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Mortality, Exploitation, Movement, and Stock Size of Saginaw Bay Walleyes, 1981–2011: 31 Years of Tag Return Analysis

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Abstract.–Walleyes are one of the primary targets of the recreational fishery in Saginaw Bay and Lake Huron. To measure mortality rates, exploitation rates, and movement patterns, about 3,000 Walleyes were jaw tagged each year since 1981. A total of 93,669 Walleyes were tagged over the time series and 9,916 tagged Walleye were reported caught by anglers. Correction factors were applied for nonreporting estimating that 24,607 tagged Walleye were actually caught by anglers during the study. The return matrix by year was analyzed by two methods: 1) a computer model (ESTIMATE) for year-specific estimates of survival and recovery rate, with the latter being functionally equivalent to exploitation rate; and 2) numerical estimation methods were employed in AD Model Builder software to derive the parameter estimates. Other fishing and natural mortality rates were derived from these estimates. Total annual mortality ranged from a high of 72% (in 1981) to a low of 21% (in 1994). Walleyes reached recovery targets in 2009 and mortality rates became more variable during that time period. Exploitation rate ranged from a low of 4% (in 1982) to a high of 38% (in 2009). These values were used to help generate estimates of total abundance of age-2 and older Walleyes in the Saginaw Bay stock; similar trends resulted from the two estimation procedures. The population peaked in 2007 (~3.6 million Walleyes). The effect of chronic tag shedding was evaluated using the numerical estimation model version and at an 8% rate, tag shedding did not significantly affect parameter estimates. Movements of Walleyes were analyzed by testing tag return proportions for independence between those from within the bay and outside the bay. Factors appearing to affect the propensity to emigrate from the bay were sex (females 12.9% of tag returns vs. males at 4.3%), size (larger fish more prone to emigrate), and density (fish more likely to emigrate in years of high density). The mortality and exploitation rates exhibited in this time series are regarded as sustainable; however, it was noted that the analysis failed to meet certain assumptions of the model.

Introduction

Walleyes *Sander vitreus* are native nearshore predators that occur throughout Lake Huron but are most abundant in Saginaw Bay (Schneider and Leach 1977; Fielder et al. 2010). Commercial exploitation of Walleye in Saginaw Bay dates to at least 1885 and the fishery was prolific until its collapse in the mid-1940s (Hile and Buettner 1959; Baldwin and Saalfeld 1962). The commercial fishery accounted for the second largest Walleye yield in the Great Lakes after that of Lake Erie, averaging about 450 tonnes per year. The collapse was primarily attributed to degradation of spawning habitat, but also the effects of invasive species such as Alewives *Alosa pseudoharengus*, Rainbow Smelt *Osmerus mordax*, and Sea Lamprey *Petromyzon marinus* (Schneider and Leach 1977). The demise of the historic population was probably hastened by intensive commercial exploitation but not likely caused by it, given that it had persisted for nearly half a century (Schneider 1977).

The ground work for recovery of the Saginaw Bay Walleye population began with the passage of the Clean Water Act in 1972. The commercial fishery was formally closed in 1970. Although Walleye fry stocking had been taking place, real gains in recruitment began with the implementation of Walleye fingerling stocking in the early 1980s, by the Michigan Department of Natural Resources (DNR) (Keller et al. 1987). A recreational fishery soon developed (Ryckman 1986; Fielder et al. 2014). Throughout the 1980s the Walleye population and fishery expanded and then plateaued. It remained stable in the 1990s but was largely dependent on continued Walleye stocking (Fielder et al. 2000; Fielder 2002). Formal recovery criteria were developed and adopted by the Michigan DNR in the early 2000s (Fielder and Baker 2004).

Enormous gains in Walleye reproductive success and subsequent recruitment began in 2003 and are primarily attributed to the collapse of Alewives in Lake Huron (Fielder et al. 2007; Fielder et al. 2008; Fielder and Thomas 2014). The Walleye recreational fishery responded accordingly (Fielder et al. 2014) and was declared recovered (Fielder and Thomas 2014) according to the criteria defined by Fielder and Baker (2004). Walleye stocking was discontinued in 2006 (Fielder and Thomas 2014).

During the initial resurgence of Walleye in Saginaw Bay, it was recognized that information was needed on mortality and exploitation rates (Keller et al. 1987). Such information is fundamental to gauging the status of a population and the management of its fisheries (Ricker 1975; Hilborn and Walters 1992), including Walleye (Schmalz et al. 2011). More specifically, stock assessment requires information on the dynamics of a fish population (Power 2007; Haddon 2001) including the vital statistics of mortality and exploitation. In the case of Saginaw Bay Walleyes, managers desired a barometer with which to gauge the sustainability of the growing fishery and to ensure that Walleye recovery was not jeopardized by exploitation.

In pursuit of estimates of mortality and exploitation rates, tag or band-based methods were developed in the 1960s and 1970s (Jolly 1965; Seber 1965; Seber 1970; Robson and Youngs 1971; Seber 1972). Cormack (1979) and Seber (1982) present detailed reviews of these works and early methods. Brownie et al. (1985) went on to further develop these methods with a series of 14 models for deriving measures of mortality and exploitation from a tagged or banded (presumably representative of the larger population) group. Choice of the most appropriate model depends on how tagged fish are recovered, with dead recoveries typically representing a catch-and-kill fishery. Other assumptions determine model options. Brownie Model 1 (Brownie et al. 1985) was developed for catch-and-kill extractions when year-specific recovery rates and survival rates are hypothesized or desired. Model 1 methods include statistical tests to evaluate if the observed data conform to this model structure and some of the assumptions.

The objective of this study was to generate estimates of total annual survival and exploitation rate for the Walleye population in Saginaw Bay. Instantaneous rates of mortality, as opposed to just annualized rates, were also desired, along with estimates of both the fishing mortality and natural mortality components. This analysis also included an examination of the significance of tag shedding on estimation. The analysis also served as a means to test parameter estimation methods between analytical derivation and numerical search methods. It was also the objective of this analysis to use tag-based metrics to generate estimates of Walleye stock size for the Saginaw Bay population. Secondary objectives for this study were to also learn something about movement of Walleye by virtue of tag returns. Data from this study also afford some unique opportunities for examination of demographics of one of the main spawning runs of Saginaw Bay Walleyes that were used as the source for tagging fish. In the early years of this study, an additional objective was to quantify growth of Walleyes based on changes in length of tagged fish over time. Since then, other studies have offered better means to examine growth and that objective is no longer part of this study and is not reported on here.

Some of the findings from this work have been reported previously. Keller et al. (1987) reported some values of exploitation and survival for 1981–1986. Mrozinski et al. (1991) reported total annual mortality, exploitation, movement, and growth drawing upon tag return data from 1981–1988. Fielder et al. (2000) reported on total annual mortality, exploitation, and movement and offered a demographic summary of the tagged lot for 1981–1997. Most recently, Fielder and Thomas (2006) reported on total annual mortality, exploitation rate, movement, and demographics of the tagged fish for the years 1981–2004. The purpose of this report is to review all findings to date, and provide a more holistic examination in light of the recent recovery of Walleye in the bay. Presented is a more thorough suite of mortality values such as instantaneous (per capita) rates including recreational fishing mortality and estimates of natural mortality. Also developed are estimates of absolute abundance (population size). Movement and demographics of the tagged lot are also updated. Lastly, recommendations about the future of this work are offered.

Methods

Tagging

Each year since 1981, Walleyes were tagged in the Tittabawassee River, a tributary to the Saginaw River (Figure 1). Walleyes were collected by 230-volt DC electrofishing during the height of their annual spring migration for spawning. The assumption, confirmed by tag returns, is that these are Saginaw Bay Walleyes that use the Tittabawassee River for spawning purposes and principally inhabit the bay outside the spawning period. In most years, tagging took place the last week of March or the first week of April. Walleyes were tagged with a #12 butt end monel band 5.26 mm wide and 0.51 mm thick (Figure 2). Tags were stamped with a unique number and a return address. During the tagging process, Walleyes were externally sexed and measured for total length. Beginning in 1994, a subsample of one day's tagging effort (usually about 700 fish) was selected near the peak of the run (when sex ratios were closest to one-to-one) for scale or dorsal spine collection for later age determination. Between 1981 and 1993, Walleyes were subsampled by inch group and total numbers aged were around 200 per year. Initially, aging was performed with scales but was switched to spines beginning around 1998.

Number tagged each year was less than 1,000 until 1983 when a tagging goal was set at approximately 3,000 per year for the remainder of the study (Table 1). Tagging was limited to fish 381 mm or larger to ensure vulnerability to the fishery (381-mm minimum length limit in recreational fishery). Tagging was usually completed within five days. Tagged fish were released at the tagging site (Dow Dam) on the Tittabawassee River for all years except three years when tagging included some fish at Sanford Dam (also on the Tittabawassee River but above Dow Dam). During a few years of this project, mostly before 1991, Walleyes were also tagged in various locations around the bay and for three years in the Flint River (another tributary to the Saginaw River). This analysis does not include those numbers and their returns as they were not consistently tagged over a sufficient time period. Because this analysis was particularly interested in trends over time, it was decided that inclusion of these other locations would not strengthen the inferences drawn from these data.

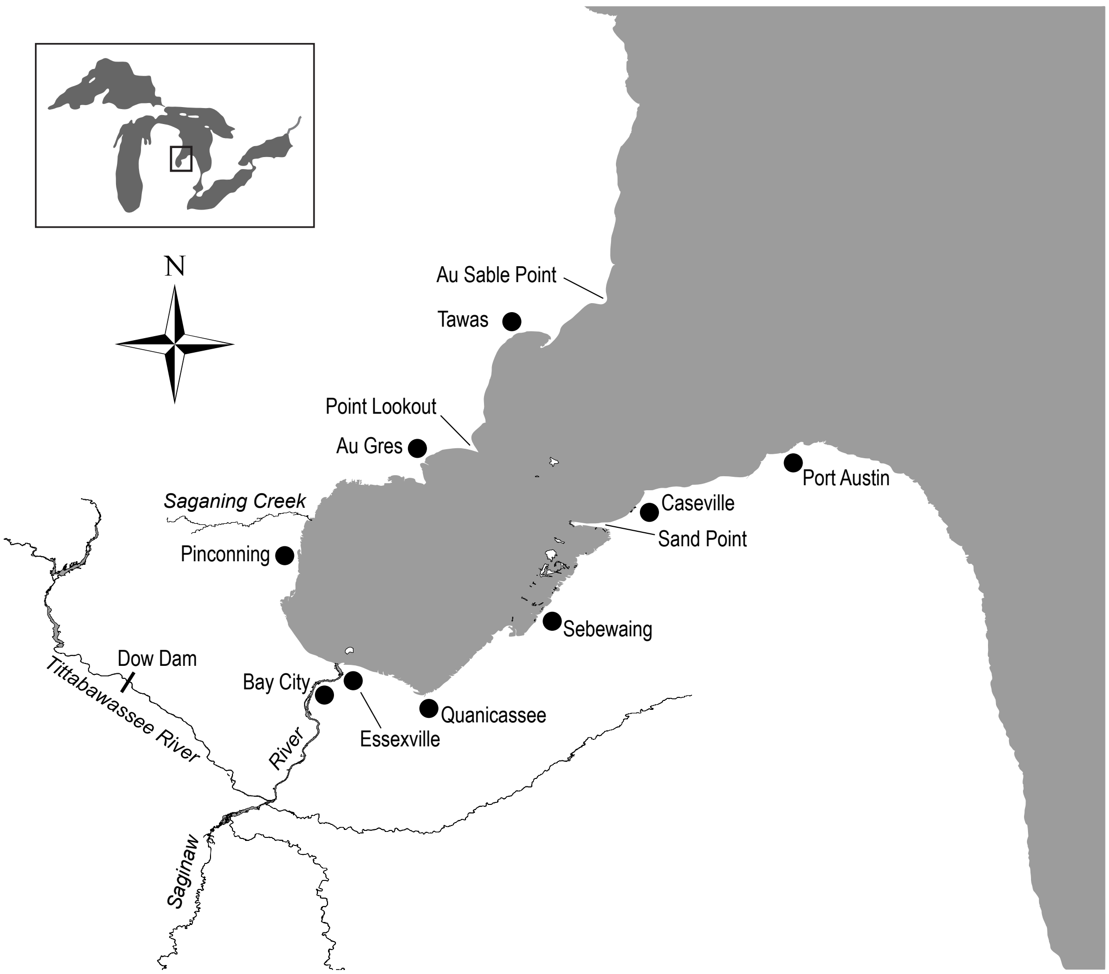


Figure 1.–Saginaw Bay, Lake Huron.

Figure 2.–Monel jaw tag in position on the maxillary and premaxillary of a Saginaw Bay Walleye.

Table 1.–Numbers of Walleyes jaw tagged in the Tittabawassee River 1981–2011, those tags remaining after initial tag shedding (post 21 days) and numbers of tags reported by anglers after expanding by annual correction factors (from Appendix A) for nonreporting. Yearly tagging numbers for three years included Walleyes tagged at Sanford Dam on the Tittabawassee River (1985: 531, 1986: 608, and 1989:497).

Year	Number tagged	Number post 21d	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
1981	400	396	24	4	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1982	727	720		15	17	4	3	8	3	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1983	3,430	3,396			147	73	51	56	41	20	29	12	14	13	9	4	2	0	0	2	2	0	0	0	0	3	0	0	0	0	0	0	0
1984	3,550	3,515				95	124	93	82	49	33	15	12	9	9	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1985	3,866	3,827					188	163	98	58	22	8	7	14	6	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986	3,531	3,496						211	146	56	33	26	19	22	13	2	4	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0
1987	6,020	5,960							436	177	102	38	33	41	22	12	10	0	4	9	7	2	3	5	0	0	0	0	0	0	0	0	0
1988	4,036	3,996								244	135	53	45	36	28	21	14	2	9	0	10	2	5	0	0	0	0	0	0	0	0	0	0
1989	2,991	2,961									111	89	62	93	37	25	10	8	11	2	10	2	0	0	0	0	0	0	0	0	0	0	0
1990	2,488	2,463										96	90	93	60	18	12	8	11	2	2	7	0	0	0	3	0	0	0	0	0	0	0
1991	3,079	3,048											119	195	92	31	18	23	24	9	17	5	3	8	3	0	0	0	3	3	0	0	0
1992	2,995	2,965												296	155	58	43	30	24	27	26	15	5	3	0	0	0	3	0	0	7	0	0
1993	2,990	2,960													280	99	63	51	37	30	36	22	13	8	6	9	0	0	0	0	0	0	0
1994	2,999	2,969														148	105	93	79	41	38	30	5	0	6	3	6	0	0	0	0	0	0
1995	2,970	2,940															107	106	99	69	76	20	8	5	14	6	3	3	0	0	0	0	0
1996	2,992	2,962																150	163	121	112	50	26	24	20	12	0	0	7	0	0	0	0
1997	2,993	2,963																	185	188	138	45	28	32	39	18	9	3	3	0	4	0	0
1998	2,490	2,465																		213	162	60	52	35	36	26	9	3	3	0	0	0	0
1999	2,998	2,968																			305	92	72	67	65	61	24	22	7	3	7	4	0
2000	3,302	3,269																				243	155	164	174	120	61	44	26	38	14	4	4
2001	3,000	2,970																					204	237	140	137	58	32	33	24	43	7	4
2002	2,993	2,963																						410	236	208	85	60	33	58	36	11	8
2003	3,000	2,970																							320	324	164	76	76	76	75	22	8
2004	2,997	2,967																								555	192	140	165	117	147	26	23
2005	2,998	2,968																									353	197	188	182	222	30	31
2006	2,996	2,966																										434	301	213	290	56	23
2007	2,886	2,857																											532	323	405	71	54
2008	2,993	2,963																												774	835	179	66
2009	2,999	2,969																													1139	228	89
2010	2,969	2,939																														657	319
2011	2,991	2,961																															552

Tag return

Tags were reported by anglers harvesting Walleye in the recreational fishery. Tags were rarely returned outside the recreational fishery as no commercial extraction is permitted within Saginaw Bay. Most returns occurred within the bay but some came from areas outside the bay in other parts of Lake Huron allowing the analysis of movement, at least within the recreational fishery. Cooperation with tag returns was encouraged in early years with a public awareness campaign. Over time, anglers became accustomed to reporting jaw tags. Most mailed the tag along with capture information to the address stamped on the tag. Since 2008, a web page on the Internet has been maintained to facilitate electronic reporting by anglers. Information recovered from anglers included location of capture and each tag return was assigned a latitude / longitude in the tag return database as accurately as reasonably possible to facilitate analysis of movement. Anglers returning tags were contacted if additional information was needed to complete the report. All anglers received a follow up thank you letter that included information on the history of their fish such as when and where it was first tagged.

Correction for nonreporting

Tagging programs rely on angler participation for the notification of a tagged Walleye (tag return or recovery). A common problem with tagging operations is noncompliance with tag returns especially with ongoing programs where anglers may grow complacent with their participation (Brownie et al. 1985; Haas et al. 1988; Pollock et al. 1991; Brenden et al. 2010; Vandergoot et al. 2012). A nonreporting correction factor of 2.33, based on $100 reward tags, was previously derived for the Saginaw Bay Walleye fishery (Fielder and Thomas 2006). The correction factor was based on 300 reward tags in the year 2000. The correction factor was derived by comparison of the difference in return numbers between the reward tags and the normal nonreward tags. The correction factor was derived based on returns in the first year at large only.

