

Including independent estimates and uncertainty to quantify total abundance of fish migrating in a large river system: walleye (*Sander vitreus*) in the Maumee River, Ohio

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Abstract: Walleye (*Sander vitreus*) in Lake Erie is a valuable and migratory species that spawns in tributaries. We used hydroacoustic sampling, gill net sampling, and Bayesian state-space modeling to estimate the spawning stock abundance, characterize size and sex structure, and explore environmental factors cuing migration of walleye in the Maumee River for 2011 and 2012. We estimated the spawning stock abundance to be between 431 000 and 1 446 000 individuals in 2011 and between 386 400 and 857 200 individuals in 2012 (95% Bayesian credible intervals). A back-calculation from a concurrent larval fish study produced an estimate of 78 000 to 237 000 spawners for 2011. The sex ratio was skewed towards males early in the spawning season but approached 1:1 later, and larger individuals entered the river earlier in the season than smaller individuals. Walleye migration was greater during low river discharge and intermediate temperatures. Our approach to estimating absolute abundance and uncertainty as well as characterization of the spawning stock could improve assessment and management of this species, and our methodology is applicable to other diadromous populations.

Résumé : Le doré jaune (*Sander vitreus*) dans le lac Érié est une espèce migratoire de valeur qui fraye dans les affluents. Nous avons utilisé l'échantillonnage acoustique, l'échantillonnage au filet maillant et la modélisation despaces d'états bayésiens pour estimer l'abondance du stock reproducteur, caractériser la taille et la structure sexuelle et explorer les facteurs ambiants qui ont signalé le début de la migration des dorés jaunes dans la rivière Maumee pour 2011 et 2012. Nous avons estimé l'abondance du stock reproducteur à de 431 000 à 1 446 000 individus en 2011, et de 386 400 à 857 200 individus en 2012 (intervalles de crédibilité bayésiens à 95 %). Un rétrocalcul à partir d'une étude concurrente de larves de poisson a produit une estimation de 78 000 à 237 000 reproducteurs en 2011. Le rapport des sexes présentait une asymétrie vers les mâles au début de la période de frai pour s'approcher de 1:1 plus tard, et les individus plus grands entraient dans la rivière plus tôt dans la saison que les individus de plus petite taille. La migration du doré était plus importante en période de faible débit de la rivière et de températures intermédiaires. Notre approche pour estimer l'abondance absolue et l'incertitude et caractériser le stock reproducteur pourrait améliorer l'évaluation et la gestion de cette espèce, et cette méthodologie se prête à d'autres populations diadromes. [Traduit par la Rédaction]

Introduction

Migratory fishes require diverse but connected habitats to complete their life cycles; thus, they must be managed over large spatial extents spanning multiple habitat types and often multiple jurisdictional boundaries (McDowall 1992, 1999). Globally, threats such as overexploitation, habitat degradation, loss of connectivity, and climate change contribute to the imperilment and decline of migratory fish (Jelks et al. 2008; Limburg and Waldman 2009; Rothlisberger et al. 2010). Estimates of abundance allow managers to identify changes in stocks in relation to threats. However, fisheries managers frequently lack fishery-independent information necessary to estimate abundance, leading to poor assessment and mismanagement of fish stocks (Walters and Maguire 1996; Botsford et al. 1997). Furthermore, abundance estimates of migratory animals involve much uncertainty because of spatiotemporal variability within populations and sampling error (Hilborn and Mangel 1997). Hence, an approach to estimating migratory fish abundance that includes multiple independent measures and that quantifies uncertainty can improve the realism and interpretation of estimates and improve management.

Stock assessment and management can benefit from information such as size and sex structure of spawning stocks, which improves estimates of biomass, growth, and assessment of harvest and fishery quality (Anderson and Neumann 1996). Also, environmental conditions influence the timing of fish migrations (Lucas and Baras 2001), and the relationships between movements and environmental conditions can generate predictive models of migration (Paragamian and Kruse 2001). Thus, combining abundance information with stock structure and environmental information can be useful for understanding population dynamics and assessing stocks (Cardinale and Arrhenius 2000).

In Lake Erie, walleye (*Sander vitreus*) are highly migratory (Wang et al. 2007) and managed in a coordinated effort by agencies from four states (Michigan, Ohio, Pennsylvania, and New York) and one province (Ontario) (WTG 2012). Walleye spawn in many of Lake Erie's tributaries as well as on open-lake reefs (Goodyear et al. 1982), and some of the spawning groups may be genetically distinct (Strange and Stepien 2007). Moreover, walleye abundance and fishing mortality vary through space in Lake Erie (Berger et al. 2012). Thus, identifying, assessing, and conserving individual

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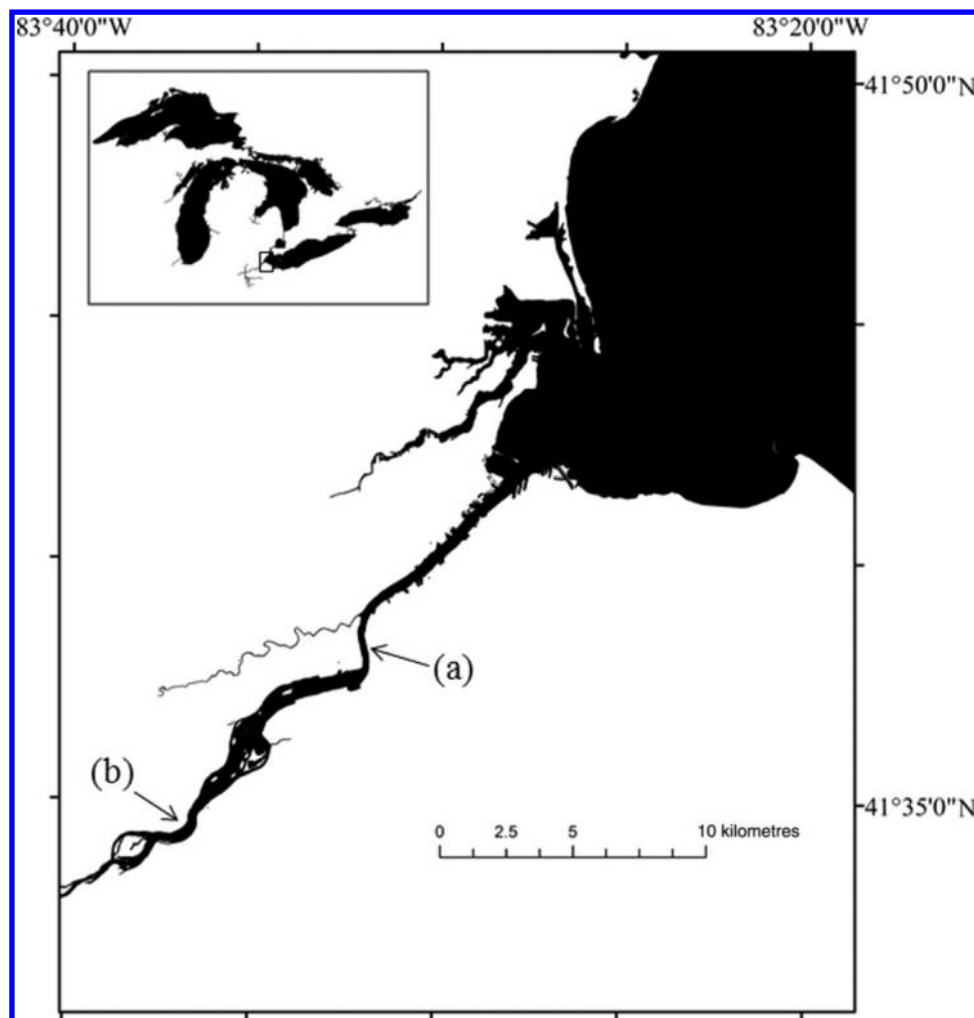
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Fig. 1. (a) Lower Maumee River hydroacoustic and gill net sampling site and (b) larval fish sampling site.



stocks are goals for walleye management in Lake Erie (Locke et al. 2005). Unfortunately, absolute abundance estimates do not exist for any of Lake Erie's walleye spawning stocks, stock-specific size and sex structure information is lacking, and the environmental factors cuing movement are unclear, thereby hindering stock-specific management.

