes. In this study, we demonstrated that age distributions derived from otolith age estimates accurately portrayed the variable recruitment of Walleyes in the Winnebago system, with each generation containing multiple strong yearclasses that collectively compose the majority of the adult stock. Due to the relatively high fishing mortality rates exerted on the Winnebago system Walleye fishery, especially on females, the robustness of the population is dependent on these regular strong year-classes. By underestimating age with dorsal spines, fish from abundant year-classes were mistakenly assigned to adjacent weaker and younger year-classes, which in turn reduced estimates of interannual variability in recruitment. Bradford (1991) further described this process and stated that underestimating fish age through the use of unvalidated aging techniques can affect recruitment estimates and severely hinder studies to assess the environmental influences on recruitment.

The mean age estimates from dorsal spines and otoliths were very similar for adult males <457 mm and adult females <508 mm, but dorsal spines yielded significantly lower age estimates than otoliths for fish larger than these critical lengths. Kocovsky and Carline (2000) observed similar results in Pymatuning Sanctuary, where scales yielded relatively accurate age estimates for Walleyes <500 mm but otoliths were required to accurately estimate the ages of fish >500 mm. The results from our study can be used to develop an age sampling protocol in which dorsal spines are used to estimate the ages of smaller Walleyes (females <508 mm and males <457 mm) with relative accuracy but otoliths are required to accurately estimate the ages of larger fish.

Underestimating the ages of larger Walleyes by using dorsal spines had little impact on the von Bertalanffy growth models for both sexes. Most of the somatic growth among the Walleyes inhabiting the Winnebago system has already occurred by age 7, the age at which dorsal spines begin to underestimate age. Similar results were reported by Kocovsky and Carline (2001) for Walleyes in Pymatuning Sanctuary, where fish attained approximately 67% of their terminal length before reaching maturity and grew very slowly following maturity. These results demonstrate that most fish growth has taken place by the age at which nonlethal structures begin to underestimate fish age, such that the growth models were relatively unaffected by aging error. Therefore, the use of dorsal spines to estimate growth

rates and von Bertalanffy growth model parameters is acceptable in scenarios where the sacrifice of fish is not possible and yield-per-recruit models are not utilized.

Spine- versus otolith-specific von Bertalanffy model parameters were used along with structure-specific estimates of natural mortality to examine the yield estimates for male and female Walleyes at various exploitation levels through sex- and structure-specific yield-per-recruit models. Despite our failure to find differences between von Bertalanffy models based on spine ages as opposed to otolith ages, yield-per-recruit modeling showed that the minimum size limits to maximize yield inferred from model results based on spine age data would be lower (implying younger ages) for both male and female Walleyes than with otolith age-based models. Also, the yield at any age or size was estimated to be much lower using models based on spine age data. The importance of these findings (assuming that otolith-derived ages are accurate) is that the type of aging error exhibited by spines, i.e., underestimating age after maturity or attainment of a certain size, would likely move a fisheries manager's decision on a minimum size limit to fish that are too small to maximize yield. This phenomenon could have serious ramifications for a fishery, especially if it is managed for maximum sustainable yield, as often is the case in commercial fisheries.

In any assessment, the ultimate use and application of age data need to be considered when determining which aging structure should be used to estimate fish age. Although age estimates derived from scales and dorsal spines are likely inaccurate to varying degrees, they may be acceptable for indicating general trends in age and growth for young, fast-growing fish populations. Such fish are typically more accurately aged because their annuli are easier to identify (Erickson 1979; Belanger and Hogler 1982; Frie et al. 1989). However, otoliths should be used to estimate fish age when populations contain a large percentage of older fish and age data are used to estimate mortality or growth rates used to set harvest regulations. Based on the results from this study, otoliths will be exclusively used to estimate the age of Walleyes in the Winnebago system, as this species is the primary focus of a sport fishery in this system, which annually contributes \$234 million to the local economy and receives national recognition (Cook and Neiswender 2007).

Collecting and utilizing accurate age data are critical to the efficiency and effectiveness of any fisheries management program, as any aging error inherent in scale and dorsal spine age estimates reduces the accuracy of the estimated rates of growth, mortality, recruitment, and yield (Bradford 1991; Mertz and Myers 1997). Effective management hinges on the accurate estimation of growth, mortality, and recruitment, which are the driving forces behind the population dynamics of a fish stock, while yield-per-recruit estimates are often used by managers to set size limits in both commercial and recreational fisheries for Walleyes and many other species. Collecting only spines from Walleyes to derive age estimates is not recommended due to the inaccurate and misleading results from models utilizing spine age data and the erroneous management decisions that

stem from flawed model results. In cases in which the sacrifice of large numbers of fish for age estimation is not possible, dorsal spines can be used to estimate the ages of male Walleyes <457 mm and female Walleyes <508 mm, but otoliths should be used to estimate the ages of larger fish. Although there would be some aging error with this protocol, the number of fish that would have to be sacrificed to estimate age, growth, mortality, and yield would be reduced while maintaining a relatively high degree of accuracy.