Walleye movement is the subject of a study underway that also used $100 rewards for the reporting of telemetry tags. That study documented a reporting rate for Tittabawassee River-implanted Walleyes in 2011 that was 4.03 times that of the jaw tag return rate for the same year (USGS Great Lakes Science Center, unpublished data). This provided an updated nonreporting value and it indicates that noncompliance has grown since 2000. For adjustment of jaw tag return values for this study, a time-varying nonreporting value series was developed as a power function since tagging began, employing the two know values of 2.33 for 2000 and 4.03 for 2011. The resulting function is reported in Appendix A. Tag recoveries in subsequent years of the study, treated as the observed returned or reported tags, were then the product of the actual number returned and the year-specific correction factor.

Tag return data analysis

Analysis reported in past publications of this data series made use of the computer program ESTIMATE Model 1 or Model 0. ESTIMATE is a Fortran77 language program operated from DOS (Brownie et al. 1985). Beginning in 2010, the formulation of Brownie et al. (1985) Model 1 (year specific survival and reporting rates) was programmed in Microsoft Excel. This offered the same output as ESTIMATE, better facilitated the calculation of additional derived forms of mortality estimates, and was easier to update.

Reported tags were compiled into a tag return matrix of number reported by year for each year tagging was conducted. The yearly interval was from tagging occasions (approximately April to April) and not on a strict calendar year cycle. This better represented the year at large and is regarded as one "fishing year". Use of a fishing year has the advantage of spanning the time period of a single age for

Walleyes as opposed to having fish age one year within the analysis period and was consistent with the fishing year designation used in the harvest reporting for the fisheries (Fielder et al. 2014).

While these methods allow for the partitioning of maturity groups and sexes in separate analyses, no such delineation was attempted here. Ages and sexes were pooled to yield an overall representation of the Walleye population at large. Walleyes 381 mm and larger are generally sexually mature within the Saginaw Bay Walleye population or likely would be first time spawners the following year. Consequently, it was inappropriate to try and delineate by maturity group as offered by Brownie et al. (1985).

Brownie et al. (1985) characterizes the analysis as a stochastic (probabilistic) analysis since tag recoveries are treated as a random event. The recovery of tags from those tagged in year *i* can come from that year and subsequent years. The year of recovery can be denoted by *j* such that $R_{i,j}$ denotes the number of tags reported from tagging year *i* in fishing year *j*. Brownie et al. (1985) treats $R_{i,j}$ as a binomial random variable (recovered or not recovered) of sample size N_i (the original number tagged in year *i*) that follows a multinomial distribution with the addition of f_j (a recovery rate parameter specific to recovery year *j*). The last parameter is an annual survival rate S_j. Brownie et al. (1985) offers several tag recovery model forms but the Model 1 year-specific version results in the *j* notation of the parameters meaning they are allowed or hypothesized to vary by year, resulting in a more realistic model in most instances.

The derivation of parameters f_j and S_j are estimated based on the principles of maximum likelihood. In Brownie's model ESTIMATE, the maximum likelihood estimators (MLEs) of the parameters are derived according to the formulas developed by Seber (1970) and Robson and Youngs (1971) as follows:

$$\hat{f}_j = \frac{R_i}{N_i}\frac{C_j}{T_j} \qquad [1]$$

where R_i is the row totals of the recoveries over the life of the tagged cohort, and C_j is the column total recoveries for the year of recovery. From these T_j (an intermediate statistic) is;

$$T_j = R_i + T_{j-1} - C_{j-1} \qquad [2]$$

except for T_1 which equals R_1. Parameter $\hat{f}_j$ is already an unbiased estimator and requires no further expression. Parameter S_j is calculated as:

$$\tilde{S}_j = \frac{R_i}{N_i}\left(\frac{T_j - C_j}{T_j}\right)\frac{N_{i+1}+1}{R_{i+1}+1} \qquad [3]$$

where $\tilde{S}_j$ is the unbiased estimator of S_j. The means of these parameters is the quotient of their sums and k-1 where k is the number of years of tagging. The variance of $\hat{f}_j$ is:

$$\operatorname{var}(\hat{f}_j) = (\hat{f}_j)^2\left[\frac{1}{R_i} - \frac{1}{N_i} + \frac{1}{C_j} - \frac{1}{T_j}\right] \qquad [4]$$

The variance of $\widetilde{S}_i$ is given by:

$$\operatorname{var}(\widetilde{S}_j) = (\widetilde{S}_j)^2 \left[\frac{1}{R_i} - \frac{1}{N_i} + \frac{1}{R_{i+1}} - \frac{1}{N_{i+1}} + \frac{1}{T_{j+1} - R_{i+1}} - \frac{1}{T_j} \right] \quad [5]$$

The standard error (SE) of each parameter is then the square root of the variance and the 95% confidence interval is approximated as ±1.96(SE).

The MLEs of parameters $\widetilde{S}_j$ and $\hat{f}_j$ as developed by Seber (1970) and Robson and Youngs (1971) are analytical solutions to the estimation. By contrast, numerical methods can iteratively solve for the parameters (Miranda and Bettoli 2007). Parameters were estimated both ways, using the Excel version of the Brownie Model ESTIMATE and by numerical methods in AD Model Builder (ADMB-Project.org 2011; Fournier et al. 2012) software.

The AD Model Builder (ADMB) software made use of the same tag return matrix and the same nonreporting values as the ESTIMATE analysis. This numerical parameter search method was also based on MLE but in the form of an objective function. The ADMB software minimized the negative log likelihood (thus maximizing the overall likelihood) of a multinomial function given as:

$$NLL = -1\sum \left(R_{i,j} \left(\ln p_{i,j} \right) + UR_i \left(\ln \left(1 - totp_i \right) \right) \right) \quad [6]$$

where $p_{i,j}$ is the probability of the tag recovery for the i^{th} tagging year in the j^{th} recovery year; $totp_i$ is the total probability of the individual $p_{i,j}$ values summed across the i^{th} tagging year; UR_i is the number of tags not recovered from the original lot tagged in year *i*; and $R_{i,j}$ is as defined before, the number of tags recovered from tagging year *i* in recovery year *j*.

Besides distinguishing the two estimation methods by their parameter derivation, an additional difference was the treatment of varying tag retention or tag shedding. Tag loss or shedding is an issue in all tagging studies. Because of the difficulty in quantifying tag shedding, the issue is most often dealt with by making the assumption that tag shedding is zero (Brownie et al 1985; Hoenig et al. 1998; Eveson et al. 2009; Vandergoot et al. 2012). There have been a number of studies that have tried to quantify tag shedding with results (ranging from no tag shedding to as much as 60%) varying across species, tag type, and method used to apply the tag (Fabrizio et al. 1996; Miranda et al. 2002; Isermann and Knight 2005; Vandergoot et al. 2012). Vandergoot et al. (2012) developed tag shedding estimates for Lake Erie Walleye including rates specific to the methods employed by the Michigan DNR in this study. That study distinguished between initial tag shedding (within the first 21 d) and long term or chronic shedding (occurring each year). The initial tag shedding for the Michigan DNR was 1% and the long-term chronic (annual) tag shedding was 8%, meaning that 8% of the study Walleyes at large each year shed their tags. While substantial, there is no allowance for annual tag retention rates less than 1.0 in Brownie computer model formulations thus no adjustment was made in the ESTIMATE analysis to try and compensate for this form of tag shedding. However, the numbers initially tagged each year in the ESTIMATE analysis were reduced by 1% to compensate for initial tag shedding and the reduced value was used for subsequent computations.

Because the numerical estimation method is based on probabilities of tag recoveries, the accounting for annual or chronic tag shedding is possible. This is accomplished by applying a 92% tag retention value in the tag recovery probability calculation. That formula comes from Brownie et al. (1985) as:

$$p_{i,j} = \left(\prod_{i=1}^{j-1} S_{i,j} \theta \right) f_{i,j} \quad [7]$$

where the values are as defined previously and θ is the tag retention value. As with the ESTIMATE-based analysis, tag recoveries were expanded by the nonreporting values. The significance of tag shedding was evaluated by comparing the tag recovery rate estimates f_j and estimates of survival S_j derived by analytical and numerical estimation methods. The ADMB code for this analysis appears in Appendix B. Significant difference was identified when values from the two estimation methods differed by more than 2SEs.

The model fit for both ESTIMATE and the ADMB version (fitting the assumptions) was tested using the Chi-square goodness of fit test where the expected (predicted) values populate a matrix of recoveries as the product of N_i and the associated year-specific $\tilde{S}_j$ and $\hat{f}_j$ values. The Chi-square test statistic is then the sum of the squared difference of the observed less the expected values divided by the expected values. When cells in the matrix of expected values were less than 2, remaining neighboring cells were pooled. The pooling was then matched in the observed data as necessary to keep the two matrices aligned. The corresponding degrees of freedom are given by the expression:

$$df = (k(k+1)/2) + (l-k)k - (k+l-1) \qquad [8]$$

where k is as defined above and l is the number of years of recovery. The Chi-square goodness of fit test allowed the testing of the null hypothesis that the model assumption of year specific survival and recovery rates was appropriate as judged by a probability α value greater than 0.05.

Population and fishery statistics from tag return analysis

For both estimation methods used, tag return analysis results in estimates of two relevant statistics that are in turn used to generate others. Survival (S) is directly estimated as an annual value. In the tag return matrix, the expected number for the first year of returns from the same year of tagging does not result in the estimation of S for that year. Survival in this format is treated as survival from the previous year to the next year and used in the next cell of the matrix to calculate the expected value but is notated as the survival attributable to the first year (Brownie et al. 1985; Cooch and White 2009). In this regard, S might be thought of as the survival over winter to the following year. Consequently, there is no S value for the last year of the matrix and associated mortality statistics derived from S also then lag one year behind.

Recovery rate f is the second statistic; it is analogous to exploitation rate u and can be treated and used as such [$u = f_j$ assumes that the constant *1* is 1.0 from Pine et al. (2003) equation 3]. Recovery rate, however, from Brownie et al. (1985) draws upon tag returns from the multiple years of cohorts at large, computationally accounting for numbers remaining at large from previous years tagging efforts by applying corresponding survival values. Consequently, recovery rate f may vary from the traditional calculation of exploitation rate which is the proportion of tags returned in the first year ignoring any natural mortality or more specifically assuming that natural mortality in year 1 is nil. In this regard, recovery rate f should be a more robust expression of exploitation rate. Exploitation rate derived from first year returns were also calculated for comparison to f and termed "direct expression of exploitation rate".

With estimates of S_j and u_j derived from tagging studies, other related mortality components can easily be derived (Pine et al. 2003). Annual mortality A was derived as A = 1-S. Instantaneous (per capita) total mortality rate Z was then derived as ln(A)/-1. Instantaneous fishing mortality F was derived as (Zu)/A where u is the exploitation rate. Instantaneous natural mortality M was computed as Z-F, and total annual natural mortality rate as v = MA/Z. Estimates of total annual mortality (A) are contrasted with the same values estimated by catch curve and cohort based analysis as reported by Fielder and Thomas (2014). Tagged-based estimates of natural mortality M were also be compared to those derived based on the Pauly equation (Pauly 1980) and based on longevity (Hoenig 1983). The Pauly equation makes use of Von Bertlanaffy growth parameters and temperature data. Time-varying growth parameters of L_∞ and K were obtained from survey data for Saginaw Bay Walleyes (Fielder et al. 2000; Fielder and Thomas 2006; Fielder and Thomas 2014) and limited the analysis to the years since 1989. Natural mortality *M* for the Pauly equation was derived using mean annual air temperature data as recommended by Pauly (1980), and was obtained from climate data for Midland-Bay City-Saginaw (MBS) airport. Analysis of natural mortality following Hoenig (1983) methods requires maximum age by year in the population's age structure; and were obtained from spawning run/tagging operation in the Tittabawassee River. That method was limited to data since 1986 since the age structure in year priors was not fully mature from the initial resurgence of fish and consequently didn't meet the assumptions of the method.

Estimates of abundance

The customary format for estimating abundance in a tagging study is to structure the analysis based on live recoveries in short term studies. Such analysis lends itself to a variety of estimation options (Pine et al. 2003; Hayes et al. 2007). Because this study only used dead recovery data form of tag returns, such methods were not possible. Size in number of the Saginaw Bay stock of Walleye was estimated by two methods. First was to use the fishery itself as a second sampling period and dead recoveries (reported tags) as the sample of the $\frac{m_2}{n_1}$ tagged population. The simplest two sample population estimation method is the Lincoln-Peterson formulation, given by Ricker (1975) as:

$$\widehat{N} = \frac{n_1 n_2}{m_2} \qquad [9]$$

where the initial number tagged is n_1, the estimate of harvest in the fishery for that year is n_2, and m_2 is the number of tags observed (reported) by anglers producing that fishery in the same year as the harvest estimate. Note that the quotient (the number of tags reported in the first year out of the initial number tagged) is one definition of exploitation rate *u*. Equation 9 above is then functionally equivalent to:

$$\widehat{N} = \frac{n_2}{u} \qquad [10]$$

where in this analysis year-specific *u* can be obtained as f_j from equation 1. This method of estimating a fish population from the quotient of harvest and exploitation rate has been used by others (Hasbrouck et al. 2000). This methodology requires several assumptions including: (1) survival of tagged fish is 1.0 in the first year of life (i.e. natural mortality is not a factor until the conclusion of the fishery); (2) the population is closed to immigration and emigration; and (3) capture probability is equal amongst all the Walleye in the tagged group.

While precise compliance with these assumptions is improbable, they may not be entirely unreasonable. In fact, most natural mortality is probably not realized until over winter or during the spawning period, both of which occur after the vast majority of the fishery has taken place. While immigration and emigration are known to occur to and from Saginaw Bay by Walleyes, tag returns can also be realized from outside the bay and thus representation of the second assumption (tags representing fish at large) is not fully violated. Lastly, the representativeness of the tagged fish, which reflect the larger population, is a fundamental assumption to all tagging or marking studies; specifically that the mortality rates exhibited by Walleyes in the Tittabawassee spawning run of fish is the same as Walleyes in the rest of the Saginaw Bay population. A more likely assumption violation would be heterogeneity in capture probability by fish size, age, or sex (Pine et al. 2003). Such heterogeneity in capture probability could be a serious bias.

The first estimate of population size was based on equation 10, using the annual estimates of adult Walleye harvest from the Michigan DNR Statewide Angler Survey Program (creel survey). The population estimation made use of the exploitation rate originating from the recovery rate values based on the ESTIMATE program analysis. Because tags are reported by the recreational fishery from both within Saginaw Bay and from outside it, the harvest estimates used were those of all the Michigan waters of Lake Huron, not just those of the bay. While there is undoubtedly some local Walleye production outside of Saginaw Bay, this analysis made the assumption that it was negligible and attributed the majority of the harvest to migrants from the Saginaw Bay stock. The creel survey estimates up to 2010 in the bay are described by Fielder et al. (2014) but are supplemented by Michigan DNR unpublished data to complete the composite harvest. Complete estimates were only available for the years 1986–2011, so population estimates were limited to those 26 years. There was no creel survey in 1990 so neighboring values were averaged to allow an estimate for that year and an uninterrupted time series.

Bence and Dobiesz (2000) estimated the abundance of Walleye in Saginaw Bay and the southern main basin of Lake Huron to aid in the estimate of predator consumption demand for the lake. They constructed an age-structured representation of the population through cohort analysis for the main basin fish and via exponential population formulation for the bay, the latter of which made use of some of the mortality and exploitation rates from this study. Their estimation was for the years 1981–1999.

The second approach to population estimation using tag return metrics sought to approximate the methodology used by Bence and Dobiesz (2000). This approach was fundamentally different from the recapture-based estimation, offering additional estimates for comparison. I repeated the analysis because the Bence and Dobiesz (2000) work only offered estimates up through 1999 and also because their approach sought to recreate an age and year-specific fishing mortality rate (*F*) so as to generate a predicted fishery with which to estimate the population size by iteratively adjusting an age-specific population to generate a fishery for comparison to the observed. My methods followed a similar tactic but elected to use the primary two parameters estimated by the ESTIMATE-derived tag return analysis; survival rate S (yielding instantaneous total mortality rate *Z*) and recovery rate f (yielding exploitation rate), thereby tying the estimation back to the tag return data.

As in Bence and Dobiesz (2000), population size was given by the formula:

$$N_{a+1,y+1} = N_{a,y} e^{-Z_{a,y}} \qquad [11]$$

with starting values for *N* from 1980 set as parameters to be solved for along with the annual recruitment to the population at age 2 (for each year). The annual population size was then the sum of the individual numbers of each age within a year. The population was constructed for years 1981–2011. The values $Z_{a,y}$ in equation 11 were the instantaneous total mortality rates from the tag return analysis by year and the same values were applied across all ages.

The predicated fishery generated from this population was simply the product of the exploitation rate and the abundance of each age each year as:

$$Pred\_Harv_{a,y} = (N_{a.y})(\mu_y) \qquad [12]$$

where $N_{a,y}$ is the age and year-specific estimate of Walleyes from equation 11 and μ_y is the year specific recovery rate (f_i) from the tag return analysis. The observed Walleye fishery made use of the same estimates of harvest from the first methods of population estimation described above for equation10. The harvest, however, was expressed across ages 2–13 by applying the age composition of the harvest as reported by Fielder et al. (2014) and supplementing with Michigan DNR unpublished data for those ports in the Michigan waters of Lake Huron outside Saginaw Bay.