Our goal was to develop widely applicable methods for estimating abundance and structural and behavioral characteristics of riverine spawning stocks. Our objectives were to (i) estimate the absolute abundance of the Maumee River, Ohio, walleye spawning stock using two independent methods and quantify uncertainty in those estimates, (ii) describe the size and sex structure of walleye, and (iii) determine environmental factors that influence walleye migration. We employed hydroacoustic sampling, gill net sampling, acoustic telemetry, Bayesian state-space modeling, and information from a concurrent larval fish study to achieve these objectives.

Methods

Study site

The Maumee River is the largest tributary of the Great Lakes by watershed area. The lower 25 km is considered a freshwater estuary, as it is heavily influenced by its proximity to Lake Erie (Herdendorf 1990). The Maumee River has large runs of migratory fish from multiple species (Trautman 1981) and supports a popular and economically important recreational walleye fishery during the spring spawning season. The spawning habitat used by wall-

eye begins approximately 25 km from the river mouth and continues upstream for another 25 km. We used a "gateway" sampling design; because fish migrate upriver many kilometres before spawning, we applied all of our effort to quantify walleye migrations through a 1 km study section located between the river mouth and spawning grounds (Fig. 1). We selected our study site because of its amenability to hydroacoustic sampling. The site is part of a dredged shipping channel, and as a result it is approximately 9 m deep, homogenous in depth, and lacks structure (large rocks or woody debris) that could provide refuge to fish.

Hydroacoustic sampling

We used hydroacoustics as our primary tool to measure spawning stock abundance of walleye in the Maumee River. We sampled approximately three times per week from March through May (encompassing the spawning season of walleye in Lake Erie) of 2011 and 2012, using a combination of mobile transects and stationary data collections at the 1 km study reach. Mobile transects allowed us to sample throughout the study reach and quantify fish abundance, whereas stationary data collections allowed us to obtain target strength distributions for individual fish and measure swimming speed and direction of movement. Hydroacoustic sampling was conducted with a 430 kHz downward-facing split-beam transducer with a beam angle of 6.9°, pulse duration of 0.2 ms, and a ping rate of 10 pings·s⁻¹. The same BioSonics DT-X echosounder (BioSonics Inc., Seattle, Washington) was used for mobile and stationary collections. The echosounder was cali-

brated at the beginning and end of the each sampling season with a standard 17 mm tungsten carbide sphere. In 2011, observed target strength (TS) values on the calibration sphere were close to expected (<0.2 dB difference), and no offset was applied to hydroacoustic data. In 2012, observed values were slightly greater than expected, and a 0.2 dB offset was applied to mobile and stationary TS data in Echoview 4.90 (Myriax, Tasmania, Australia) prior to analysis. The mobile transects were conducted in a zig-zag pattern moving from upstream to downstream at approximately $1 \text{ m}\cdot\text{s}^{-1}$. Typically, 700–900 m^3 of water were sampled with each transect. One set of six to eight transects was sampled during each event in 2011, and two sets of six to eight transects were sampled during each event in 2012. Stationary collections were made during most sampling events at one or two points in the study reach for 15–20 min at each point. In total, mobile hydroacoustic transects were conducted on 24 sampling events in 2011 (stationary hydroacoustics collections were made on 17 of those sampling events) and on 27 sampling events in 2012 (stationary collections were made on 21 sampling events).

Gill net sampling

Species identity cannot be ascertained from hydroacoustics; consequently, we conducted gill net sampling to augment acoustic data. Netting was conducted in conjunction with hydroacoustic sampling three times per week. High river discharge prevented gill net sampling on several occasions, particularly during 2011. The gill net was 76.2 m in length by 2.4 m high, with stretch mesh sizes of 5.1, 7.6, 10.2, 12.7, and 15.2 cm. The gill net was deployed perpendicular to the river channel, and set for 1–2 h to reduce mortality of captured fish. Fish were measured for total length, identified to species, sex, and spawning condition (i.e., prespaw or postspaw), and released.

Estimating migration rate

Our abundance estimates depended heavily on the rate at which fish migrated upstream. Consequently, we used two independent measures of walleye movement: a small-scale rate of movement measured using stationary hydroacoustics and large-scale rate derived from acoustic telemetry tags. For the stationary hydroacoustic method, we calculated the swimming speed and direction of movement for each fish track that met the potential walleye criteria (Appendix A). We observed 13 individual fish in 2011 and 12 individuals in 2012 that met walleye criteria and moved in an upstream direction. We observed that fish typically followed a meandering path upstream rather than swimming directly upstream. For each fish track, we measured the angle of the path to directly upstream and then used trigonometry to measure the upstream component of movement. The mean upstream migration rate for 2011 and 2012 combined was $7.5 \text{ km}\cdot\text{day}^{-1}$ and ranged from 0.8 to $19.6 \text{ km}\cdot\text{day}^{-1}$. The stationary hydroacoustic measurement of swimming speed was advantageous as it allowed us to measure the swimming speed for many individual fish; however, there were several drawbacks. For example, the scale of observation (1–2 m) was much smaller than the unit of interest (1 km). Also, although we applied our TS criteria for walleye, the species identity for measured fish could not be absolutely determined; thus, some of the swimming speed measurements may have been from species other than walleye.

To estimate adult walleye movement at a larger spatial scale, we used data collected as part of a concurrent Great Lakes Fishery Commission acoustic telemetry tagging study in which 200 adult walleye were tagged in the Maumee River in 2011 (C. Vandergoot, unpublished data). In March 2012, two receivers were placed in the study reach, 1 km apart from each other. The receivers had a range of approximately 500 m and could thus detect tagged fish over approximately 2 km of river. By determining which receiver first located tagged fish and calculating the amount of time it took for tagged fish to move through the 2 km receiver area, we were

able to deduce direction and approximate speed of upstream movement. We observed 14 individuals moving upstream, with a mean speed of $12.5 \text{ km}\cdot\text{day}^{-1}$ and ranging from 4.8 to $23.0 \text{ km}\cdot\text{day}^{-1}$. The telemetry measurements allowed us to be certain only wall-eye swimming speeds were measured and the scale of the observations was similar to the scale of interest. However, only a small number of fish were observed, and detection probability of tags near the periphery of the range of the receivers is known to be variable (Bergé et al. 2012), which could limit the precision of swimming speed measurements. The hydroacoustic and telemetry methods provided complementary means of measuring swimming speed, and using the two methods in concert limited the potential bias resulting from the shortcomings of each.