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#### REFERENCES

- Allen, M. S., L. E. Miranda, and R. E. Brock. 1998. Implications of compensatory and additive mortality to the management of selected sportfish populations. Lakes and Reservoirs 3:67–79.
- Belanger, S. E., and S. R. Hogler. 1982. Comparison of five ageing methodologies applied to Walleye (*Stizostedion vitreum*) in Burt Lake, Michigan. Journal of Great Lakes Research 8:666–671.
- Bettoli, P. W., and L. E. Miranda. 2001. Cautionary note about estimating mean length at age with subsampled data. North American Journal of Fisheries Management 21:425–428.
- Beverton, R. J. H. 1987. Longevity in fish: some ecological and evolutionary considerations. Pages 161–185 in A. D. Woodhead and K. H. Thompson, editors. Evolution of longevity in animals: a comparative approach. Plenum, New York.
- Bradford, M. J. 1991. Effects of ageing errors on recruitment time series estimated from sequential population analysis. Canadian Journal of Fisheries and Aquatic Sciences 48:555–558.
- Campbell, J. S., and J. A. Babaluk. 1979. Age determination of Walleye, Stizostedion vitreum vitreum (Mitchill), based on the examination of eight different structures. Department of Fisheries and the Environment, Fisheries and Marine Service, Technical Report 849, Winnipeg, Manitoba.
- Cook, C., and C. Neiswender. 2007. The economic impact of angling on the Lake Winnebago system. University of Wisconsin Extension, Winnebago County, Oshkosh.
- Erickson, C. M. 1979. Age differences among three hard tissue structures observed in fish populations experiencing various levels of

- exploitation. Manitoba Department of Natural Resources, Report 79-77, Winnipeg.
- Erickson, C. M. 1983. Age determination of Manitoban Walleyes using otoliths, dorsal spines, and scales. North American Journal of Fisheries Management 3:176–181.
- Frie, R. V., J. K. Anderson, and M. J. Larson. 1989. Age verification of Walleyes from Lake of the Woods, Minnesota. Journal of Great Lakes Research 15:298– 305.
- Guy, C. S., H. L. Blankenship, and L. A. Nielsen. 1996. Tagging and marking. Pages 353–383 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Kocovsky, P. M., and R. F. Carline. 2000. A comparison of methods for estimating ages of unexploited Walleyes. North American Journal of Fisheries Management 20:1044–1048.
- Kocovsky, P. M., and R. F. Carline. 2001. Dynamics of the unexploited Walleye population of Pymatuning Sanctuary, Pennsylvania, 1997–1998. North American Journal of Fisheries Management 21:178–187.
- Koonce, J. F., T. B. Bagenal, R. F. Carline, K. E. F. Hokanson, and M. Nagięć. 1977. Factors influencing year-class strength of percids: a summary and a model of temperature effects. Journal of the Fisheries Research Board of Canada 34:1900–1909.
- Lai, H. L., and D. R. Gunderson. 1987. Effects of ageing errors on estimates of growth, mortality and yield per recruit for Walleye Pollock (*Theragra chalcogramma*). Fisheries Research 5:287–302.
- Leaman, B. M., and D. A. Nagtegaal. 1987. Age validation and revised natural mortality rate for Yellowtail Rockfish. Transactions of the American Fisheries Society 116:171–175.
- Maceina, M. J., P. W. Bettoli, S. D. Finely, and V. J. DiCenzo. 1998. Analyses of the Sauger fishery with simulated effects of a minimum size limit in the Tennessee River of Alabama. North American Journal of Fisheries Management 18:66–75
- Mertz, G., and R. A. Myers. 1997. Influence of errors in natural mortality estimates in cohort analysis. Canadian Journal of Fisheries and Aquatic Sciences 54:1608–1612.
- Newman, S. J., M. Cappo, and D. M. Williams. 2000. Age, growth, mortality rates and corresponding yield estimates using otoliths of the tropical red snappers, *Lutjanus erythropterus*, *L. malabaricus* and *L. sebae*, from the central Great Barrier Reef. Fisheries Research 48:1–14.
- Priegel, G. R. 1969. Age and growth of the Walleye in Lake Winnebago. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 57:121–133.
- Reeves, S. A. 2003. A simulation study of the implications of age-reading errors for stock assessment and management advice. ICES Journal of Marine Science 60:314–328.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.
- Rien, T. A., and R. C. Beamesderfer. 1994. Accuracy and precision of White Sturgeon age estimates from pectoral fin rays. Transactions of the American Fisheries Society 123:255–265.
- Robson, D. S., and D. G. Chapman. 1961. Catch curves and mortality rates. Transactions of the American Fisheries Society 90:181–189.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10:181–213.