This approach allowed for the creation of a predicted and observed age-specific harvest by year for Walleyes in Lake Huron, again treating the main basin fish as a likely extension of the Saginaw Bay stock of Walleyes, as a result of seasonal emigration. Following Bence and Dobiesz (2000), cell-specific residual sums of squares (RSS) were then calculated as observed harvest minus predicted harvest and totaled. The total RSS was then minimized by iteratively solving for the parameters of annual recruitment (age-2 abundance) and the initial population in 1980 in the population model (equation 11). Model fitting was limited to the years 1986–2011 when there were observed measures of Walleye harvest but population estimation began in 1981. The Solver utility from Microsoft Excel was used to derive the estimates and run consecutively until it reported that all constraints and optimality conditions were satisfied. Initial attempts at optimization indicated that Solver wanted to set some year classes to negative values or to zero if constrained to zero. In the final version, I constrained the minimum age-2 recruitment to 10,000 Walleyes to prevent any year class from being completely absent.

In the Michigan waters of Lake Huron, the recreational length limit of 381 mm corresponded approximately to an age-2 Walleye until about 2006, when the recovery of the Walleye population resulted in slower growth (Fielder and Thomas 2014). To ensure that population estimates represented age-2 and older fish across the years, the length-at-age was examined. Beginning in 2006, the population estimates from both methods had to be expanded for the proportion of age-2 fish not represented in the fishery. That proportion was taken from Fielder and Thomas (2014) fishery-independent assessment of the proportion of the entire age structure represented by age-2 Walleyes less than 381 mm. That fraction was multiplied by the unadjusted population estimates and added back to them. This resulted in a population estimate of age-2 and older Walleyes that are attributable to the Saginaw Bay stock of fish.

The approach employed in this second population estimation differed from the first in that it iteratively solved for the population to generate a fishery that conformed to the known fishery using both the mortality and exploitation rates generated by the tag return analysis. While assumptions of equal mortality and exploitation across ages are unlikely, attempts to further derive an age-structured population or fishery model would likely not reflect the tag return metrics as the drivers in the population estimation. Population estimates were compared among methods and also averaged to offer a single joint estimate.

Some Walleyes from Lake Erie are known to make seasonal migrations into Lake Huron and Saginaw Bay supplementing the fishery there (Wolfert 1963, Ferguson and Derksen 1971, Haas et al. 1988, Todd and Haas 1993, McParland et al. 1999, Thomas and Haas 2005, Wang et al. 2007). To generate accurate estimates of the population size of the Saginaw Bay stock of Walleyes, the annual contribution from Lake Erie had to be estimated and accounted for. The Lake Erie contribution of Walleyes to Lake Huron (and Saginaw Bay) was based on the estimated abundance of the population of western and central basin Walleyes as annually reported by the Lake Erie Walleye Task Group (WTG) of the Great Lakes Fishery Commission (C. Vandergoot, Ohio DNR, personal communication). The five year running average of tag returns were used to create a smoothing effect on the Lake Erie data so as to allow for less variability. The tag return values of Lake Erie fish in Lake Huron ranged from zero to 2.4% (of tagged Walleyes at large) and were also supplied by the Lake Erie WTG. The annual age composition of the Lake Erie Walleye population (expressed over 13 age classes) was used to represent the Lake Erie Walleye population by age and adjusted according to the proportion of fish believed to make the migration which was set to 1.0 for each age 5 and older but only at 0.5 for age 4 fish and zero for Walleye younger than age 4. These adjustments were based on findings from Wolfert (1963), Ferguson and Derksen (1971), and Wang et al. (2007) who observed that younger Lake Erie Walleyes were less prone to movement. The resulting total number of Lake Erie Walleyes in Lake Huron by year was then just the sum across ages. The formulation was as follows:

$$ne_y = \sum_{a=1}^{13}(E_y P_{y,a} T_y R_y C_a) \qquad [13]$$

where

ne_y = the number of Walleyes in Lake Huron that results from Lake Erie migrants

E_y = the total Walleye population in the central and western basins of Lake Erie

$P_{y,a}$ = the year specific age distribution of Walleye from the Lake Erie population

T_y = the year specific proportion of Walleyes migrating to Lake Huron (tag return percent)

R_y = the year-specific correction (expansion) factor for nonreporting of tags from the recreational fishery in Lake Huron (from Appendix A)

C_a = the contribution (expressed as a proportion) of each age that is thought to migrate from Lake Erie

Analysis of population size included comparison to a fishery-independent measure of relative abundance so as to validate the estimation process. The Walleye-catch-per-unit-of-effort (CPUE) in the annual fish community gill-net survey (Fielder et al. 2000; Fielder and Thomas 2006; Fielder and Thomas 2014) was used for fish age 2 and older. This allowed a direct comparison of survey CPUE to population estimates by year. Linear regression was performed with the resulting coefficient of determination (R^2) serving as an indicator of agreement. The analysis was limited to the years 1994–2011 because Fielder and Thomas (2006) concluded a change in catchability of the survey nets had occurred beginning in 1993 due to changes in water clarity stemming from zebra mussel *Dreissena polymorpha* colonization of the bay beginning that year.

Movement

Movement was analyzed by plotting Walleye jaw tag recovery locations (as reported by anglers) in a geographic information system (ESRI 2012). The geographic maps of tag returns allow visual inspection of distribution of Walleyes and was expressed by season; spring (March–May), summer (June–August), fall (September–November) and winter (December–February) and all returns over the entire time series. Fielder et al. (2000) already examined distribution of Walleyes pre- and post-dreissenid colonization and concluded no apparent effect on distribution. Of key interest was emigration of Walleyes from Saginaw Bay (defined by a line between Au Sable Pt. and Port Austin). This was tested across three criteria. First, temporal examination was stratified by two time periods of interest: 1) 2006–2011 represented the recovered Walleye population that was dominated by wild fish at high density with an absence of Alewives in the main basin; and 2) years before 2003 representing Walleye distributions at lower density and dominated by stocked fish and the availability of an Alewife prey base in the main basin (Fielder and Thomas 2014). Second, differences in emigration were examined (for all years combined) by sex. Last, size was tested with 508 mm total length the dividing point between smaller and larger fish. Significant differences were tested based on independence using the Chi-square test (Sokal and Rohlf 1981). Because of the large sample sizes involved, normality assumption of the test was assumed and Yate's correction for continuity was employed because the 2x2 tables had only 1 degree of freedom. Significance was determined at $\alpha \leq 0.05$.

Demographics

Biological data from tagged Walleyes were examined by year to characterize the age and sex structure of the fish represented by tagging. Scales in early years, switching to dorsal spines in the mid-1990s, were collected to allow age assignment.

Results

Mortality and Exploitation Rates

Since study inception, a total of 93,669 Walleyes have been jaw tagged and released in the Tittabawassee River (Table 1, Appendix C). Of those, a total of 9,916 have been reported back by anglers (Appendix C). Applying the initial 21 day tag shedding estimate from Vandergoot et al. (2012), an estimated 92,732 tags were at large for the study (Table 1). Applying the nonreporting correction factors from Appendix A, the estimated actual recovery total was 24,607 tags or 25.9% of the total at large (Table 1). The Chi-square test statistic confirmed a satisfactory fit of the ESTIMATE model ($P = 0.9945$, df = 435) meaning the data fit the model assumptions of year specific survival and recovery rates.

Annual survival (S) ranged from a low of 0.2796 in 1981 to a high of 0.8172 in 1984 based on the ESTIMATE analysis (Table 2). The mean survival rate over the study period was 0.6174. The corresponding total annual mortality rate varied accordingly over time and compared reasonably closely with that estimated by Fielder and Thomas (2014) except for the years 2004–2006 when there was a consistent departure (Figure 3). A similar comparison of total annual mortality rate to that developed for the cohort method by Fielder and Thomas (2014) had somewhat greater agreement (Figure 4). The recovery rate f ranged from a low of 0.0236 in 1982 to a high of 0.3790 in 2009 based on the ESTIMATE analysis (Table 2). The mean recovery rate was 0.1039.

Estimates of survival and recovery rate were not significantly different between those estimated analytically by the program ESTIMATE and those estimated numerically in ADMB. From this it appears that there is no significant effect on these metrics stemming from the tag retention rate of 0.92 for Michigan DNR tag attachment practices as reported by Vandergoot et al. (2012).

Annual and instantaneous mortality rates can be determined from the estimates in Table 2 along with the estimated exploitation rate which is the same as f (Table 3). Exploitation rate as estimated by the annual recovery rates f and that from the direct expression of exploitation rate varied little between methods (Table 4). Exploitation rate and total annual mortality rate (A) did not trend consistently together ($R^2 = 0.06$) suggesting that total mortality was influenced by more than just recreational harvest patterns (Figure 5). A similar comparison of exploitation as a predictor of fishing mortality resulted in a predictably strong relationship ($R^2 = 0.96$).

Population estimation

The population of the Saginaw Bay stock of Walleye in Lake Huron (age-2+) as estimated by the direct calculation method (equation 8) ranged from an estimated low of 284,238 (1987) to a high of 3,761,189 (2007) over a 15 year time span (Figure 6A, Table 5). The population estimates from the iteratively-solved method (equations 9 & 10) predicted the same approximate population trend (Figure 6A). Similar to the direct calculation method, abundance was lowest and peaked in the same years (228,067 in 1987 and 3,443,862 in 2007) for the iteratively-solved method of population estimation. The estimated Walleye population from the iteratively solved method infused minimal year classes on five occasions (1989, 1990, 1994, 1997 and 2007) to construct the population yielding the observed fishery. Some of these years, in fact, matched weak year classes identified by Fielder and Thomas (2014) but not consistently. The model average of the two population estimates may offer the best prediction for comparison with that from Bence and Dobiesz (2000) (Figure 6B).

Table 2.–Estimates of annual survival rate (S) and recovery rate (f) for Saginaw Bay Walleyes (1981–2011) derived by two methods; from analytical solutions in the program ESTIMATE and numerically derived in the AD Model Builder version. Last year is not estimable for the survival rate.

	ESTIMATE estimates						Numerical solution estimates					
	Survival rate			Recovery rate			Survival rate			Recovery rate		
Year	Estimate	CV	95% CI (±)	Estimate	CV	95% CI (±)	Estimate	CV	95% CI (±)	Estimate	CV	95% CI (±)
1981	0.2796	0.3651	0.2001	0.0603	0.1984	0.0234	0.3119	0.3655	0.2234	0.0603	0.1985	0.0235
1982	0.3636	0.1624	0.1158	0.0236	0.2280	0.0106	0.4088	0.1638	0.1312	0.0236	0.2282	0.0105
1983	0.6323	0.0657	0.0814	0.0452	0.0766	0.0068	0.6733	0.0678	0.0895	0.0451	0.0767	0.0068
1984	0.8172	0.0582	0.0932	0.0295	0.0791	0.0046	0.8699	0.0597	0.1018	0.0297	0.0793	0.0046
1985	0.6824	0.0582	0.0779	0.0425	0.0587	0.0049	0.7506	0.0602	0.0885	0.0432	0.0589	0.0050
1986	0.6456	0.0539	0.0682	0.0565	0.0525	0.0058	0.6720	0.0565	0.0744	0.0568	0.0533	0.0059
1987	0.5567	0.0528	0.0576	0.0670	0.0404	0.0053	0.5788	0.0556	0.0631	0.0674	0.0410	0.0054
1988	0.6051	0.0600	0.0712	0.0565	0.0494	0.0055	0.6383	0.0637	0.0797	0.0569	0.0505	0.0056
1989	0.6524	0.0649	0.0830	0.0492	0.0574	0.0055	0.6741	0.0689	0.0911	0.0488	0.0595	0.0057
1990	0.6830	0.0615	0.0823	0.0392	0.0657	0.0051	0.7253	0.0652	0.0926	0.0395	0.0680	0.0053
1991	0.5861	0.0528	0.0606	0.0446	0.0580	0.0051	0.6102	0.0559	0.0669	0.0442	0.0602	0.0052
1992	0.6094	0.0518	0.0619	0.0988	0.0426	0.0083	0.6298	0.0552	0.0681	0.0990	0.0440	0.0085
1993	0.7037	0.0552	0.0761	0.0892	0.0451	0.0079	0.7238	0.0590	0.0837	0.0899	0.0465	0.0082
1994	0.7837	0.0573	0.0881	0.0489	0.0568	0.0054	0.8263	0.0611	0.0989	0.0495	0.0588	0.0057
1995	0.5837	0.0539	0.0616	0.0406	0.0596	0.0047	0.6132	0.0574	0.0689	0.0405	0.0621	0.0049
1996	0.7524	0.0489	0.0721	0.0548	0.0523	0.0056	0.7880	0.0519	0.0802	0.0551	0.0542	0.0059
1997	0.6755	0.0506	0.0670	0.0690	0.0468	0.0063	0.7034	0.0535	0.0737	0.0686	0.0486	0.0065
1998	0.6606	0.0502	0.0650	0.0806	0.0469	0.0074	0.6979	0.0532	0.0728	0.0816	0.0485	0.0077
1999	0.4335	0.0451	0.0383	0.1070	0.0404	0.0085	0.4576	0.0487	0.0436	0.1055	0.0421	0.0087
2000	0.7634	0.0394	0.0590	0.0840	0.0434	0.0071	0.7981	0.0426	0.0666	0.0816	0.0454	0.0073
2001	0.6230	0.0374	0.0456	0.0690	0.0457	0.0062	0.6481	0.0400	0.0508	0.0684	0.0475	0.0064
2002	0.6870	0.0349	0.0471	0.1220	0.0349	0.0084	0.7239	0.0374	0.0531	0.1228	0.0361	0.0087
2003	0.5681	0.0328	0.0365	0.1230	0.0344	0.0083	0.5962	0.0353	0.0412	0.1212	0.0358	0.0085
2004	0.6683	0.0329	0.0431	0.1890	0.0281	0.0104	0.6974	0.0355	0.0486	0.1876	0.0293	0.0108
2005	0.6481	0.0322	0.0409	0.1174	0.0351	0.0081	0.6707	0.0345	0.0454	0.1168	0.0365	0.0083
2006	0.6630	0.0300	0.0389	0.1227	0.0337	0.0081	0.6926	0.0318	0.0431	0.1237	0.0348	0.0084
2007	0.5115	0.0265	0.0265	0.1647	0.0292	0.0094	0.5325	0.0280	0.0292	0.1661	0.0301	0.0098
2008	0.7648	0.0264	0.0396	0.2504	0.0231	0.0113	0.7986	0.0275	0.0430	0.2508	0.0238	0.0117
2009	0.3359	0.0430	0.0283	0.3790	0.0205	0.0152	0.3499	0.0447	0.0306	0.3796	0.0208	0.0155
2010	0.5817	0.0546	0.0623	0.2233	0.0306	0.0134	0.6048	0.0581	0.0689	0.2238	0.0310	0.0136
2011				0.1701	0.0393	0.0131				0.1864	0.0384	0.0140

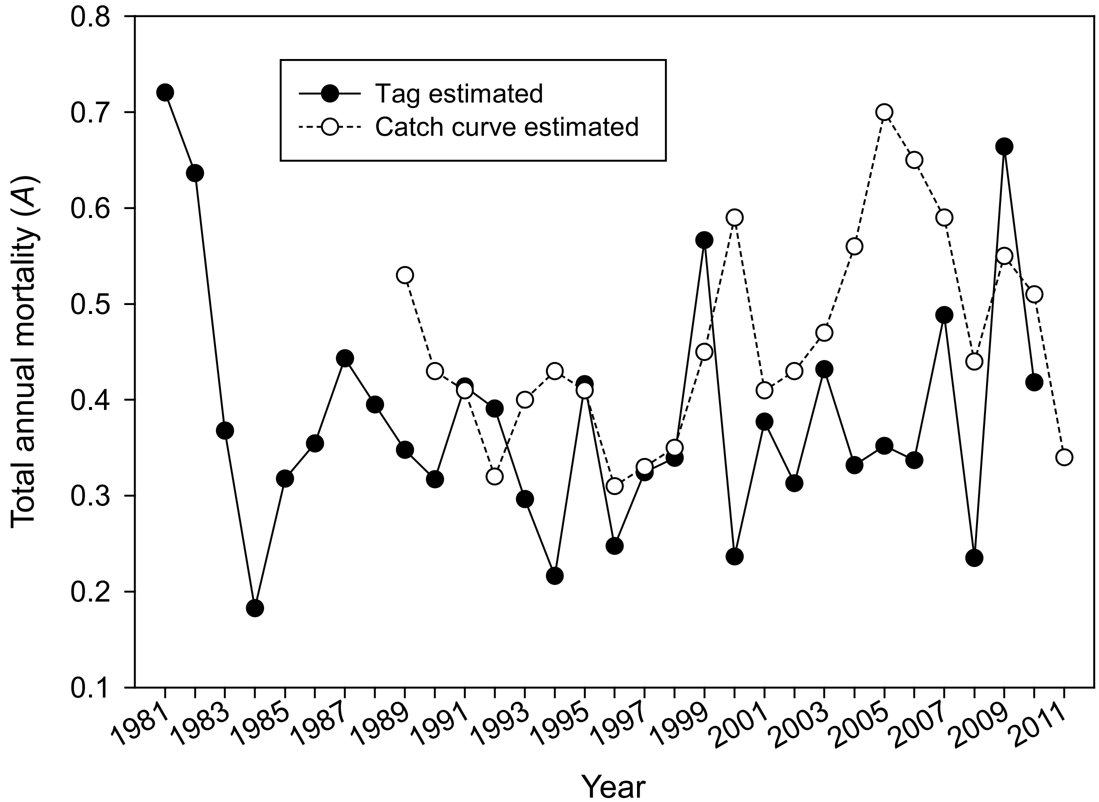


Figure 3.–Total annual mortality rate (*A*) for Saginaw Bay Walleyes estimated by two methods; from tag returns using ESTIMATE analysis (1981–2010) and by catch curves (1986–2011) from Fielder and Thomas 2014.