We incorporated both the stationary hydroacoustic and telemetry estimates into a composite estimate of migration rate. Since the hydroacoustic and telemetry observations were made in the same location over the same period of time, we assumed that these two sets of observations sampled the same movement process, and we used both data sets in a hierarchical gamma model (Ntzoufras 2009) to generate a single estimate of migration rate, described by a gamma distribution. In this model each individual observation was described by a gamma distribution, where the means of those distributions were drawn from larger groups (i.e., sampling method), also described by gamma distributions. Both sets of measurements were given equal weight in the model. The estimated migration rates from different sampling methods shared global hyperparameters (α , β) in their distributions. The mean of the final gamma distribution describing migration rate was $10.7 \text{ km}\cdot\text{day}^{-1}$, with a standard deviation of $10.1 \text{ km}\cdot\text{day}^{-1}$, capturing the great amount of variability in the measurement of migration rate observed with each method. Past studies have measured walleye migration rates in other systems and reported values have ranged from approximately $4 \text{ km}\cdot\text{day}^{-1}$ (Palmer et al. 2005) to $10 \text{ km}\cdot\text{day}^{-1}$ (Paragamian 1989; DePhilip et al. 2005), which are contained within the modeled migration rate distribution used in this study.

Hydroacoustic data analysis

We used echo-counting to calculate fish density for each individual mobile hydroacoustic transect by 2 m depth strata. To accomplish this task, single targets were detected from each transect using the Single Target Detection Method 2 algorithm in Echoview 4.90, using established parameter settings for Great Lakes hydroacoustic applications (Parker-Setter et al. 2009; Appendix A). Next, we used the α - β fish tracking algorithm in Echoview to identify individual fish. We used fish tracking algorithm parameters similar to the Echoview defaults, with α set to 0.7 and β set to 0.5 for minor and major axes and range. Weights in the fish tracking algorithm were set to 30% for the major axis, 30% for the minor axis, and 40% for the range. We then visually analyzed all hydroacoustic data to verify the software's fish track identification. Finally, we calculated the mean TS of all identified fish tracks in Echoview.

After individual fish tracks were identified, we sought to identify potential walleye. We matched season-wide mean TS–frequency histograms for fish tracks from our stationary hydroacoustic surveys and length–frequency histograms from our gill net surveys and calculated expected TS for captured fish from a TS–length equation (Frouzova et al. 2005; Appendix A). From these analyses, we set threshold values to identify the smallest walleye size classes of -30.0 dB for 2011 and -29.5 dB for 2012; all fish tracks with mean TS greater than the threshold value were considered potential walleye and included in further analysis. Once fish tracks were narrowed to only potential walleye, we calculated 2 m strata-specific density of potential walleye for each transect by dividing the number of potential walleye by the water volume sampled during that transect.

We made several important assumptions in our estimate of fish abundance. (1) Fish density was the same below the acoustic bottom dead zone (~0.2 m in our surveys) as it was immediately above the dead zone. The mean distance above the bottom dead zone for potential walleye targets from our mobile hydroacoustic transects was 1.2 m, indicating that most fish migrated far enough from the bottom to be detected. (2) Fish were far enough apart from one another to be distinguished. We used a high-frequency transducer and a short pulse duration (0.2 ms), which maximizes vertical resolution and minimizes the bottom dead zone and the possibility that overlapping targets are not discernible. Also, large fish were generally low in density, and no schooling behavior was observed. (3) No walleye migrated shallower than 2 m. At shallow depths, the hydroacoustic near-field dead zone limits the ability to detect fish. However, adult walleye are typically demersal (Bozek et al. 2011), and in this study we observed most walleye at depths greater than 5 m (see Appendix A). (4) Gill nets provided an accurate depiction of the large-bodied fish (>400 mm) community. (5) Fish were constantly migrating through the study reach. (6) Fish migrated independent of diel cycle. We conducted a total of five paired day–night collections over the two sample years and compared average large fish (fish tracks > -30.0 dB TS in 2011 and > -29.5 dB in 2012) densities with a paired *t* test. We found no significant difference with time of day (two-tailed paired *t* test; *t* = 0.74, *df* = 4, *p* = 0.50), validating this assumption. We also conducted a *t* test to compare the migration rate (km·day⁻¹) of day- vs. night-moving fish on 14 upstream-moving walleye tagged as a part of the concurrent telemetry study. Of those tagged fish, nine were observed to move during the day (0601–1800) and five were observed to move at night (1801–0600). The mean upstream migration rate was 12.46 km·day⁻¹ for day-moving fish and 12.54 km·day⁻¹ for night-moving fish, and no significance was found with a two-tailed *t* test (*t* = 0.02, *df* = 12, *p* = 0.98). (7) Fish behavior was unaffected by the presence of the research vessel or the use of the hydroacoustics. (8) Walleye were unevenly distributed in the sample reach, and individual transects are independent measurements of fish abundance in the study reach. We excluded ~5 m at the beginning and end of each transect to remove spatial autocorrelation near the vertices of the zig-zag transects (Simmonds and MacLennan 2005).

Bayesian state-space model

We first extrapolated the abundance of potential walleye in our study reach from hydroacoustic analysis of individual transects. Individual transects were analyzed by 2 m depth strata, and strata-specific densities were multiplied by the volume of water in that depth stratum from the entire study reach:

$$(1) \quad a_{\text{transect}} = \sum (d_{\text{strata}} \cdot v_{\text{strata}})$$

where *a* is the abundance extrapolated from an observed transect, *d* is the density of potential walleye by depth strata, and *v* is the water volume of the study reach by depth strata. This resulted in six to eight estimates of potential walleye abundance in the study reach on a given sample day in 2011 and 12 to 16 estimates per sample day in 2012 (because two sets of transects were conducted).

Next, we used a Bayesian state-space model (Ntzoufras 2009; Kery and Schaub 2012) to generate a single daily abundance estimate (*A*_{day}) of potential walleye in our sample area from the individual transect estimates (*a*_{transect}). A Poisson–gamma mixture was used to accommodate variation in the data caused by the assumed uneven spatial distribution of fish in the sample reach. We assumed temporal autocorrelation in *A*_{day} among days and therefore structured our model to share information among sampling days. Thus, each unsampled day was estimated from data collected in the days preceding and following it, and estimates on

sampled days were also informed by surrounding estimates. This model structure allowed us to estimate potential walleye abundance within our sampling reach while accounting for both temporal and spatial variability (DuFour 2013).

Finally, we rescaled *A*_{day} within the sampling reach to include only prespawnd walleye migrating upstream on a daily basis. *A*_{day} were multiplied by the proportion of potential walleye that are likely prespawnd. A migration rate was then applied, ultimately generating an estimate of daily spawning stock abundance (*SS*_{day}, fish·day⁻¹):

$$(2) \quad SS_{\text{day}} = A_{\text{day}} \cdot p_{\text{month or week}} \cdot m_{\text{season}}$$

where *SS*_{day} is the spawning stock abundance on given day, *A*_{day} is the daily abundance of potential walleye in the sampling reach, *p* is the monthly (2011) or weekly (2012) proportion of fish >460 mm (2011) or >500 mm (2012) in our gill net samples that were prespawnd walleye (in 2011 sparse sampling precluded finer temporal resolution), and *m* is a migration rate, calculated as the upstream migration rate of upstream migrating fish (km·day⁻¹ from the stationary hydroacoustic collections and telemetry observations) divided by the length of the study reach (1 km). We then estimated the seasonal spawning stock abundance (*S*) by summing daily estimates of abundance:

$$(3) \quad S_{\text{season}} = \sum (SS_{\text{day}})$$

We used several distributions in the Bayesian model to best describe our data inputs. Extrapolated transect-specific abundance of potential walleye (*a*_{transect}) was modeled with a Poisson–gamma mixture, a form of the negative binomial distribution that accounts for spatial aggregation of organisms. Next, the proportion of prespawnd walleye (*p*) was modeled with a beta distribution, allowing for potential variation in this value. Finally, the migration rate (*m*) was modeled with a gamma distribution, which has a right-tailed skew and allows for the possibility that some individuals move faster than others. The Bayesian state-space model and subsequent analysis were carried out in the Markov chain Monte Carlo (MCMC)-based software OpenBUGS, which facilitated the mixture of multiple distributions and propagation of uncertainty (Lunn et al. 2009).