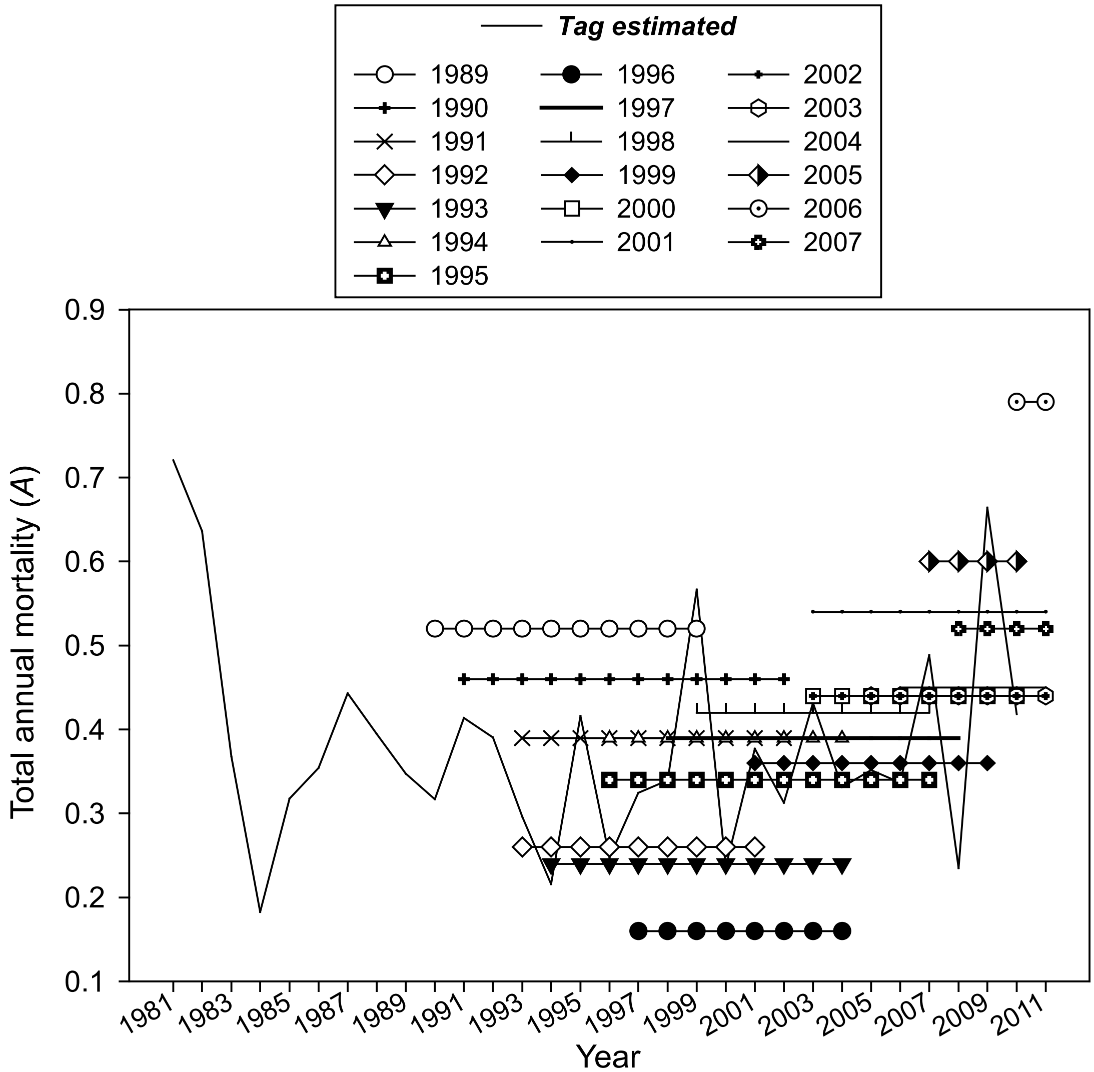


Figure 4.–Total annual mortality rate (*A*) for Saginaw Bay Walleyes as estimated by tag returns ESTIMATE analysis (1981–2010) and for individual cohorts over time from cohort analysis (Fielder and Thomas 2014).

Table 3.–Exploitation, total annual survival and corresponding mortality metrics for Saginaw Bay Walleyes (1981–2011) based on ESTIMATE tag return analysis. Survival and mortality rates are not estimable for the last year. Included for comparison are independent (not based on tagging) estimates of instantaneous natural mortality (*M*) from the Pauly (1980) and Hoenig (1983) equations.

		Total annual			Instantaneous mortality				
Year	Exploitation (*u*)	Survival (*S*)	Mortality (*A*)	Natural mortality (*v*)	Total (*Z*)	Fishing (*F*)	Natural (*M*)	*M* from Pauly equation	*M* from Hoenig equation
1981	0.0603	0.2796	0.7204	0.6601	1.2744	0.1067	1.1678		
1982	0.0236	0.3636	0.6364	0.6128	1.0117	0.0376	0.9741		
1983	0.0452	0.6323	0.3677	0.3225	0.4584	0.0563	0.4021		
1984	0.0295	0.8172	0.1828	0.1533	0.2019	0.0326	0.1693		
1985	0.0425	0.6824	0.3176	0.2751	0.3822	0.0512	0.3310		
1986	0.0565	0.6456	0.3544	0.2979	0.4376	0.0698	0.3678		0.49
1987	0.0670	0.5567	0.4433	0.3763	0.5857	0.0886	0.4972		0.49
1988	0.0565	0.6051	0.3949	0.3383	0.5023	0.0719	0.4304		0.49
1989	0.0492	0.6524	0.3476	0.2984	0.4272	0.0605	0.3667	0.23	0.49
1990	0.0392	0.6830	0.3170	0.2778	0.3813	0.0472	0.3341	0.27	0.49
1991	0.0446	0.5861	0.4139	0.3693	0.5342	0.0576	0.4767	0.22	0.44
1992	0.0988	0.6094	0.3906	0.2918	0.4953	0.1253	0.3700	0.18	0.32
1993	0.0892	0.7037	0.2963	0.2071	0.3514	0.1058	0.2456	0.28	0.40
1994	0.0489	0.7837	0.2163	0.1674	0.2437	0.0551	0.1886	0.18	0.40
1995	0.0406	0.5837	0.4163	0.3757	0.5384	0.0525	0.4859	0.24	0.37
1996	0.0548	0.7524	0.2476	0.1928	0.2845	0.0630	0.2215	0.18	0.40
1997	0.0690	0.6755	0.3245	0.2555	0.3924	0.0835	0.3089	0.22	0.32
1998	0.0806	0.6606	0.3394	0.2588	0.4146	0.0985	0.3162	0.24	0.34
1999	0.1070	0.4335	0.5665	0.4596	0.8360	0.1578	0.6781	0.21	0.32
2000	0.0840	0.7634	0.2366	0.1526	0.2700	0.0958	0.1741	0.20	0.34
2001	0.0690	0.6230	0.3770	0.3080	0.4733	0.0867	0.3866	0.21	0.32
2002	0.1220	0.6870	0.3130	0.1910	0.3754	0.1463	0.2291	0.23	0.32
2003	0.1230	0.5681	0.4319	0.3089	0.5654	0.1610	0.4044	0.24	0.30
2004	0.1890	0.6683	0.3317	0.1427	0.4030	0.2296	0.1734	0.23	0.32
2005	0.1174	0.6481	0.3519	0.2345	0.4337	0.1447	0.2890	0.26	0.32
2006	0.1227	0.6630	0.3370	0.2143	0.4109	0.1496	0.2613	0.23	0.32
2007	0.1647	0.5115	0.4885	0.3238	0.6704	0.2261	0.4444	0.32	0.32
2008	0.2504	0.7648	0.2352	0.0000	0.2681	0.2854	0.0000	0.19	0.32
2009	0.3790	0.3359	0.6641	0.2852	1.0910	0.6226	0.4685	0.39	0.32
2010	0.2233	0.5817	0.4183	0.1950	0.5418	0.2892	0.2526	0.21	0.22
2011	0.1701							0.24	0.28

Table 4.–Exploitation rates and their coefficient of variation (CV) for Saginaw Bay Walleyes from 1981–2011 by two methods; from recovery rate as estimated by the ESTIMATE tag return model and from the direct expression method of first year tag returns.

Year	Recovery rate f estimate	CV	Direct expression	CV
1981	0.0603	0.1984	0.0603	0.1984
1982	0.0236	0.2280	0.0215	0.2517
1983	0.0452	0.0766	0.0434	0.0805
1984	0.0295	0.0791	0.0272	0.1009
1985	0.0425	0.0587	0.0492	0.0711
1986	0.0565	0.0525	0.0603	0.0668
1987	0.0670	0.0404	0.0731	0.0461
1988	0.0565	0.0494	0.0610	0.0621
1989	0.0492	0.0574	0.0375	0.0931
1990	0.0392	0.0657	0.0389	0.1001
1991	0.0446	0.0580	0.0390	0.0899
1992	0.0988	0.0426	0.0998	0.0552
1993	0.0892	0.0451	0.0946	0.0569
1994	0.0489	0.0568	0.0498	0.0802
1995	0.0406	0.0596	0.0365	0.0947
1996	0.0548	0.0523	0.0506	0.0796
1997	0.0690	0.0468	0.0623	0.0713
1998	0.0806	0.0469	0.0864	0.0655
1999	0.1070	0.0404	0.1028	0.0542
2000	0.0840	0.0434	0.0744	0.0617
2001	0.0690	0.0457	0.0688	0.0675
2002	0.1220	0.0349	0.1382	0.0459
2003	0.1230	0.0344	0.1077	0.0528
2004	0.1890	0.0281	0.1872	0.0383
2005	0.1174	0.0351	0.1190	0.0499
2006	0.1227	0.0337	0.1465	0.0443
2007	0.1647	0.0292	0.1861	0.0391
2008	0.2504	0.0231	0.2612	0.0309
2009	0.3790	0.0205	0.3837	0.0233
2010	0.2233	0.0306	0.2234	0.0344
2011	0.1701	0.0393	0.1864	0.0384

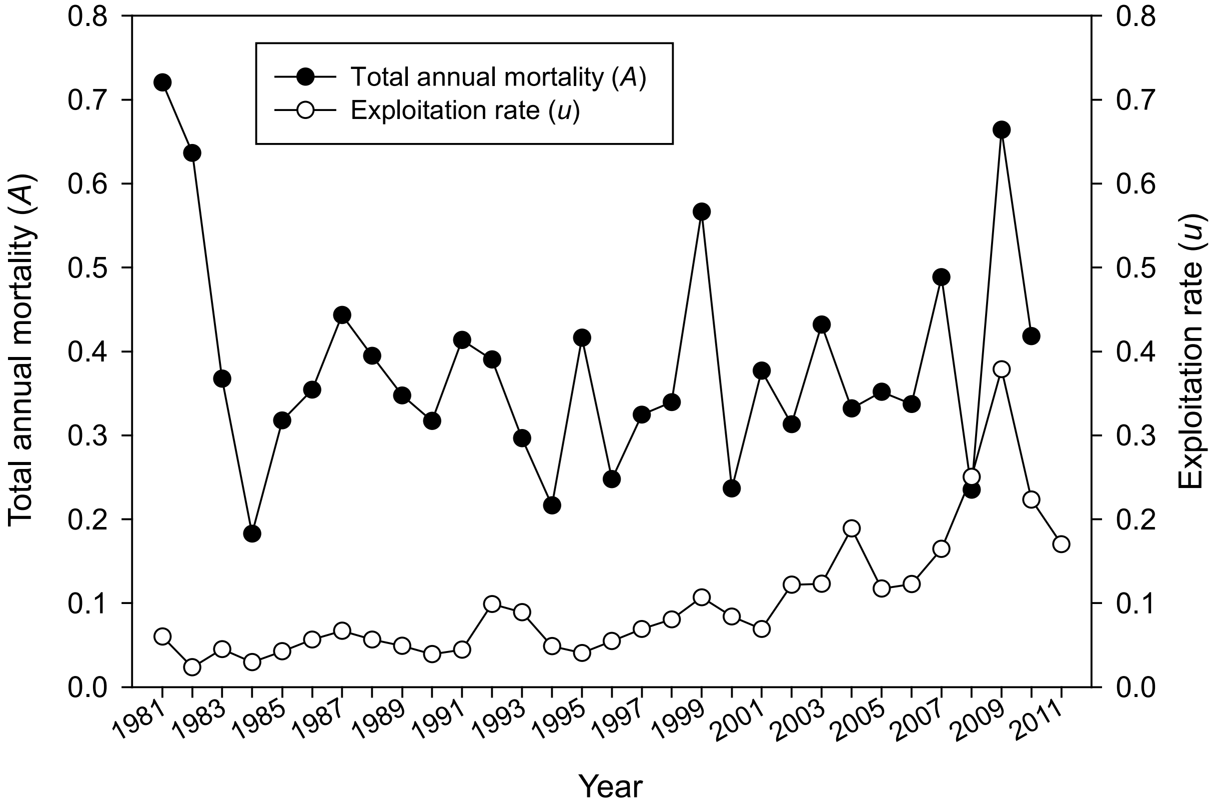


Figure 5.–Total annual mortality rate (*A*) for Saginaw Bay Walleyes from ESTIMATE analysis (1981–2010) of tag returns and the exploitation rate (*u*) for 1981–2011.

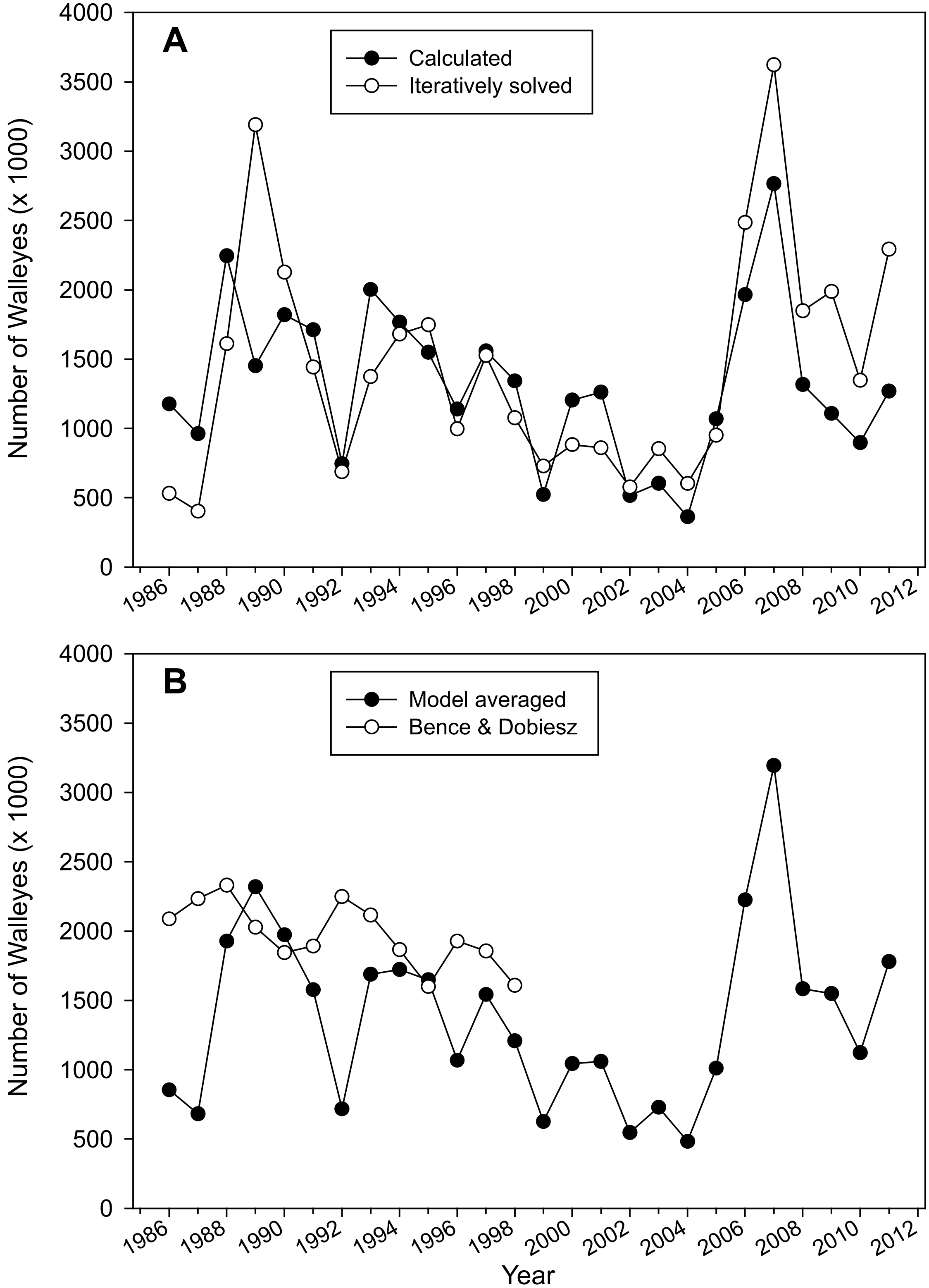


Figure 6.–(A) Estimated numbers of age 2+ Saginaw Bay stock of Walleyes 1986–2011 using two methods; the directly calculated method (from equation 8) and iteratively solved method (using equations 9 and 10). (B) Model averaged estimate (from the two methods in A, with that from Bence and Dobiesz (2000) for comparison).