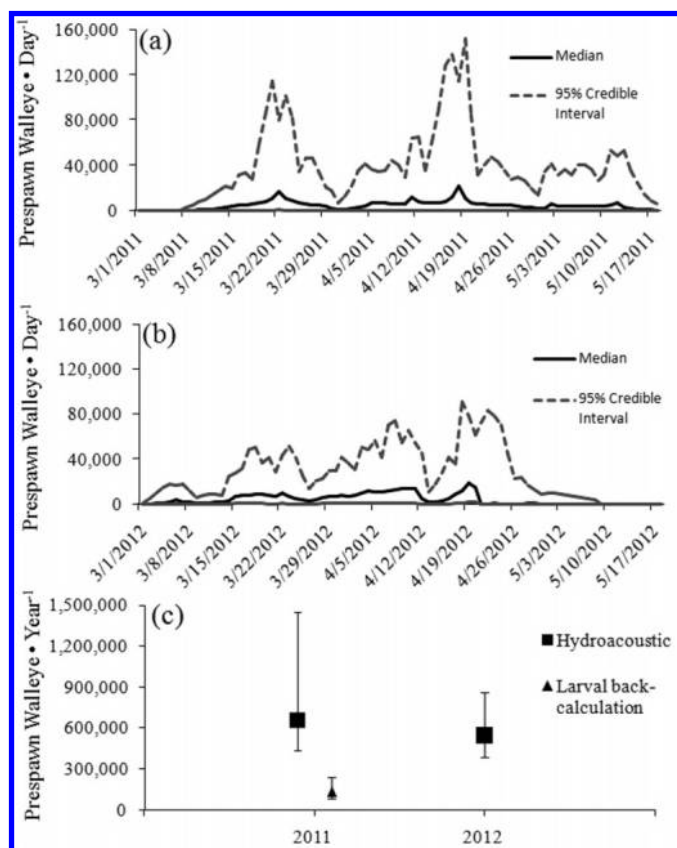
Larval fish sampling and stock-size back-calculation

A second, independent estimate of walleye spawning stock size was generated for 2011 through a back-calculation from larval fish abundance estimate. Larval fish were sampled three times per week from March to June 2011 with paired ichthyoplankton nets outfitted with flow meters (DuFour 2013). Larval fish were collected with 3–5 min tows in the upstream direction at two to three locations just downstream of the spawning riffles (Fig. 1b). Larval fish production was estimated by multiplying larval fish density by river discharge, and a Bayesian state-space model was used to estimate production during unsampled days (DuFour 2013). We then estimated total walleye egg production in the Maumee River for each sample year by applying egg mortality rates based on river temperature and velocity (Cheng et al. 2006). Then, using a fecundity–length relationship (Muth and Ickes 1993) and length frequency information from our gill net samples, we estimated the number of female walleye spawning in the river each year (see Roseman et al. 2012). Finally, we multiplied the number of females by the ratio of males to females observed in our gill net samples to estimate the total walleye spawning stock size for each year.

Size and sex structure of walleye spawning stock

We visually analyzed boxplots of lengths for male and female walleye by week from the 2011 and 2012 gill net catches. We then

Fig. 2. Daily median spawning stock abundance estimates and 95% credible intervals for (a) 2011 and (b) 2012 and (c) seasonal median spawning stock abundance estimates and 95% credible intervals from the Bayesian hierarchical model for 2011 and 2012 and larval fish back-calculation (2011 only).



used simple linear regression with mean length of males and females from each sample year as response variables and Julian week as the independent variable to identify trends in size structure through the course of the spawning season. We also used visual analysis and simple linear regression to identify trends in the sex ratio through the spawning season.

Environmental factors influencing walleye movement

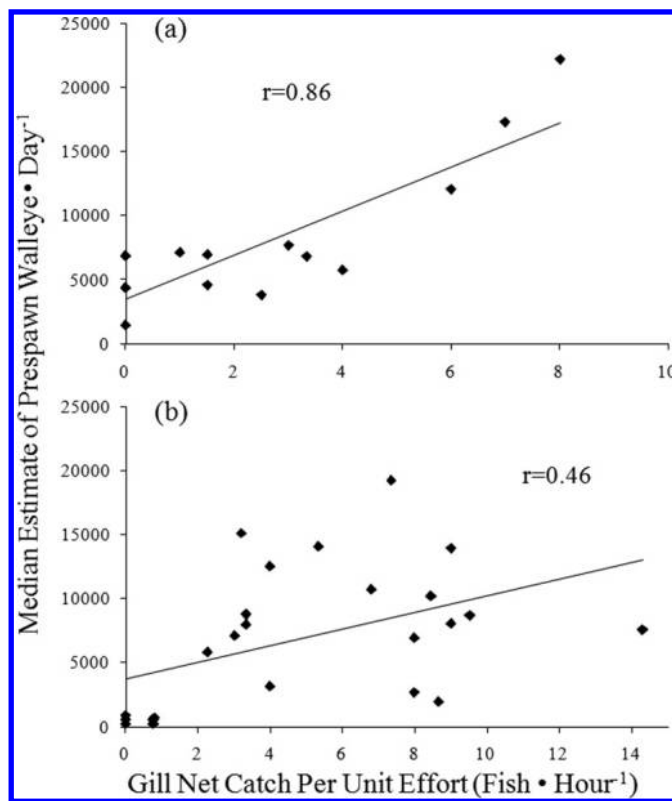
We used simple linear regression to model the relationship between walleye daily abundance and discharge and used polynomial regression for the nonlinear relationship between daily abundance and water temperature to explore possible environmental factors influencing movement. Both discharge and temperature may influence the performance of migrating adults (Budy et al. 2011) as well as their reproductive success (i.e., the survival of eggs and larvae; Smith and Koenst 1975; Mion et al. 1998). Since the small number of sample years precludes more sophisticated statistical modeling techniques, we sought only to quantify the strength of relationships between walleye movement and these two environmental factors.

Results

Hydroacoustic estimates of abundance

We estimated the total spawning stock abundance for Maumee River walleye to be 651 000 in 2011 and 543 000 in 2012 (medians from Bayesian model; Fig. 2). The 95% credible interval for abundance was 431 000 to 1 446 000 individuals in 2011 and 386 400 to 857 200 individuals in 2012 (Fig. 2). Median daily migrant estimates varied widely during both years, ranging from 556 to

Fig. 3. Gill net CPUE and daily walleye spawning stock abundance estimates for (a) 2011 and (b) 2012. Each gill net observation was for one net fished per 1–2 h.



15 460 prespawm walleye per day in 2011 and 199 to 22 120 prespawm walleye per day in 2012 (Fig. 2). Gill net catch per unit effort (CPUE) of prespawm walleye was positively correlated with the daily estimate of prespawm walleye migration from the Bayesian state-space model in both 2011 ($r = 0.86$) and 2012 ($r = 0.46$; Fig. 3).