Table 5.–Estimated population size (numbers) of Saginaw Bay stock of Walleyes from 1986 to 2011 for two methods of estimation [calculated (equation 8) and iteratively solved (equations 9 and 10)], and their average estimate. Also included are various intermediate values used in the estimation process.

Year	Harvest	Number of Lake Erie Walleyes in Lake Huron	Proportion of population age 2 but below 381 mm	Estimated population of Saginaw Bay stock of Walleyes (calculated)	Estimated population of Saginaw Bay stock of Walleyes (iteratively solved)	Model averaged population estimate
1986	71,297	317,355	0.0000	524,411	439,939	482,175
1987	83,440	553,234	0.0000	284,238	228,067	256,152
1988	159,747	351,556	0.0000	1,261,582	1,490,433	1,376,008
1989	240,406	247,627	0.0050	850,796	3,097,725	1,974,260
1990	129,619	376,423	0.0100	1,063,243	1,977,557	1,520,400
1991	97,346	277,105	0.0000	1,113,206	1,327,127	1,220,167
1992	118,366	487,865	0.0140	292,370	468,813	380,592
1993	163,220	260,692	0.0310	1,442,621	1,249,085	1,345,853
1994	108,207	324,025	0.0000	1,271,079	1,523,681	1,397,380
1995	85,702	178,578	0.0090	1,240,973	1,656,183	1,448,578
1996	63,302	175,995	0.0090	931,759	903,006	917,382
1997	112,736	88,109	0.0100	1,424,682	1,477,776	1,451,229
1998	97,250	100,474	0.0360	1,258,966	1,016,811	1,137,889
1999	63,842	19,839	0.0190	529,108	716,539	622,824
2000	68,350	0	0.0090	1,296,707	883,252	1,089,980
2001	53,112	0	0.0000	1,404,500	859,783	1,132,141
2002	61,678	52,373	0.0130	565,177	543,464	554,321
2003	90,541	132,250	0.0100	655,289	766,758	711,023
2004	96,171	128,062	0.0100	383,517	517,375	450,446
2005	64,691	47,101	0.3480	1,362,693	909,257	1,135,975
2006	165,477	49,477	0.3700	2,619,773	2,439,726	2,529,749
2007	300,370	179,451	0.4350	3,761,189	3,443,862	3,602,526
2008	317,620	215,897	0.0510	1,811,679	1,687,529	1,749,604
2009	335,061	0	0.4210	1,702,821	1,989,658	1,846,239
2010	153,283	0	0.2210	1,437,084	1,346,766	1,391,925
2011	161,230	0	0.3900	2,205,684	2,293,323	2,249,504

The abundance of Lake Erie Walleyes in Lake Huron has declined in recent years, requiring an adjustment to derive population estimates of the Saginaw Bay stock (Table 5). The prevalence of age-2 Walleyes in the population but outside the fishery due to length limits has grown since the recovery of the Walleye population. When regressed with the fishery independent gill-net survey CPUE of age-2+ Walleyes from Fielder and Thomas (2014), the calculated population estimate explained 69% of the variability in the fishery independent gill-net CPUE $P < 0.0001$, $R^2 = 0.69$); and 67% of the variability was explained by the iteratively solved population estimate ($P < 0.0001$, $R^2 = 0.67$) suggesting the two population estimation methods perform equally well. Predictably, the model average prediction was intermediate in its predictive ability at 68% ($P < 0.0001$, $R^2 = 0.68$).

Movement

Of the tag returns reported by anglers, 9,719 or 98% included sufficient information to assign a latitude and longitude to their capture location (Figure 7). Of those, 860 (8.8%) were reported from locations outside the mouth of Saginaw Bay. There were significantly (Chi-square $P = 0.0217$) more Walleyes reported from outside the bay after recovery of the Saginaw Bay Walleye population (2006–2011; 9.3%) compared to years before recovery was achieved (1981–2002; 7.8%) (Figure 8). When the frequency of tag recoveries were compared across sex of fish for all years, females were strongly more prevalent outside the bay at 12.9% vs. 4.3% for males (Figure 9, Chi-square $P < 0.0001$). Similarly, Walleyes greater than 508 mm in total length were significantly more likely to be reported from outside the bay than those less than 508 mm (Figure 10, Chi-square $P < 0.0001$). Walleye tag recoveries were most frequent in the summer months and least in the fall (Figure 11) although seasonality of tag reports is highly dependent on temporal distribution of fishing effort.

Demographics

There was some trend in the size and age structure of the Walleye tagged in the Tittabawassee River between 1981 and 2011. Walleye mean length peaked between 1996 and 2001 for males and females and then began to decline, likely reflecting the increased reproductive success (Table 6). The tagging series began early enough to characterize the earliest stages of the initial Walleye resurgence in Saginaw Bay as evidenced by the low mean age and few year classes in 1981 (Table 7). Like mean length, the age structure steadily matured over time, peaking in 1997 for males and in 2000 for females. Mean age then declined with recovery of natural reproduction, reaching a second period of lows in 2007/2008 from increased recruitment before beginning to increase again.

Discussion

Total annual mortality rate of the Saginaw Bay Walleye stock was relatively consistent in most years, in the 30% to 50% range. The rate averaged 38% over the time series and would have to be regarded as typical of an exploited Walleye population. Escanaba Lake in Wisconsin averaged 50% (1967–2007), Oneida Lake in New York 27% (1957–2007) and Lake Erie 48% (1978–2008) (Nate et al. 2011). Three approximate periods may be observed from the trends in total annual mortality (Table 3, Figure 3); an initial period of very high but declining total mortality for the years 1981–1982, then a period of stability for the years 1983–2006, and most recently a period of greater variability with at least one very high year (2009) for the years 2007–2010. The initial high mortality may have reflected a smaller, younger Walleye population early in the initial resurgence period that was more vulnerable to exploitation. There is some suggestion that the same phenomenon may have occurred in Lake Erie early in its recovery (1978) (Nate et al. 2011). The Saginaw Bay recreational Walleye fishery had resumed by 1981 and was fully developed by 1986 (Fielder et al. 2014), but the population was still maturing (Table 7).

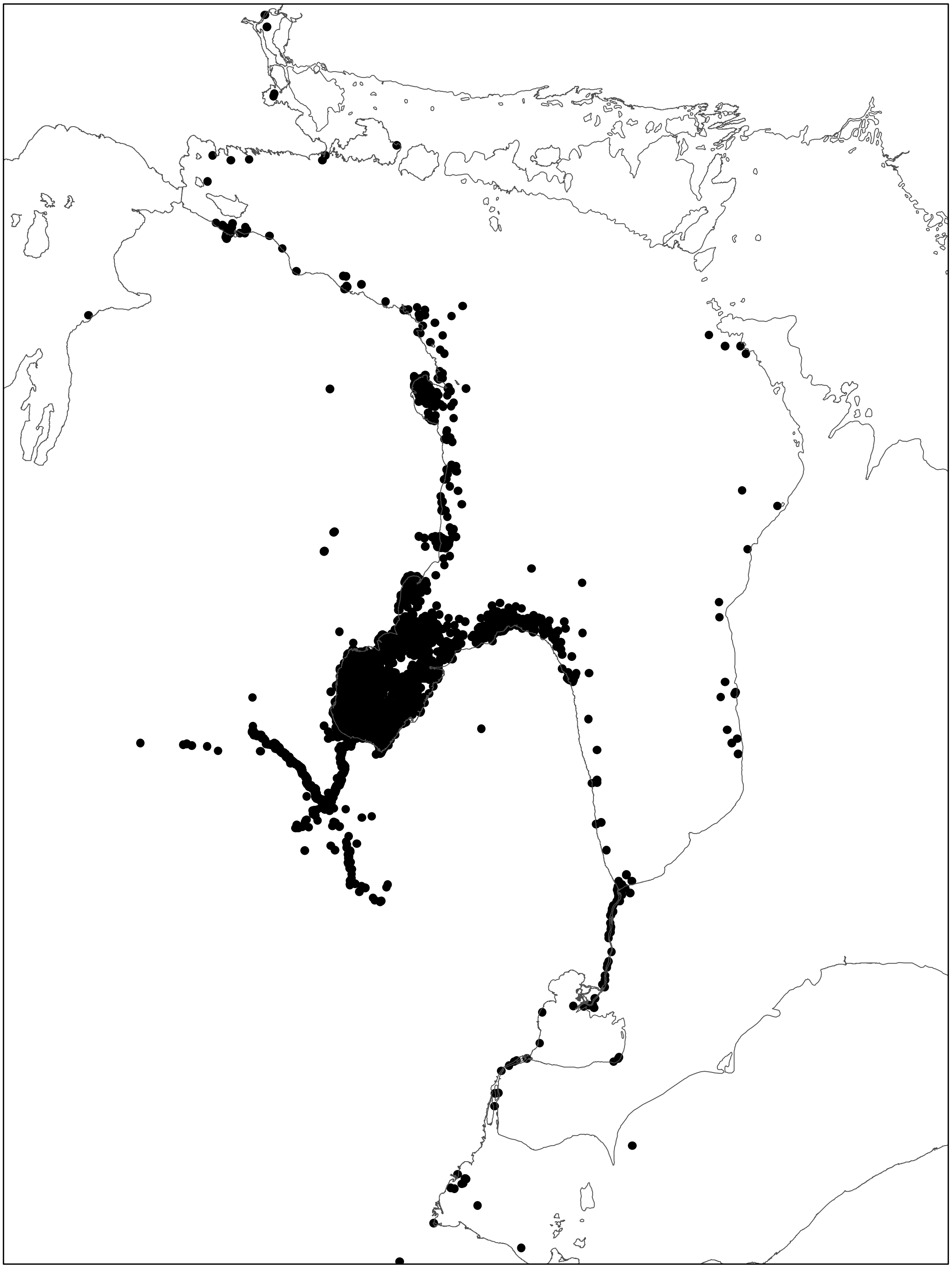
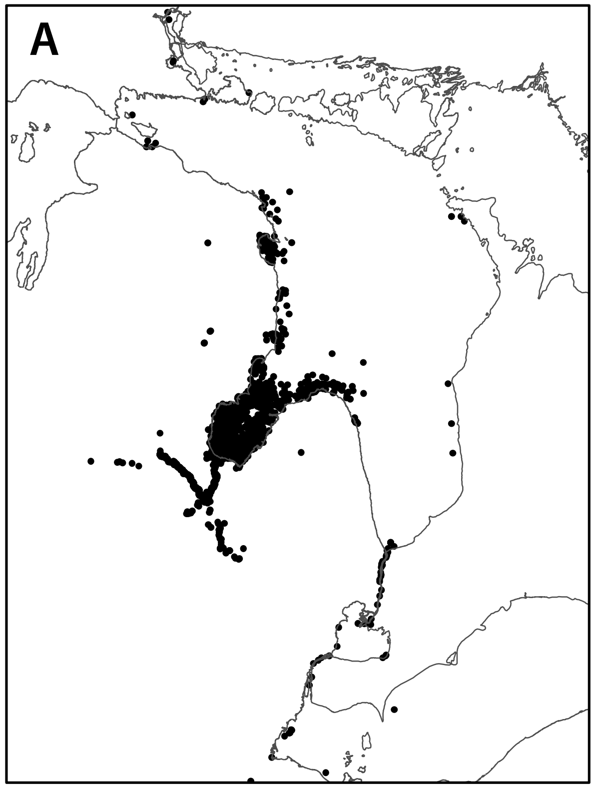


Figure 7.–Capture location of angler reported Walleye jaw tags (each dot = one fish) 1981–2011 N = 9,719.



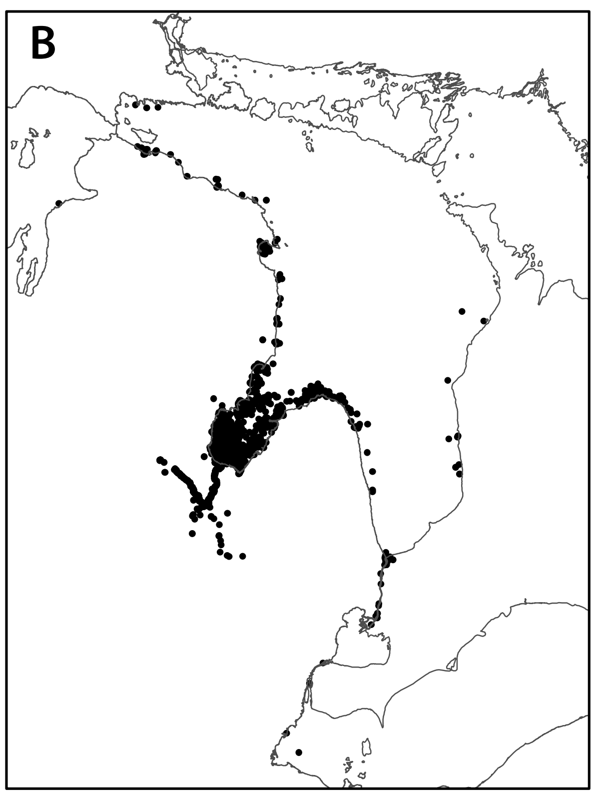


Figure 8.–Capture location of angler reported Walleye jaw tags (each dot = one fish) 1981–2002 (lower density; A), and 2006–2011 (higher density; B).

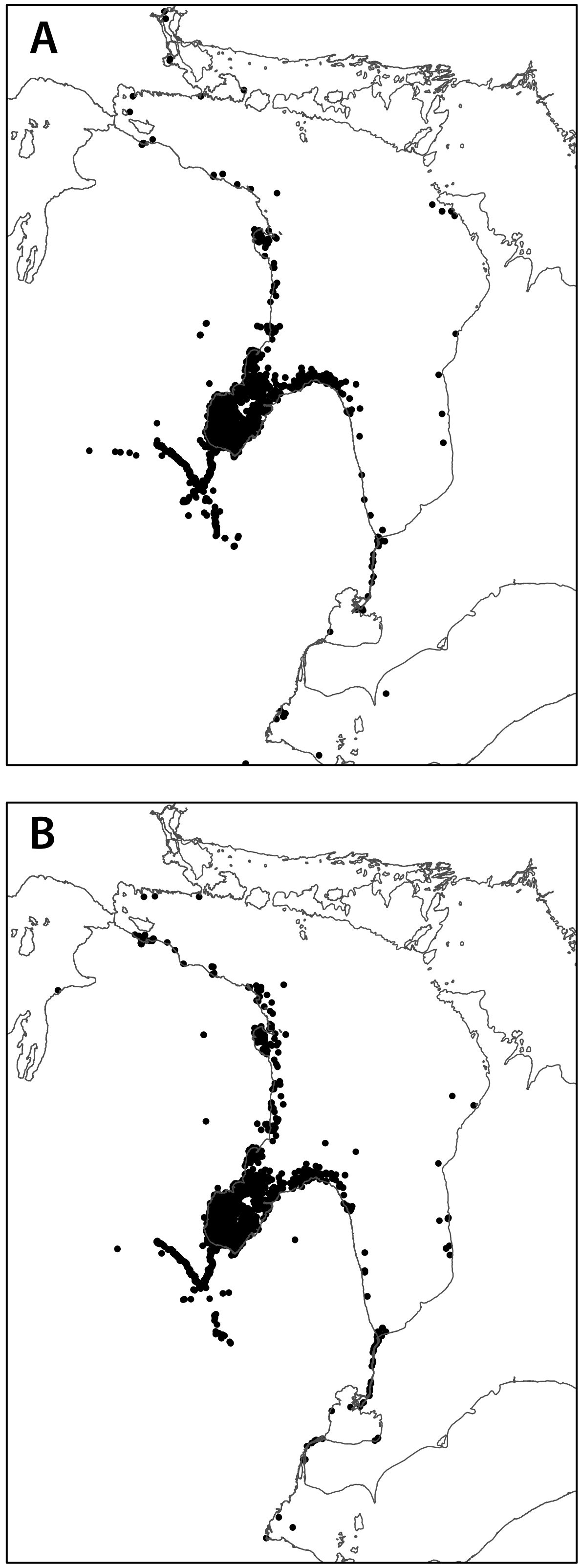


Figure 9.–Capture location of angler reported Walleye jaw tags (each dot = one fish) 1981–2011 by sex; males (A), females (B).