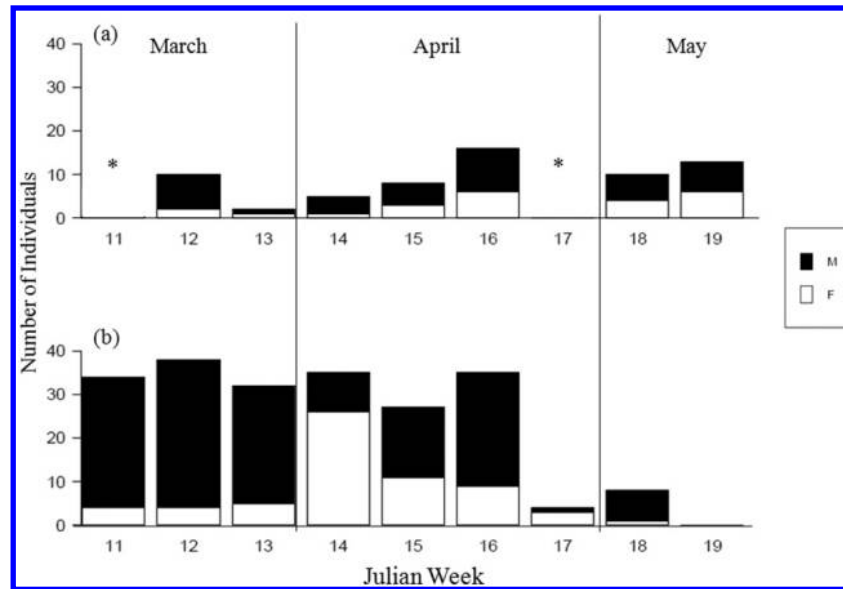
Larval fish back-calculated estimate of abundance

Larval walleye production in 2011 was estimated at between 58.3 and 177 million individuals (95% Bayesian credible interval from DuFour 2013), with a median estimate of 94.1 million. The spring of 2011 was characterized by very high discharge and river velocities over $1 \text{ m} \cdot \text{s}^{-1}$. Therefore, we assumed walleye egg mortality to be 99% (Cheng et al. 2006). The mean female walleye length from our gill net sampling was 590 mm in 2011, and from Muth and Ickes's (1994) length–fecundity relationship, the approximate fecundity of the mean female is 225 000 eggs. Thus, by back-calculating from the lower bound of the 95% credible interval, approximately 26 000 females were needed to produce the estimated larval walleye, from the upper bound of the credible interval 79 000 females were needed, and from the median 42 000 females were needed. At the seasonal 2:1 male to female ratio, as observed in our gill net samples, we estimated the total spawning stock abundance of walleye to be between 78 000 and 237 000, with a median value of 126 000 individuals (Fig. 2).

Size and sex structure

There was high variability in walleye catch in terms of abundance, sex ratio, and distribution of total lengths; however, some trends were apparent through time. Walleye catch was generally dominated by males early in the season (sampling weeks 1–3), but the sex ratio shifted to near 1:1 for the remainder of the season (Fig. 4). Simple linear regressions showed that walleye male to female ratio decreased over time in both 2011 ($R^2 = 0.80$, $p = 0.039$) and 2012 ($R^2 = 0.73$, $p = 0.014$). In addition, large fish, both males

Fig. 4. Sex ratio and gill net catch (total number of individuals captured) through time in (a) 2011 and (b) 2012. Asterisks denote weeks that did not contain any samples.



and females, were the first to enter the river. The size of both sexes found in the river decreased towards the end of the season in both sample years (Fig. 5). We detected significant decreases in size through the sampling season in females in 2011 ($R^2 = 0.78$, $p = 0.046$) and 2012 ($R^2 = 0.61$, $p = 0.039$), as well as males in 2012 ($R^2 = 0.64$, $p = 0.017$). The decrease in size for males in 2011 was not statistically significant ($R^2 = 0.52$, $p = 0.106$). In general, prespawn fish dominated catches early in the season, and postspawn fish became more prevalent late in the season (Fig. 6). Also, walleye were typically the dominant large-bodied species early in the season, and other species made up a larger portion of the gill net catch later in the season (Fig. 6).

Environmental factors influencing migration

Daily migration rates had a negative relationship with discharge in both 2011 and 2012 and had a nonlinear relationship with temperature in both sample years (Fig. 7). In general, more walleye migrated during intermediate water temperatures, and migration was reduced at low and high temperatures (Fig. 7).

Discussion

Estimates of absolute abundance support some management objectives more effectively than indices of relative abundance (Hayes et al. 2007). In the case of walleye in Lake Erie, stated research goals of management agencies include assessing population trends, determining stock-specific fishing mortality, determining the contribution of each stock relative to the Lake Erie population, and exploring size-selective management (Locke et al. 2005). These management objectives can be aided by fishery-independent estimates of absolute abundance and description of stock size and sex structure, such as generated by this study.

Overharvest is a common threat facing many fisheries (Botsford et al. 1997), and in Lake Erie, managing the walleye fishery to ensure sustainability is the primary goal (Locke et al. 2005). The Maumee River walleye spawning stock provides a very popular and economically important recreational fishery. Spring harvest of walleye in the Maumee River is typically approximately 40 000 fish (ODW 2012). According to our estimate, this spring harvest represents 5%–10% of the total Maumee River spawning stock, although additional harvest on this spawning stock occurs in Lake Erie over the rest of the season. This estimate of exploitation during the spawning season provides information to aid future

stock-specific management efforts and regulations aimed at preventing overharvest of a popular and valuable stock.

Although we have generated abundance estimates for walleye spawning in the Maumee River, there are no estimates for any other Lake Erie walleye spawning stocks. However, absolute abundance estimates for the entire west-central Lake Erie population are generated each year. The total estimated number of age-3+ individuals was approximately 20 million in 2011 and 16 million in 2012 (WTG 2012). Our estimates suggest that the Maumee River spawning population is approximately 2%–5% of the total Lake Erie west-central population, which is similar to previously hypothesized values for walleye spawning in western Lake Erie tributaries (Cheng et al. 2006; Hayes et al. 2009). It is also important to note that not all individuals spawn in all years (Henderson et al. 1996), and if these nonspawning fish do not migrate, the percentage of the total Lake Erie walleye population that spawns in the Maumee River across years may be greater than our 2%–5% estimate. In addition, estimates of absolute abundance for other walleye spawning stocks are needed to achieve stock-specific management of the lake-wide population.

Absolute abundance estimates can be more useful for assessing population trends than indices of relative abundance, which may be sensitive to changes in efficiency or catchability of traditional fisheries sampling gear (Hayes et al. 2007; Stapanian et al. 2009; Kocovsky and Stapanian 2011). In this study, gill net CPUE of walleye was much greater in 2012 than in 2011. Mean river discharge during the sampling season was almost three times greater in 2011, and we posit that heavy debris loads and high river velocity reduced the effectiveness of the gill nets in that year compared with 2012. Nonetheless, the hydroacoustic estimates of walleye abundance were very similar between the two sample years. Because of the large size of walleye (most fish are over 500 mm), they are still discernible on hydroacoustics even in noisy (i.e., high flow) environments. Thus, population trends of walleye in the Maumee River assessed strictly from gill nets may lead to erroneous conclusions because of year to year differences in gear efficiency. Our study shows that hydroacoustics may be useful in conjunction with traditional sampling gears to provide a stock assessment tool even in rivers that have frequent flood pulses and diverse (>10 species) migratory fish communities. However, changes in fish behavior as a result of high river discharge, such as movement of fish nearer the bottom, may influence hy-

Fig. 5. Total length (mm) through time of (a) 2011 females, (b) 2011 males, (c) 2012 females, and (d) 2012 males.

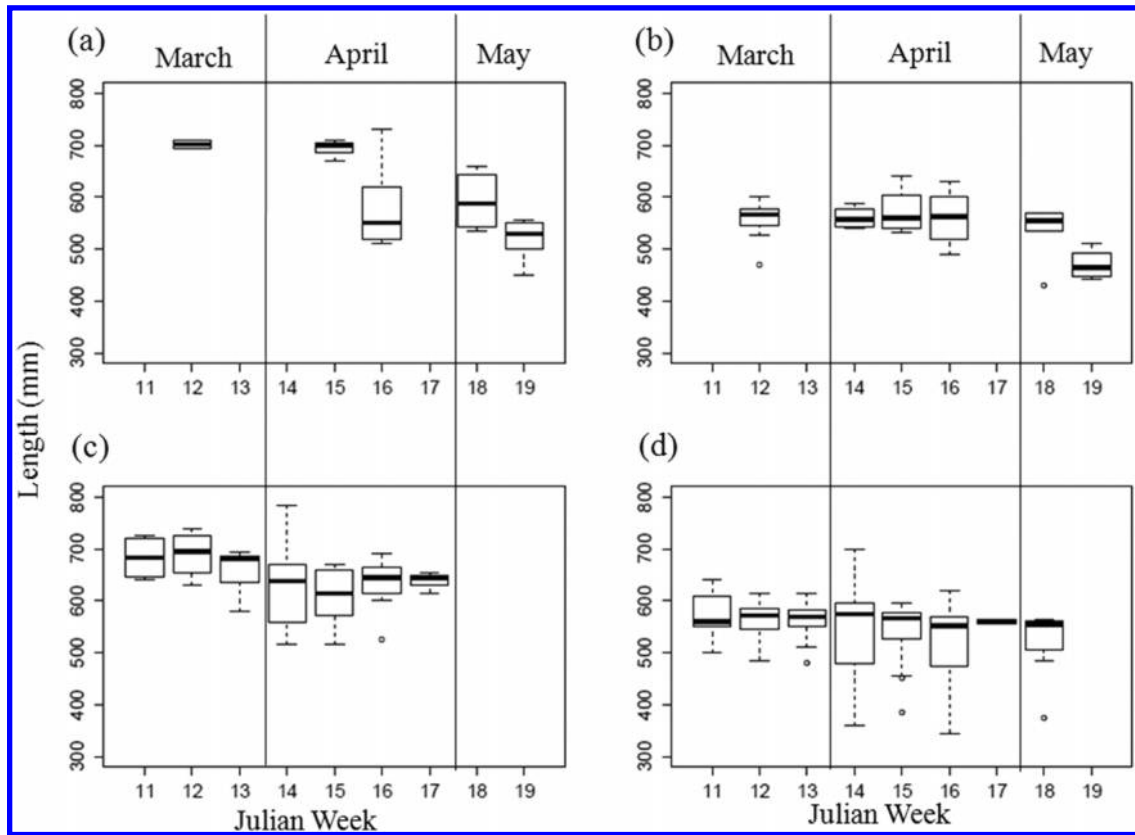


Fig. 6. Proportion of prespawn and postspawn walleye in gill net samples from (a) 2011 and (b) 2012 and proportion of gill net catch consisting of walleye and other species in (c) 2011 and (d) 2012.

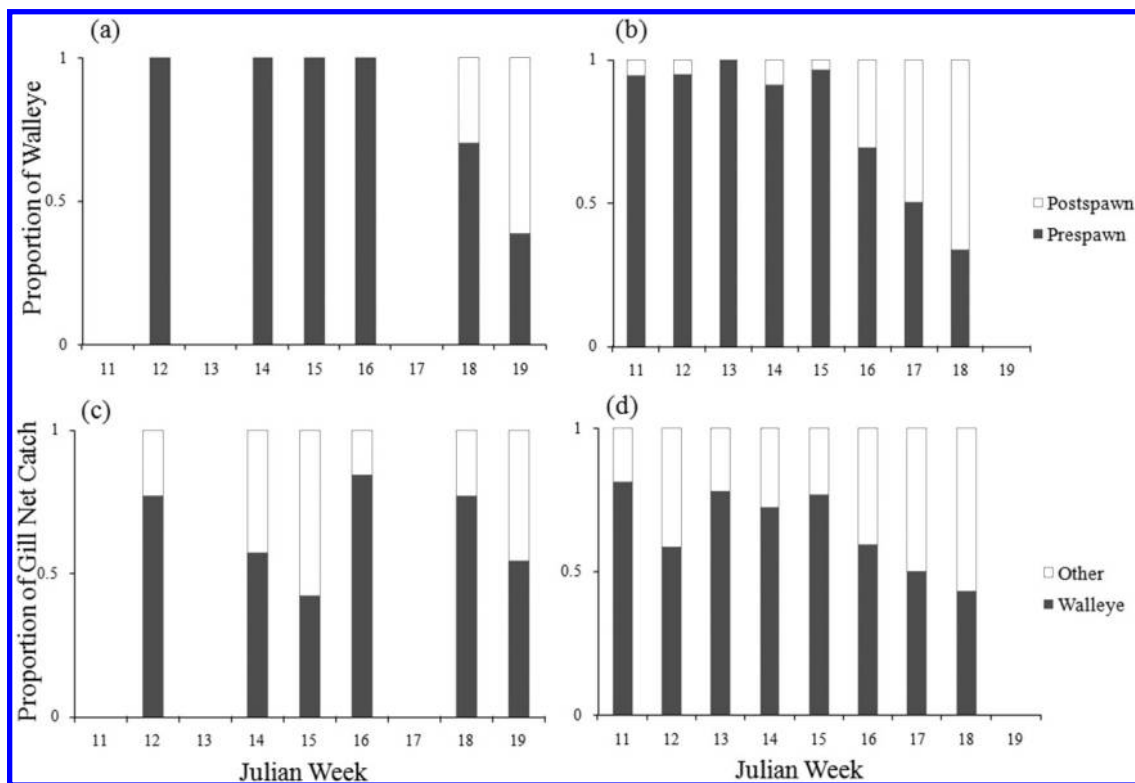
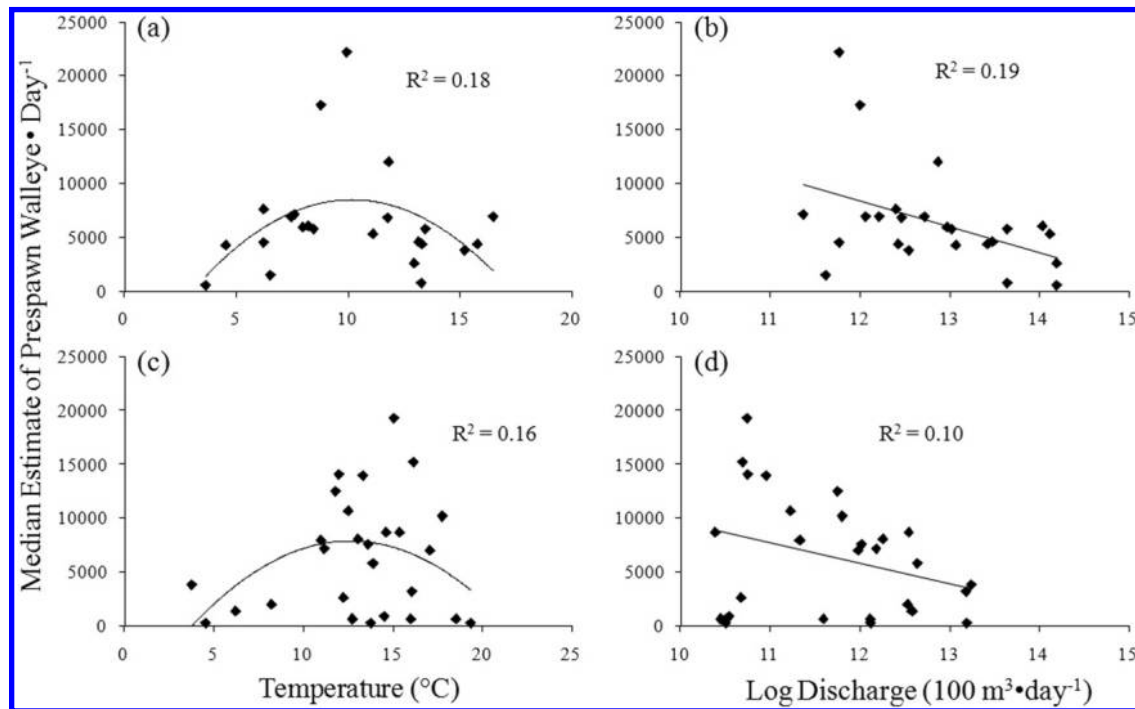