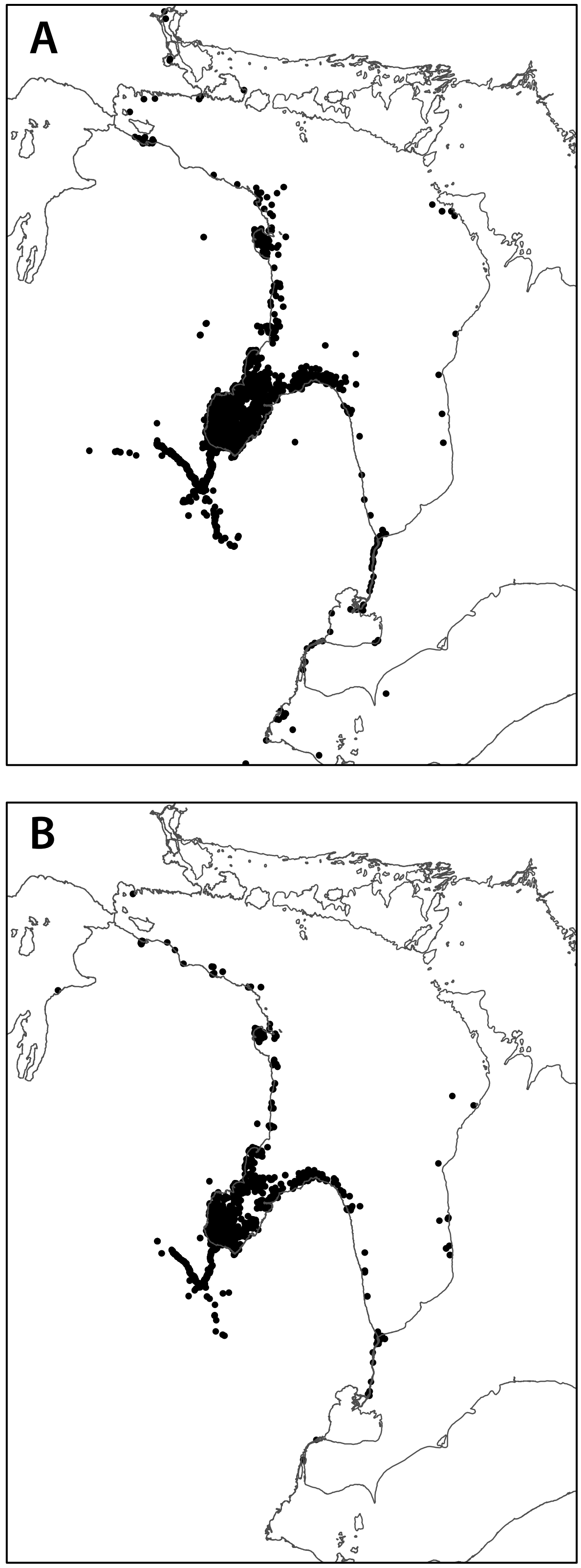


Figure 10.–Capture location of angler reported Walleye jaw tags (each dot = one fish) 1981–2011 by size; Walleyes ≤ 508 mm, (A) and Walleyes > 508 mm (B).

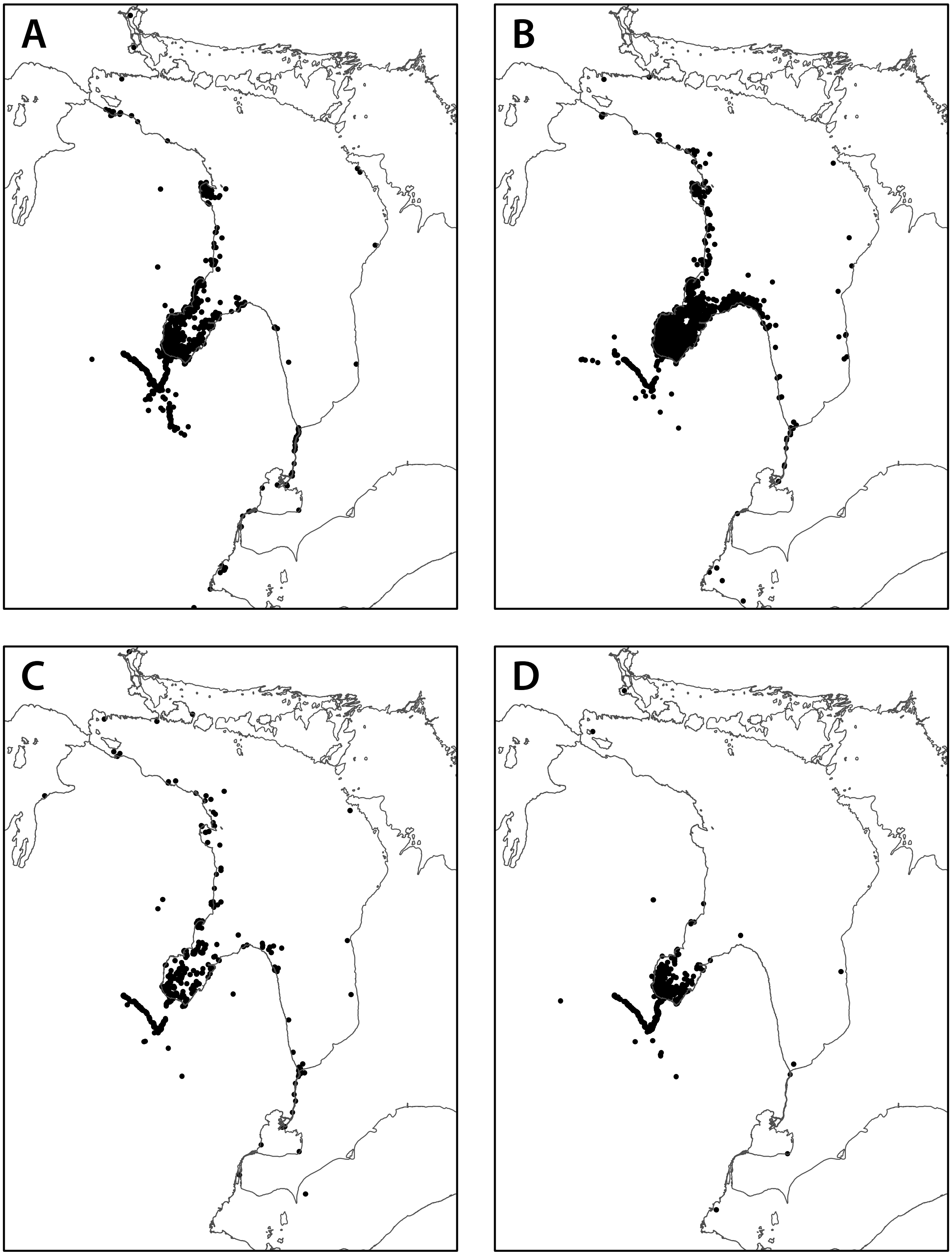


Figure 11.–Capture location of angler reported Walleye jaw tags (each dot = one fish) 1981–2011 by season; Spring (A), Summer (B), Fall (C), and Winter (D).

Table 6.–Average total length (mm) of Walleyes collected by electrofishing below Dow Dam, Tittabawassee River, March–April, 1981–2011.

	Female		Male		Total	
Year	Length	Number	Length	Number	Length	Number
1981	528	87	350	272	394	399
1982	516	179	452	513	467	697
1983	549	2,082	498	1,300	528	3,413
1984	584	1,052	472	2,421	505	3,540
1985	531	1,322	457	1,662	490	2,984
1986	536	1,370	465	2,023	493	3,574
1987	546	1,736	472	3,829	485	5,976
1988	582	549	477	3,338	490	4,033
1989	561	1,774	485	1,244	528	3,064
1990	582	972	493	1,481	528	2,467
1991	584	2,232	488	843	559	3,079
1992	610	1,491	483	1,497	556	2,995
1993	582	1,323	488	1,666	531	2,989
1994	599	1,452	531	1,534	564	2,999
1995	589	962	538	2,003	556	2,970
1996	627	1,376	556	1,614	589	2,992
1997	630	1,905	554	1,088	604	2,993
1998	589	1,170	544	1,311	564	2,489
1999	620	957	549	2,031	569	2,995
2000	630	531	540	2,756	555	3,299
2001	635	576	518	2,421	540	2,997
2002	594	809	536	2,178	551	2,993
2003	615	967	525	2,028	554	2,994
2004	602	1,095	529	1,902	556	2,997
2005	604	1,586	531	1,412	570	2,998
2006	584	760	492	2,174	515	2,997
2007	545	658	490	2,208	502	2,887
2008	561	1,752	471	1,238	524	2,993
2009	550	1,513	473	1,484	512	2,999
2010	547	1,157	478	1,810	505	2,969
2011	544	1,486	479	1,505	511	2,991

Table 7.–Age composition (percent) of Walleyes sampled from Tittabawassee River (Dow Dam) during spring electrofishing, 1981–2011.

		Age														Mean
		1	2	3	4	5	6	7	8	9	10	11	12	13	14+	age
1981		0.3	56.0	22.6	20.0	1.1	–	–	–	–	–	–	–	–	–	2.7
1982		–	–	79.2	13.6	7.2	–	–	–	–	–	–	–	–	–	3.3
1983		–	–	0.7	85.3	4.4	3.7	3.7	1.5	0.0	0.7	–	–	–	–	4.3
1984		–	14.7	18.2	22.1	33.8	8.2	3.0	–	–	–	–	–	–	–	4.1
1985		0.1	8.6	48.3	20.3	19.2	3.3	0.2	–	–	–	–	–	–	–	3.6
1986		–	3.1	28.4	39.1	17.3	5.9	5.2	1.0	0.1	–	–	–	–	–	4.2
1987		–	10.4	1.9	46.9	29.9	5.0	3.7	1.9	0.3	–	–	–	–	–	4.4
1988:	Female	–	–	4.0	18.5	32.8	25.7	10.5	5.7	3.0	–	–	–	–	–	5.5
	Male	–	0.5	29.5	22.8	25.5	14.5	3.8	2.3	1.1	–	–	–	–	–	4.5
1989:	Female	–	–	1.5	41.4	27.3	23.1	5.7	1.1	–	–	–	–	–	–	4.9
	Male	–	0.8	5.8	58.5	20.4	8.2	4.4	1.2	0.6	–	–	–	–	–	4.5
1990:	Female	–	0.1	0.1	1.2	37.1	34.7	22.9	3.6	0.4	–	–	–	–	–	5.9
	Male	–	3.1	5.0	14.0	49.2	21.1	7.1	0.5	0.1	–	–	–	–	–	5.0
1991:	Female	–	–	0.1	18.8	19.2	45.7	11.5	2.6	1.5	0.6	–	–	–	–	5.7
	Male	–	0.1	43.8	9.6	19.6	20.5	3.6	2.6	0.2	–	–	–	–	–	4.4
1992:	Female	–	0.1	0.0	9.4	14.5	12.1	17.9	13.7	10.2	12.9	4.6	3.0	1.7	0.2	7.5
	Male	–	0.6	19.5	30.8	17.4	17.6	11.4	1.0	1.0	0.3	0.4	–	–	–	4.8
1993:	Female	–	–	1.6	13.7	31.8	11.7	18.6	14.6	6.5	1.2	0.3	–	–	–	6.1
	Male	–	–	33.3	25.6	14.2	12.6	9.0	2.9	1.1	1.3	–	–	–	–	4.6
1994:	Female	–	–	1.3	17.3	32.7	16.0	7.7	12.2	7.7	1.9	1.3	0.6	–	–	6.0
	Male	–	–	4.9	18.9	12.8	10.4	13.4	17.1	12.8	4.9	1.2	–	–	–	6.5
1995:	Female	–	–	–	9.4	53.1	13.4	9.1	7.1	3.9	2.4	1.2	0.4	–	–	5.8
	Male	–	–	1.3	9.0	20.5	21.0	12.7	14.0	12.5	7.6	0.7	0.4	0.2	–	6.7
1996:	Female	–	–	–	0.2	9.1	18.4	22.6	13.1	12.6	15.9	6.9	1.3	–	–	7.8
	Male	–	–	0.6	0.8	6.3	16.1	18.9	21.9	18.4	13.0	3.1	0.9	–	–	7.8
1997:	Female	–	–	0.4	4.1	1.3	11.8	26.8	22.9	12.4	8.4	7.1	4.9	–	–	7.9
	Male	–	–	–	1.5	0.3	15.2	23.6	27.3	16.1	9.2	4.0	2.0	–	0.6	7.9
1998:	Female	–	–	1.7	22.8	11.0	6.6	11.3	19.6	12.8	7.3	4.0	2.7	0.3	–	7.0
	Male	–	–	6.8	9.3	3.4	4.8	16.4	22.7	17.7	10.3	6.2	1.5	0.9	–	7.6
1999:	Female	–	–	0.4	8.0	13.3	4.9	4.5	11.4	21.2	18.6	9.8	6.8	0.4	0.4	8.3
	Male	–	0.6	1.7	13.2	8.5	5.2	7.4	23.5	19.8	12.4	4.5	1.2	0.8	–	7.6
2000:	Female	–	–	–	0.6	11.2	14.9	10.6	4.3	13.0	20.5	13.7	8.1	2.5	–	8.7
	Male	–	4.4	11.7	2.2	9.0	11.4	5.8	8.2	21.8	14.1	8.3	2.5	0.6	–	7.4
2001:	Female	–	–	2.7	7.5	5.8	8.4	13.3	8.0	9.7	15.5	14.6	11.5	2.2	0.9	8.6
	Male	–	–	25.4	9.5	3.0	9.1	10.5	11.0	14.2	9.5	5.4	1.9	0.5	–	6.6
2002:	Female	–	–	–	16.5	38.0	15.2	9.5	3.8	4.4	3.8	3.8	2.5	1.9	0.6	6.3
	Male	–	–	0.8	31.4	28.9	7.1	7.9	7.5	2.9	7.1	4.2	0.8	1.3	–	6.0
2003:	Female	–	–	–	4.5	25.9	17.7	9.1	10.7	9.1	6.6	8.2	5.8	1.6	0.8	7.4
	Male	–	1.2	5.5	13.1	26.2	17.7	12.8	11.9	4.9	4.0	2.0	0.6	–	–	6.1
2004:	Female	–	–	0.3	10.5	28.0	28.6	11.0	3.7	5.1	5.4	3.7	2.5	0.8	0.4	6.5
	Male	–	–	9.7	6.3	16.2	25.2	13.3	11.7	4.5	6.5	3.8	1.8	0.7	0.4	6.6

Table 7.–Continued.

		Age														Mean
		1	2	3	4	5	6	7	8	9	10	11	12	13	14+	age
2005:	Female	–	–	–	14.2	18.1	30.3	13.6	6.2	5.7	3.7	1.7	3.1	2.3	1.1	6.6
	Male	–	–	6.1	13.3	12.4	26.1	11.2	7.9	8.5	8.1	3.8	1.6	1.1	–	6.6
2006:	Female	–	2.1	0.5	10.9	36.5	20.8	10.4	7.3	5.2	3.6	0.5	0.5	1.0	0.5	6.0
	Male	0.2	–	33.8	15.5	11.9	14.5	9.5	6.4	4.5	1.4	1.0	1.2	–	–	5.1
2007:	Female	–	–	1.0	34.7	30.7	10.9	7.9	4.0	5.0	2.0	–	1.0	2.0	1.0	5.6
	Male	–	–	13.2	33.6	16.4	7.8	5.2	8.6	6.9	3.7	2.0	1.7	0.6	0.3	5.6
2008:	Female	–	–	–	10.6	44.9	15.8	9.5	5.6	5.2	3.7	0.9	1.3	0.2	2.1	6.2
	Male	–	–	7.7	34.1	40.5	5.0	4.5	1.8	4.5	–	–	0.5	0.5	0.9	5.0
2009:	Female	0.3	–	–	9.0	35.2	36.2	8.0	4.9	1.3	3.3	0.5	0.3	0.5	0.5	5.9
	Male	–	–	2.2	14.4	29.8	31.5	13.2	3.2	3.2	1.2	0.2	–	0.7	0.2	5.8
2010:	Female	–	–	0.4	7.8	37.1	22.0	17.2	3.4	3.4	2.2	2.2	2.2	–	2.1	6.3
	Male	–	–	2.7	7.9	25.9	27.8	16.1	3.8	4.0	4.0	0.8	3.1	1.0	3.0	6.6
2011:	Female	–	–	0.2	8.4	16.6	29.3	19.3	14.5	2.3	3.5	0.7	2.4	1.0	1.8	6.8
	Male	–	–	2.4	18.3	16.7	25.4	11.9	11.9	7.1	3.2	1.6	1.9	–	–	6.3

This analysis permits the calculation of the instantaneous fishing mortality rate (*F*). What exactly that value represents, however, requires careful consideration. Most clearly these values of *F* represent a recreational fishing mortality given that Walleye jaw tags are rarely reported by any of the commercial fisheries that operate in Lake Huron. MacMillan and Roth (2012) documented that in 2010, there was bycatch mortality of Walleyes in Saginaw Bay amounting to 21,500 for May–August, which may amount to as much as 101,872 for the entire year. This expanded value was two-thirds as much as the recreational harvest of Walleye in the Michigan waters of Lake Huron. Given the movement and habitation Saginaw Bay Walleyes are exhibiting in the main basin of the lake, it's also likely that they are being commercially exploited by provincial licensed commercial Walleye fisheries in the Ontario waters of Lake Huron, especially in the southern basin of the lake. Tribal commercial and subsistence harvest of Walleye in northern Lake Huron may also exploit Saginaw Bay stock of Walleyes. Tittabawassee River spawning genotypes, for example, figured prominently in a mixed stock analysis of Walleyes in the commercial take in the Ontario southern Lake Huron waters in the mid-1990s (McParland et al. 1999). The mortality generated by these fisheries is almost certainly expressed as part of the natural mortality in the reported values (Table 3) because of their failure to return jaw tags.