Fig. 7. Daily walleye migration rates for 2011 (a) temperature and (b) discharge and 2012 (c) temperature and (d) discharge.



droacoustic measurements and were not considered in our analysis.

Careful accounting of natural and sampling variability provides decision makers with an explicit measure of uncertainty. Our approach included estimates of uncertainty encompassing error from multiple sources. Uncertainty stemmed from variability in (i) estimates of fish density among hydroacoustic transects, (ii) hydroacoustic estimates of fish density among sampled days, (iii) the proportion of large fish that were prespawn walleye, and (iv) the movement rates of individual walleye. The Bayesian state-space model and MCMC analysis allowed us to propagate this uncertainty through each step of the model and quantify the precision of our estimate. Furthermore, the Bayesian framework used to generate our estimates can be further refined in future years by incorporating prior information. Although we provided an estimate of uncertainty for the abundance of the Maumee River spawning stock, uncertainty in other areas of Lake Erie walleye research presents challenges for incorporating our estimate into the current body of knowledge. For example, uncertainty in the west-central Lake Erie population estimate is not documented, and it is therefore difficult to evaluate our estimate in the context of this unaccounted for uncertainty.

The spawning stock abundance estimate generated from the larval fish back-calculation was somewhat lower than the hydroacoustic estimate, though the two estimates were of similar magnitude, suggesting that neither is radically flawed. Several possible explanations could account for the lower number generated by larval back-calculation. First, the effective spawning stock size, or the number of individuals that actually contribute to the next generation, can be substantially smaller than the total spawning stock abundance. If many walleye do not contribute to the next generation through lack of spawning success, the effective spawning stock estimate generated from the larval fish back-calculation would be expected to be lower than the hydroacoustic estimate of total abundance. Also, the egg mortality rate and fecundity values used in the larval fish back-calculation are derived from previous studies and were not empirically measured, which could limit their accuracy in the current study. Therefore, the larval back-calculation is likely a measure of a subset of the total

number of fish entering the river (i.e., the effective spawning stock for a given year) rather than the total abundance estimated by hydroacoustics.

Size and sex structure of walleye progressed similarly during both sampling seasons. Larger individuals and relatively more males migrated early in the season, and the size of fish and relative number of males decreased as the season progressed. Based on walleye length-at-age observations (ODW 2012), larger, early-migrating individuals are likely older than individuals migrating later in the spawning season. Several mechanisms may be responsible for early migration of larger fish and males. For example, larger individuals may have more energy that can lead to faster gonad development (Henderson et al. 1996). Size- and age-induced differences in the timing of spawning have been observed for many marine fishes (Berkeley et al. 2004). The increased complexity in spawning behaviors in a mixed-size population and contributions from large, older individuals may be important for maintaining fish populations (Berkeley et al. 2004). Therefore, management that protects a diverse size and age structure may benefit Lake Erie's walleye fishery.

The change in size and sex structure through time could also have implications to management and assessment of the spawning stock. First, if managers wish to protect a particular segment of the population, that segment may be more vulnerable to harvest at particular times of the year, and fine-scale temporal regulations (closures or special regulations) may be justified. Also, the Ohio Department of Natural Resources collects walleye from the Maumee River for gametes for hatchery production of walleye and saugeye (*Sander vitreus* × *Sander canadense*), as well as individuals for age and growth analysis. The timing of sampling events could be informed by the size and sex structure of in-river walleye. For example, age and growth analysis conducted early in the season would yield results that differ from those later in the season. Taking these differences into account could aid in allocating sampling resources and improve walleye assessment.

Although this study was limited by having only two sample years, we identified two environmental factors that may influence migration that warrant further study. Walleye migration was greatest at intermediate temperatures and negatively correlated

with discharge in both sample years. We hypothesize that intermediate temperatures and low discharge provide the best conditions for offspring survival; therefore, migrating and spawning during those conditions improve reproductive success. For example, survival of walleye eggs and larvae has been shown to be greatest under low discharge (Mion et al. 1998; Ivan et al. 2010). Furthermore, optimal temperature for walleye egg fertilization is 6 to 12 °C and 9 to 15 °C for incubation (Smith and Koenst 1975), which coincides with intermediate temperatures in this study (Fig. 4). We also hypothesize that intermediate temperatures and low discharge represent the optimal bioenergetic conditions for adult upstream migration. Walleye have slow swimming speeds compared with other well-studied migratory fish, such as salmonids (Peake et al. 2000), and the growth potential (a measurement of performance) for walleye is best between 10 and 20 °C (Budy et al. 2011). The relationships between walleye migration and environmental factors could be incorporated into predictive models of within-season estimates of run strength. Predictions of within-season abundance would be useful for population assessment and research and timing sampling events for gathering hatchery broodstock.

Although we were able to quantify uncertainty in many of the inputs into our hydroacoustic estimate of walleye abundance, there are several inherent limitations of both hydroacoustics and traditional gears. First, we attempted to assign TS cutoffs for analysis based on histogram matching (Appendix A). The TS distributions for the walleye and non-target species in the Maumee River has not been characterized; thus, some error in classifying targets as potential walleye is likely and could bias estimates. For example, flash-like echoes (Lilja et al. 2004) from small, non-target species could cause the erroneous inclusion of those individuals and bias estimates high. Conversely, if walleye echoes were smaller than expected based on the histogram matching and length-TS equations used in this study (see Appendix A), our estimate would be biased low. More information on length-TS relationships for walleye and other Lake Erie species could improve the interpretation of hydroacoustic results and refine abundance estimates. Another source of potential error that was not accounted for in our model of abundance is the validity of our assumptions concerning fish density in near-field and bottom dead zones. If our assumptions that no walleye migrated in the top 2 m of the water column and fish density in the bottom dead zone was the same as density immediately above it were erroneous, our estimate of walleye abundance could be biased. Next, our study design provided only a snapshot of fish abundance on each sampling day. Although we found no difference in fish density or movement in our five day-night paired hydroacoustic sampling events, we did not exhaustively examine fine-scale (i.e., within-day) fluctuations in walleye migration. Better fine-scale information could improve seasonal estimates of walleye abundance.