The ability to predict total mortality from exploitation rate depends partly on how thoroughly the total mortality is driven by recreational harvest. The predictive relationship in Saginaw Bay was low ($R^2 = 0.06$) but clearly related for fishing mortality ($R^2 = 0.96$). There was a similar lack of relationship in Escanaba Lake, Wisconsin from 1967 to 2007 but a very strong predictive relationship in Lake Erie (1978–2008). The stronger relation between exploitation and total annual mortality rate in Lake Erie might be attributed to their use of Statistical-Catch-at-Age (SCA) analysis to estimate mortality rate and exploitation (Nate et al. 2011). SCA methods can better incorporate and represent competing fisheries and more fully account for all sources of fishing mortality. Exploitation rate of Saginaw Bay Walleyes ranged from 2% (1982) to 38% (2009), with a time series mean of 10% (Table 3). These values are generally regarded as low for an exploited Walleye fishery assuming sufficient productivity (Nate et al. 2011) but again, these values almost certainly under represent the full exploitation of this stock given the lack of representation of other forms of extraction. Exploitation rate for Lake Erie Walleyes for the same time period ranged from 4.7% to 21.9 % with a time series mean of 12.9% (M. Thomas, Michigan DNR, personal communication). Those rates from Lake Erie reflect a relatively intense recreational and commercial fishery. Given the similarity in magnitude of the exploitation rates between the two systems, and the likely under estimation of the rate for the Saginaw Bay stock, it is possible that the latter is more intensively exploited relative to Walleyes in Lake Erie.

Natural mortality rates are generally difficult to assess in fish populations and are often assigned an assumed set value for population modeling (Nate et al. 2011; Quinn and Deriso 1999). This analysis affords an annual measure of natural mortality (M) but it is derived as the difference between total and fishing mortality. While computationally valid, this then translates any potential bias in the estimation of fishing mortality (F) to the values of M. Most notable is that there may be sources of fishing mortality not represented in this analysis which would then be ascribed to M. Thus, these values of M are likely over estimated compared with those forces of true natural mortality alone. Total annual natural mortality (v) ranged from none (2008) to 66% (1981), averaging 28% over the time series; instantaneous natural mortality (M) averaged 0.38. The value of zero natural mortality in 2008 is unlikely; rather, this is likely an artifact of the estimation method indicating that the higher fishing mortality for that year accounted for the total.

Independent measures of M using the Pauly (1980) and Hoenig (1983) equations offered another expression of this important metric. Hoenig's value based on longevity (maximum age in the population) was comparable to that from the tag based estimates with a mean of 0.36 since 1986. The annual value from the Pauly equation, which is derived from relationships of growth metrics and mean annual temperature, was lower, with a mean of 0.24 since 1989. By comparison, annual natural mortality for Lake Escanaba, Wisconsin averaged 20%, for Oneida Lake 13%, and for Lake Erie 24%. Lake Erie's SCA model assumes a constant annual M value of 0.32 (Nate et al. 2011). There is suspicion, however, that the Lake Erie value also suffers from under representation of some fisheries, inflating the estimate of M (M. Thomas, Michigan DNR, personal communication), not unlike the findings here for Saginaw Bay.

This analysis pools across ages and is not age specific. There are age-specific tag return analysis methods for generating age-specific mortality rates (Pine et al. 2003) such as the model BROWNIE which essentially generates group-specific rates for age groups, sexes, or however the data are stratified. However, estimates based on juveniles, are regarded as generally unreliable methods (Anderson et al. 1985). Mortality rates can vary by ages of fish within a population, however (Beverton and Holt 1959), and variability most often stems from either differing vulnerabilities in catchability (Arreguin-Sanchez 1996) or are due to size-selective predation (Lorenzen 1996). New attention is being given to the derivation of age-specific mortality rates from tag return data (Jiang et al. 2007). Understanding age-specific components of mortality can offer important clues as to what forces are affecting a population. In this analysis, Walleyes were not fully recruited to the tagging operation until age-3 or age-4 (Table 7) yet Walleyes were often recruited to the recreational fishery as early as age 2 (Fielder et al. 2014). This is at least one source of bias and would probably express itself as underestimation of mortality rates, especially fishing mortality. Comparatively, however, estimates of total mortality from tag return analysis were in line with those from catch curves (Figures 3 and 4), except for years 2004–2008 when catch curve estimates were consistently greater. This was likely due to the influence of the influx of strong year classes that steepened the slope of the catch curve and violated the assumption of equal annual recruitment for that method. The same bias was not evident with the total annual mortality rates estimated by the cohort catch curve method (Figure 4) which does not make that same assumption.

The recovery of the Walleye population is evident in the population estimates (Figure 6, Table 5). Fielder and Thomas (2014) report that recovery criteria established by the Michigan DNR were achieved in 2009. Unfortunately the derivation of these estimates doesn't allow for expression of variability so it is difficult to assess the uncertainty about these population estimates. Given that 2SEs about the mean in the estimates of harvest (Fielder et al. 2014) can be as much as the mean itself, it seems likely that the variability about these population estimates would be considerable. The Walleye population estimates peaked in 2007 which is consistent with a series of consecutive strong year classes reported by Fielder and Thomas (2014). Walleye recruitment then became more variable, likely precipitating the decline in abundance. Fielder and Thomas (2014) characterized this as a decline to a more intermediate population size as the population came to equilibrium with the carrying capacity of the bay. The overall trajectory of the Walleye population as estimated here follows the approximate trend laid out by fishery-independent assessment and angler harvest patterns alike (Fielder and Thomas 2014, Fielder et al. 2014), offering some confidence that these population estimates have correctly depicted the trend in abundance. The empirical value of the estimates, however, is less certain as there presently is no independent way to corroborate those values.

The estimates of Walleye abundance for the years 1986–1999 from Bence and Dobiesz (2000) were in line with the values estimated by the two population methodologies used here and followed the same trajectory. The two methods produced similar population estimates (Figure 6) except for the year 1989 when the iteratively solved estimate was substantially greater than the calculated estimate. This is likely because the methodology was sensitive to the magnitude of the observed fishery which was considerable that year. The same fishery data were used in the calculated method but apparently the exploitation rate that year resulted in a smaller estimate of population size. Aside from that deviation, the two methods had considerable agreement despite the differences in methods. Both, however used the same fishery data, and same adjustments for Lake Erie contributions and proportions of age-2 Walleyes smaller than 381 mm (to correct for vulnerability to the fishery). The model-averaged predictions are probably the most robust with respect to methods, since neither method had a greater predictive ability with the fishery-independent index.

The methods of calculating the abundance of Lake Erie Walleyes in Lake Huron (equation 13) used the proportion of tag returns (of total Lake Erie tag returns that same year) as the indicator of proportions making the migration to Lake Huron. This approach requires the assumption that exploitation is the same between the two lakes. Equation 13 also applied the nonreporting correction value to further attempt to correct the tag return proportions in the calculation of the number of Lake Erie fish in Lake Huron. There is no established convention for making these calculations and the method used in equation 13 served to maximize the estimate of Lake Erie Walleyes (in Lake Huron). For this reason, the population estimates of Saginaw Bay Walleye might be considered conservative.

Walleye movement appeared to be affected by sex, size, and density of the overall Walleye population with larger fish more prone to migration than smaller fish, females more prone than males, and Walleye more likely to emigrate from the bay during periods of high density. Given that females are often larger than males, it's difficult to delineate if it is sex or size (or perhaps both) that are affecting the tendency to emigrate. While tag returns differed significantly based on these characteristics, it doesn't necessarily give clues as to whether the motivation for migration might be pursuit of prey resources, temperature mediated, or something else. Given that movement beyond the bay is affected by density, this favors a prey resource explanation more than temperature.

While this analysis helps to assess frequency of emigration across strata, it is more difficult to quantify spatial distribution and or destination from these types of data (Goethel et al. 2011). Tag returns such as these are highly sensitive to the distribution of recreational fishing effort, thus tag return location is a function of both movement of Walleyes and effort by anglers. Adlerstein et al. (2007a, 2007b, 2008) attempted to assess movement of Lake Trout *Salvelinus namaycush* and Chinook Salmon *Oncorhynchus tshawytscha* by adjusting angler-based tag return data to compensate for inherent biases through a general linear model design. Hilborn (1990) offers methods based on a nonlinear likelihood approach. Landsman et al. (2011) characterize fish movement studies in the Great Lakes as not making use of more advanced technologies such as acoustic telemetry. Most of what is known about large-scale movement of Great Lakes fishes to date has been a result of tag return analysis such as jaw tags (this study) or coded wire tags (mostly salmonids). In both instances, movement analysis is typically an ancillary examination and was not the primary purpose of the original tagging study. Large scale analysis of Walleye movement in Lakes Huron and Erie is presently being conducted in a new study by the Great Lakes Fishery Commission and partner agencies and is making use of the same Tittabawassee River source of Walleyes in Saginaw Bay. That study should overcome the biases inherent in the analysis of tag returns for the purpose of understanding large scale movement, and can also aid in more accurate estimation of mortality rates (Eveson et al. 2012).

In spite of the difficulties in interpreting tag returns as evidence of spatial movement, these data do clearly illustrate that Saginaw Bay is not a closed system and that the bay's Walleye population ranges into the main basin. Since mixed-stock analysis has confirmed Tittabawassee River strain of Walleyes in the Ontario commercial harvest, it demonstrates that this stock is being exploited beyond just that of the recreational fishery in Lake Huron. Given that there is little or no reporting from these fisheries of Michigan jaw tags; this study cannot characterize the exploitation rates as being fully representative of all the exploitation and extraction taking place on this stock of Walleye. This is a very important and fundamental limitation to these methods of tag return analysis. Careful consideration has to be given to the sources of tag return data and then, in turn, what the data represent. Other serious limitations include the lack of age-specific estimates of metrics. It is highly improbable that Walleyes across all ages share exactly the same catchability and selectivity for the fisheries and in turn, their mortality rates and exploitation rates also likely differ. The current methods used for analyzing tag returns in Michigan do not allow for the derivation of age-specific rates, although analytical methods do exist. Those methods, however, are just individual analyses of groups (such as ages) and would require the aging of all tagged fish and possibly an increased tagged sample size to allow for application to the Saginaw Bay stock.

Tag analysis studies are replete with assumptions. Others have explored them in detail but the essential assumptions as presented by Brownie et al. (1985) are:

1. The sample is representative of the target population; in this case that Tittabawassee River spawning fish are in fact Saginaw Bay fish and are typical of the Walleyes in the bay not spawning in the Tittabawassee River.
2. Age and sex of individuals are correctly determined. This is more significant for models that attempt to analyze across these groups as strata, which this study did not.
3. There is no tag loss (shedding)
4. Survival rates are not affected by the tagging itself (no tag-induced mortality).
5. Tag recoveries are correctly tabulated.
6. The fate of each tagged fish is independent of the fate of other tagged individuals.
7. The fate of a given tagged fish (i.e. tag recovery in years after tagging) is a multinomial random variable.
8. All groups of individuals tagged (sex, age, size) have the same annual survival and recovery rates (homogeneity of capture probability).
9. For Brownie Model 1, that survival and recovery rates vary by year (annually).

In this study, assumptions 2, 4, 6, and 7 are reasonable and inherent in the study design. The validity of assumption 9 was tested for through the Chi-square goodness of fit test.

None of the study results would lead us to question the assumption of representativeness of the tagged lot of fish (representing the entire stock; assumption 1 above). It is worthwhile, however, to consider that since the recovery of natural reproduction in Saginaw Bay, reproduction is likely occurring in a variety of tributaries and perhaps offshore reefs in and around Saginaw Bay. Sources of reproduction have not been fully investigated since recovery in the mid-2000s and until then, this assumption is less certain than perhaps it once was.

The assumption of no chronic (annual) tag shedding is most problematic for Brownie models as all the theory and corresponding algorithms depend on knowing the original number tagged (N_i) and the computed number remaining at large each year which are the foundation for estimates of survival rates (S_j). If there is substantial tag shedding, then the estimates will have a bias in the parameter estimation. Compounding matters, the variance calculation of these rates in the Brownie model formulation (equations 4 and 5) will not reflect this uncertainty since they too are computationally dependent on the assumption of no tag shedding.

The numerical-based estimation model version (ADMB version) in this study was able to fully incorporate annual tag shedding. Both methods accounted for initial tag shedding the same, by reducing tagged numbers by 1% in advance of any other estimation. The lack of significant differences in estimated recovery rate and survival rates between the two methods, however, indicates that the estimated 8% annual tag shedding rate (92% tag retention) was not sufficient to affect the estimation process.

In an attempt to test the sensitivity of the parameter estimation in the numerical solution model, values of tag retention were varied from 92% down to just 60%. The recovery rate parameter (f_j) increased very little but survival (S_j) increased substantially. This suggests that in parameter estimation, chronic tag retention (θ) less than 1.0 has a greater effect on survival than the tag recovery rate. This was evident even at the 92% tag retention rate in this study (Table 2). Brenden et al. (2010) characterized chronic tag shedding as an influential factor in estimation of mortality rates but less so than nonreporting issues. Within the model structure, the estimation must follow the logic that the same annual tag returns for fewer tags at large constitutes better survival, and not greater exploitation of the tagged fish at large. It is not clear, however, if this is reflective of true population dynamics or an artifact of the formulation of the tag return probability (equation 7) which accounts for tag retention as the product with the annual compounding survival values.

Assumption 5 is probably best interpreted to mean that all tags encountered are reported (i.e. full compliance), which we know is not the case for this study but is compensated for via a correction factor. In tagging literature, the reporting rate is most often denoted by λ_j (Brownie et al. 1985; Eveson et al. 2009) and is typically estimated by reward studies (Henny and Burnham 1976). Unlike the issue of tag shedding, the computation of nonreporting is more straight forward, provided estimates are available. This analysis elected to make use of a time-varying correction factor (Appendix A). In past reports on the tag return analysis, correction was limited to the application of the 2.33 correction factor developed by Fielder and Thomas (2006) and applied to all years. With the availability of the much greater correction factor of 4.03 in 2011 stemming from another reward comparison, it became apparent that nonreporting is not a steady rate. The approach in this study applied a slightly curving power function on the assumption that the rate of nonreporting increases over time. This approach provided for a low nonreporting rate in early years of the study when encountering a tag was a novel experience for an angler and greater nonreporting over the time series as the tag encounter experience became more common. While the reasoning is sound, it's difficult to know if these time-varying rates are accurate given that only two measured points in time exist.

The issue of nonreporting as discussed here is really an issue of under reporting in the recreational fishery. True nonreporting appears to be an issue in the commercial fisheries that operate in the main basin of Lake Huron. Such nonreporting by commercial fisheries is common and the customary procedure for overcoming this is to use fishery observers (Eveson et al. 2007). Such methods are difficult for fisheries that occur outside the jurisdictional boundaries of the agency conducting the tagging study. If rewards are great enough, commercial reporting may begin to occur.

The final assumption that may be violated in this study is that of homogeneity in capture probability (assumption 8). As identified earlier, homogeneity in capture probability states that all fish have the same probability of capture. The most obvious type of violation of this may stem from differences by size and sex (Pine et al. 2003), but in the instances of multiple fisheries exploiting a single stock, there is likely a similar spatial heterogeneity in capture probability. Catchability variation across sex and sizes of fish are perhaps overcome by the large sample size, but the lack of participation by other fisheries and mortality sources is something not easily resolved in this or any tagging study. It is likely that movement of fishes to areas and fisheries outside the study area results in inflation of natural mortality estimates.

While a powerful technique, tag-based studies of population dynamics may seriously underestimate key population metrics and rates. Methods that can overcome these biases and limitations may include construction of age-based models that are tag independent. SCA methods are used in Lake Erie to derive age-specific metrics and population estimates as a supplement to those derived from tag studies. SCA methods, while computationally more intensive, may offer a key advantage in that they can more directly incorporate multiple sources of extraction (beyond just recreational) to encompass a more complete picture of the Walleye population and fisheries. Such models can sometimes make use of auxiliary information including some of the values derived from tag return analyses, resulting in a model superior to either alone.

Recommendations

- Develop a Statistical Catch-at-Age stock assessment model to estimate survival and exploitation rates so as to validate the tag-based values reported here and to test assumptions about homogeneity of capture probabilities.
- Continue annual tagging, maintain the tag recovery matrix and analysis but shift annual analysis to the numerical estimation method (ADMB version). While estimation results are similar, the ADMB version is easier to maintain and more accurate in model structure than the ESTIMATE model.
- Diversify tagging sources beyond the Tittabawassee River to ensure dynamics of the tagged fish are truly representative of the entire Saginaw Bay stock of Walleyes.
- Stratify the tagging and recovery data in this study by ages and sex to explore if sufficient data exist to generate age or sex-specific values of survival and exploitation rate.
- Annually evaluate nonreporting by inclusion of a yearly subset of reward tags so as to develop refined and updated trends in reporting.
- Reexamine Walleye movement using effort-corrected methodologies. Compare and contrast with forthcoming telemetry findings.

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Patrick A. Hanchin, Reviewer
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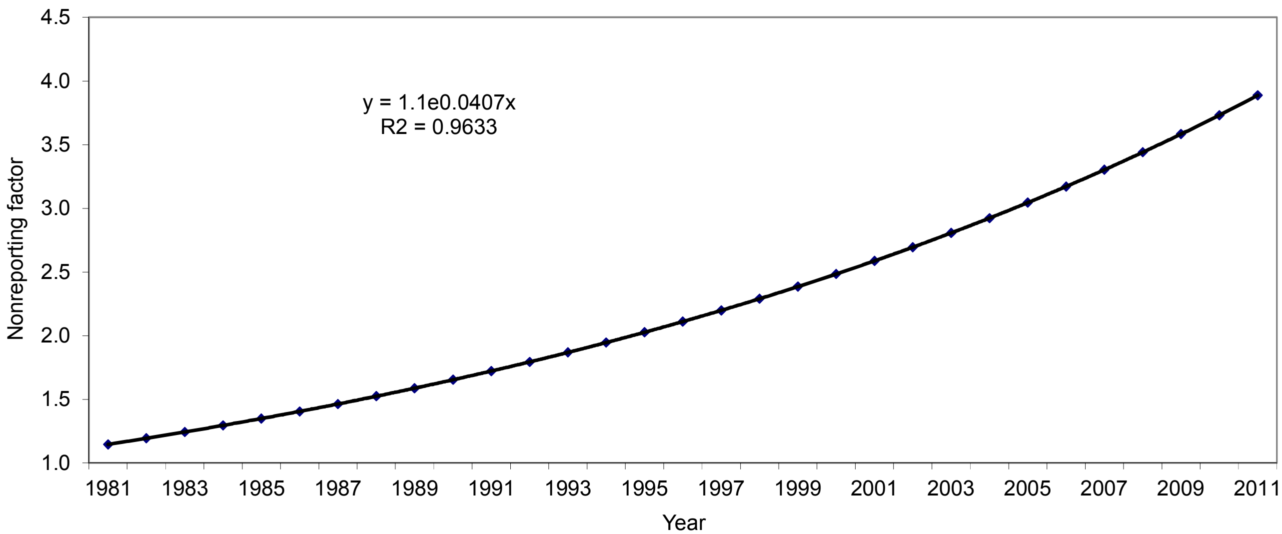

Year	Expansion factor
1981	1.1457
1982	1.1933
1983	1.2429
1984	1.2946
1985	1.3484
1986	1.4044
1987	1.4628
1988	1.5236
1989	1.5869
1990	1.6528
1991	1.7215
1992	1.7930
1993	1.8675
1994	1.9452
1995	2.0260
1996	2.1102
1997	2.1979
1998	2.2892
1999	2.3843
2000	2.4834
2001	2.5866
2002	2.6941
2003	2.8061
2004	2.9227
2005	3.0442
2006	3.1707
2007	3.3024
2008	3.4397
2009	3.5826
2010	3.7315
2011	3.8866

Appendix A.–Expansion factor used to correct for nonreporting of jaw tag returns, 1981–2011. Values were derived by fitting a power function to two measured values in 2000 and 2011, equation included.

Appendix B.–AD Model Builder programming code for the numerical solution version of tag return analysis.

```
//File first Created on 12/27/2012
//Saginaw Bay tag return analysis model.    Dave Fielder, MDNR/MSU FW QFC
//This version treating  recovery rate 'f' and survival 'S' as parameters
//according to the formulation of Brownie et al. (1985).
//now adjusting for nonreporting on tags returns (up front) by year
//now applying tag retention values in with survival calcs in accordance with Brownie et al.
(1985)  formulation
//This version with data beginning in 1981.
//All Rights Reserved by the author.



DATA_SECTION

//values in common
  init_int fyear                    //first year
  init_int lyear                    //last year


//Tag data from recreational fishery
  init_vector num_tagged(fyear,lyear)          //number jaw tagged by year
  init_int Ntag                     // number of years of tagging
  init_int recap_yrs                // number of years of recaps
  init_int startyear                //first year of tag returns
  init_int endyear                  //last year of tag returns
  init_matrix tags_returned(fyear,lyear,startyear,endyear)   //observed jaw tags returned by
year (ragged matrix)
  init_number initial_tagrent               // initial first 21 d tag retention rate
  init_number annual_tagrent                //annual tag retention rate
  init_vector nonreport(fyear,lyear)          //vector of yearly correction (expansion) factors
for nonreporting of jaw tags in recreational fishery.


//More values in common
  init_vector test(1,3)                              //test vector for ensuring data are read in
correctly
  int i                          //index for year loop
  int c
                             //index for year at large loop
  //!!cout << test << endl;
  //!!cout << "     " << endl;
  //!!cout << tags_returned << endl;
  //!!cout << "     " << endl;
  //!!exit(88);
```

```
PARAMETER_SECTION
  //Declaration of parameters to be estimated


  //parameters related to tag returns
  init_bounded_vector S(startyear,endyear,0.01,1.0,1)  //Recovery year specific Survival
  init_bounded_vector f(startyear,endyear,0.001,1.0,1)  //recovery rate specific to recovery
year



  //variables needed for comparison of tag returns
  matrix pred_tagrtns(fyear,lyear,startyear,endyear)    //matrix of predicted values in the same
ragged format as the observed
  matrix tags_returned_adj(fyear,lyear,startyear,endyear)  //tags returned after adjustment for
nonreporting
  matrix p(fyear,lyear,startyear,endyear)              //matrix of predicted recovery probabilities
  matrix S_byyear(fyear,lyear,startyear,endyear)       //matrix of compounding S values,
derived from estiamted S
  vector tot_p(fyear,lyear)                            //vector of total probabilities (summed p)
  vector tot_recov(fyear,lyear)                        //vector for adding up total recoveries. Needed
to get at tot_unrecov
  vector tot_unrecov(fyear,lyear)                      //vector of total unrecovered tags (survivors)

  //other values to be derived from estimates
  vector A(fyear,lyear)           //Total annual mortality from S
  vector Z(fyear,lyear)           //Total instantaneious mortalty
  vector F(fyear,lyear)           //recreatinoal fishing mortality
  vector M(fyear,lyear)           //instantaneious natural mortality
  number mean_M                   //mean M value (omits last year which is not estimatable)
  vector M_sub(fyear,lyear-1)     //just an intermediate value needed to get mean M
  vector exploit(fyear,lyear)     //exploitation based off of F and Z as opposed to recovery
rate f



  //variables needed for all predictions (common)

  matrix L13(fyear,lyear,startyear,endyear)
  vector L13_sub(fyear,lyear)
  number L14
  objective_function_value negLL;

INITIALIZATION_SECTION

  //done in Preliminary calcs section
```

```
PRELIMINARY_CALCS_SECTION
  //starting values for parameters

S.fill("{0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,0.6,
0.6,0.6,0.6,0.6,0.6,0.6,0.6}");

f.fill("{0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,0.1,
0.1,0.1,0.1,0.1,0.1,0.1,0.1}");
   L13=0.0;   //initializing tag return likelihood component since only partically filled by obj
fun calc.


PROCEDURE_SECTION

  get_tagrtn();
  get_rates();
  get_objective();



FUNCTION get_tagrtn


   for(i=fyear;i<=lyear;i++)   {
    for(c=startyear;c<=endyear;c++)  {
   tags_returned_adj(i,c)=tags_returned(i,c)*nonreport(i);  //accounting for nonreporting
upfront. 'Nonreporting' is yearly vector of  expansion factors
    }
     }

   tot_recov=rowsum(tags_returned_adj);  //getting the total number of tags recoered by tag
year

  //populating a matrix of compounding survivals for use in predicting the tag returns

   for(i=fyear;i<=lyear;i++)   {
    for(c=startyear;c<=endyear;c++)  {
     if(c==i)   S_byyear(i,c)=1.0*initial_tagrent;      //setting S_byyear  for first year. This
value is not ever used in calcs. Survival in first summer at large assumed to be 1.0. Mort is knife
edge over winter. Initial_tagrent included just to remind us it affects first year.
     if(c-i==1) S_byyear(i,c)=S(c-1)*annual_tagrent*initial_tagrent;  //c-1 for S_byyear
because the needed value is ascribed (labeled) to the year before. i.e survival from the start year
to next year is labeled start year. Initial_tagrent inlcuded again because calc doesn't really make
use of first S_byyear so included here (again) to keep the math right.
     if(c-i>1) S_byyear(i,c)=S(c-1)*annual_tagrent*S_byyear(i,c-1);  //calculating
compounding matrix of survival. uses S(c-1) cause it needs the survival value to the current year
from the previous year which is attributed (labeled)  to the previous year.
         }
         }
```

```
for(i=fyear;i<=lyear;i++)    //loop for all tag years (1-26)
{
for(c=startyear;c<=endyear;c++)
 {
if(c==i)  p(i,c)=f(c)*initial_tagrent;   //first year predicted tag return probabilities (only a function of recovery rate and initial tag retention). Initial_tagrent included here since easier to code in here, than to add in S value that representst that since no one is expecting an S the first year.
if(c-i>=1)  p(i,c)=(f(c)*S_byyear(i,c));    //subsequent years predicted tag return probabilities. Annual tag retention value already included back in the compounding matrix of survivals (S_byyear).

 }
}

for(i=fyear;i<=lyear;i++)    //loop for all tag years
{
for(c=startyear;c<=endyear;c++)
 {
if(c==i)  pred_tagrtns(i,c)=((num_tagged(i)*p(i,c)))/nonreport(i);  //first year predicted tag returns
if(c-i>=1)  pred_tagrtns(i,c)=((num_tagged(i)*p(i,c)))/nonreport(i);  //subsequent years predicted tag returns
//dividing by nonreporting to return values back to what was actually observed
 }
}


tot_p=rowsum(p);  //summing up the individual pred probabilities
tot_unrecov=num_tagged-tot_recov;  //getting the total number unrecovered (survivors)Trying w/o num_tagged_act since adjustment of short term tag retenction already in prob


FUNCTION get_rates

 //deriving related mortality and exploitation rates from estimated parameters
 A=1.0-S;
 Z=(log(S))/-1.0;
  for(i=fyear;i<=lyear;i++)    //loop for all tag years
  {
 F(i)=(Z(i)*f(i))/A(i);
  }
 M=Z-F;
 for (i=fyear;i<=lyear-1;i++)
 {
  M_sub(i)=(M(i));
 }
 mean_M = (sum(M_sub))/(Ntag-1.0);
```

```
    exploit=elem_prod(elem_div(F,Z),(1-exp(-Z)));     //calculating exploitation but
fundementally equivalient to f




  FUNCTION get_objective


    for(i=fyear;i<=lyear;i++)    //loop for all tag years
     {
     for(c=startyear;c<=endyear;c++)
      {
     if(c-i>=0)  L13(i,c)=-1.0*((tags_returned_adj(i,c))*log(p(i,c))); //likelihood from
multinomial for tag return probabilities
      }
    L13_sub(i)=-1.0*((tot_unrecov(i))*log(1.0-tot_p(i)));  //likelihood from multinomial for tag
survivors probabilities
     }
    L14=(sum(rowsum(L13)+L13_sub));  //summing it all up
    negLL=L14;




  REPORT_SECTION
    report.precision(4);
    //--------------------------------------------------------------------------------------------
    report << "Mortality and Recovery Rate Estimation" << endl;
    report << "Saginaw Bay Walleye jaw tag return analysis ";
    report <<fyear;
    report <<"-";
    report <<lyear<< endl;
    report <<"______________________________________________________" <<endl;
    report << " " << endl;
    report << " " << endl;
    //--------------------------------------------------------------------------------------------
    report << "pred_tagrtns" << endl;
    report <<  pred_tagrtns << endl;
    report << " " << endl;
    //--------------------------------------------------------------------------------------------
    report << "p(i,c)" << endl;
    report <<  p << endl;
    report << " " << endl;
    //--------------------------------------------------------------------------------------------
    report << "Initial tag retention value used" << endl;
    report << initial_tagrent  << endl;
    report << " " << endl;
    //--------------------------------------------------------------------------------------------
```

```
report << "Annual tag retention value used" << endl;
report << annual_tagrent  << endl;
report << " " << endl;
//-----------------------------------------------------------------------------------------------
report << "S(i) from stated year to the next year" << endl;
 for (i=fyear;i<=lyear-1;i++)
{
report <<  S(i) << endl;
}
report << "value in last year is  not estimable & therefore is omitted " << endl;
report << "     " << endl;
//-----------------------------------------------------------------------------------------------
report << "S_byyear(i,c)" << endl;
report <<  S_byyear << endl;
report << " " << endl;
 //-----------------------------------------------------------------------------------------------
report << "f(i)" << endl;
for (i=fyear;i<=lyear;i++)
{
report <<  f(i) << endl;
}
report << " " << endl;
//-----------------------------------------------------------------------------------------------
report << "exploit(i)" << endl;
for (i=fyear;i<=lyear;i++)
{
report <<  exploit(i) << endl;
}
report << " " << endl;
//-----------------------------------------------------------------------------------------------
report << "Z" << endl;
report <<  Z << endl;
report << "value in last year is  not estimable & therefore should be ignored " << endl;
report << " " << endl;
//-----------------------------------------------------------------------------------------------
report << "F" << endl;
report <<  F << endl;
report << "value in last year is  not estimable & therefore should be ignored " << endl;
report << " " << endl;
//-----------------------------------------------------------------------------------------------
report << "mean M" << endl;
report << mean_M << endl;
report << " " << endl;
//-----------------------------------------------------------------------------------------------
report << "M" << endl;
report <<  M << endl;
report << "value in last year is  not estimable & therefore should be ignored " << endl;
report << " " << endl;
//-----------------------------------------------------------------------------------------------
```

```
report << "A" << endl;
report <<  A << endl;
report << "value in last year is  not estimable & therefore should be ignored " << endl;
report << " " << endl;
```

Appendix C.–Numbers of walleye jaw tagged in the Tittabawassee River 1981-2011, and actual tag numbers recovered by year before any expansion for nonreporting. Yearly tagging numbers for three years included walleyes tagged at Sanford Dam on the Tittabawassee River (1985: 531, 1986: 608, and 1989:497).

		Actual recovery (harvest) matrix by year returned																														
Year	No. tagged	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
1981	400	17	3	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1982	727	0	11	12	3	2	6	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1983	3,430	0	0	105	52	36	40	28	13	18	7	8	7	5	2	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0
1984	3,550	0	0	0	68	88	66	56	32	21	9	7	5	5	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1985	3,866	0	0	0	0	134	116	67	38	14	5	4	8	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986	3,531	0	0	0	0	0	150	100	37	21	16	11	12	7	1	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
1987	6,020	0	0	0	0	0	0	298	116	64	23	19	23	12	6	5	0	2	4	3	1	1	2	0	0	0	0	0	0	0	0	0
1988	4,036	0	0	0	0	0	0	0	160	85	32	26	20	15	11	7	1	4	0	4	1	2	0	0	0	0	0	0	0	0	0	0
1989	2,991	0	0	0	0	0	0	0	0	70	54	36	52	20	13	5	4	5	1	4	1	0	0	0	0	0	0	0	0	0	0	0
1990	2,488	0	0	0	0	0	0	0	0	0	58	52	52	32	9	6	4	5	1	1	3	0	0	0	1	0	0	0	0	0	0	0
1991	3,079	0	0	0	0	0	0	0	0	0	0	69	109	49	16	9	11	11	4	7	2	1	3	1	0	0	0	1	1	0	0	0
1992	2,995	0	0	0	0	0	0	0	0	0	0	0	165	83	30	21	14	11	12	11	6	2	1	0	0	0	1	0	0	2	0	0
1993	2,990	0	0	0	0	0	0	0	0	0	0	0	0	150	51	31	24	17	13	15	9	5	3	2	3	0	0	0	0	0	0	0
1994	2,999	0	0	0	0	0	0	0	0	0	0	0	0	0	76	52	44	36	18	16	12	2	0	2	1	2	0	0	0	0	0	0
1995	2,970	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	50	45	30	32	8	3	2	5	2	1	1	0	0	0	0	0
1996	2,992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	71	74	53	47	20	10	9	7	4	0	0	2	0	0	0	0
1997	2,993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	84	82	58	18	11	12	14	6	3	1	1	0	1	0	0
1998	2,490	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	93	68	24	20	13	13	9	3	1	1	0	0	0	0
1999	2,998	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	128	37	28	25	23	21	8	7	2	1	2	1	0
2000	3,302	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	98	60	61	62	41	20	14	8	11	4	1	1
2001	3,000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	79	88	50	47	19	10	10	7	12	2	1
2002	2,993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	152	84	71	28	19	10	17	10	3	2
2003	3,000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	114	111	54	24	23	22	21	6	2
2004	2,997	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	190	63	44	50	34	41	7	6
2005	2998	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	116	62	57	53	62	8	8
2006	2,996	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	137	91	62	81	15	6
2007	2,886	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	161	94	113	19	14
2008	2,993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	225	233	48	17
2009	2,999	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	318	61	23
2010	2,969	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	176	82
2011	2,991		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	142
Total	93,669																															