We relied on gill netting to provide physical samples for interpreting hydroacoustic data. Gill nets are known to have size-selectivity and species-selectivity biases (Hubert 1996), which could mischaracterize the large-bodied fish community. Also, we set the gill net on the bottom of the river and therefore did not sample the water above the gill net. The Maumee River is deep and turbid, which precludes the use of many types of commonly used freshwater fisheries sampling gears, such as electrofishing. In addition, the Maumee River is an important shipping channel, and as a result, we could not set passive gears for long amounts of time or use gears that could not be quickly retrieved. Moreover, adult walleye are large and can generally avoid small trawls towed at slow speeds. Thus, we had a limited selection of gears to meet our sampling requirements and chose to use the bottom-set gill net because it could capture large fish in deep water, is fishable from small watercraft, and could be quickly set and retrieved.

Many important fish species migrate through estuaries and into rivers, habitats that have historically presented a sampling chal-

lenge. Our methodology may be applicable to other large, deep, or heavily modified river systems. Several examples of the use of hydroacoustics to estimate spawning stock abundance through echo counting exist for riverine systems. Most of these (e.g., Hewitt 2003) used side-looking fixed station hydroacoustics that collect data continuously. In the Maumee River, which is a major shipping port in an urban setting, access along the river bank is limited, and security of expensive hydroacoustic equipment was questionable, preventing a fixed station design. We therefore used mobile transects and were left with a need to estimate unsampled time periods. Other researchers have overcome this problem by sampling virtually every day for the entire day over the entire sampling season (Banneheka et al. 1995). This strategy is logistically difficult and very expensive, and it is unlikely that many research entities have the resources to implement it. In this study, we provide an alternative strategy: sampling with moderate intensity (3 days per week) and using Bayesian methods to estimate unsampled days. We believe this strategy is compatible with the time and resources available to many research and management entities and could be used to assess stocks of migratory fish in similar large riverine systems.

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Appendix A

Single target detection parameters and fish tracking sensitivity analysis

We conducted a sensitivity analysis in Echoview 4.90 to select single target detection parameters for fish tracking. We selected five sampling dates (three from 2012 and two from 2011) that spanned a range of large-fish densities. We iteratively adjusted the maximum beam compensation (using 2, 4, and 6 dB), minimum normalized pulse length (0.6 and 0.8), and angular position standard deviation (0.6, 2.0, and 10.0 SD). We then used echo counting to calculate large-fish density across all transects for each sample day using the mean target strength threshold used for 2012 (−29.5 dB). We then calculated the mean of densities across days to compare performance among parameters (Table A1). The sensitivity analysis showed that mean fish density was not strongly affected by changes in any of the parameter settings (Table A1). Overall, changes in the single target detection parameters produced 5%–10% changes in fish density (Table A1). The parameters that we selected are those recommended by the Standard Operating Procedures for hydroacoustic sampling in the Great Lakes (Parker-Setter et al. 2009). The selected settings performed similarly to other settings.

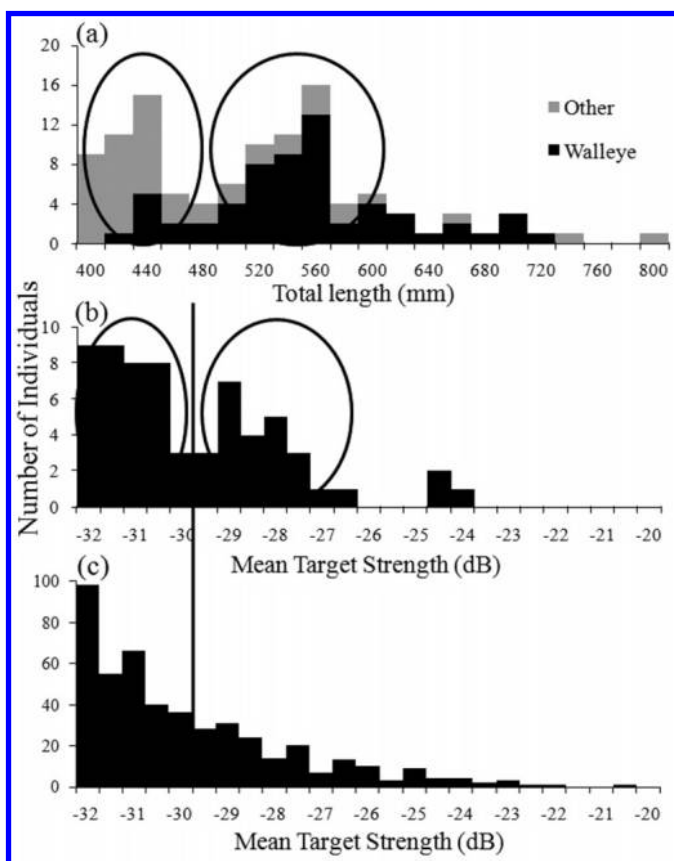
Target strength thresholds and sensitivity for fish track inclusion

We relied on paired histogram analysis to select an appropriate TS threshold. We created season-wide length–frequency histograms of our 2011 and 2012 gill net catch and mean TS–frequency histograms of our 2011 and 2012 stationary fish tracks to compare distributions of fish length and target strength (Fig. A1; Fig. A2). The 2011 length–frequency histogram had peaks at 440 and 560 mm whereas the 2012 length–frequency histogram had peaks of 460 and 580 mm. In addition, the 2011 length–frequency had a

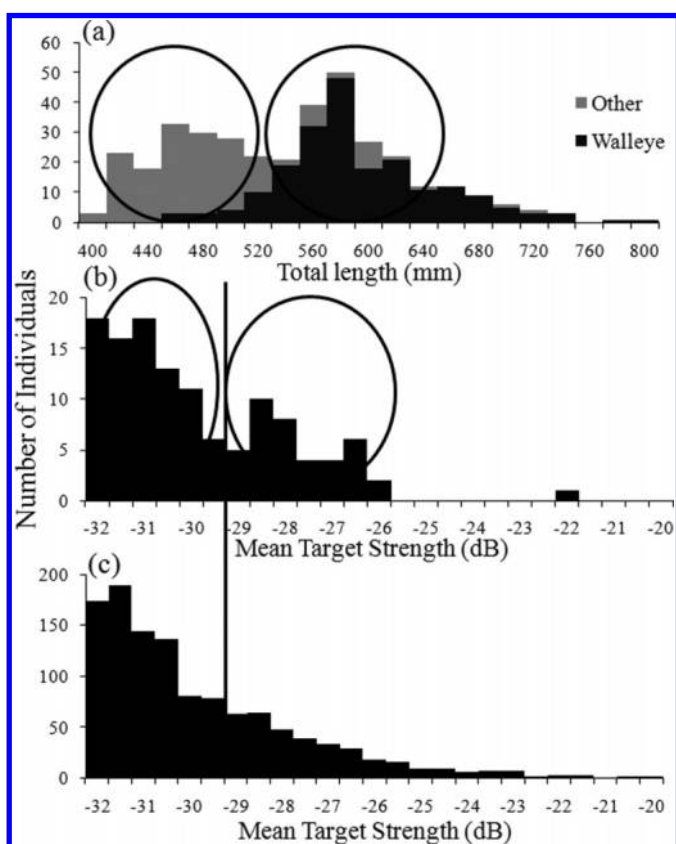
Table A1. Mean large-fish densities (> -29.5 dB) for five sampling events for different parameter settings.

Maximum beam compensation	Minimum normalized pulse length	Angle SD	Average density (fish-1000 m ⁻³)	Proportion of selected settings
2	0.6	0.6	2.07	1.01
	0.6	2	1.96	0.96
	0.8	0.6	2.01	0.98
4	0.6	0.6	2.10	1.02
	0.6	2	2.01	0.98
	0.6	10	2.13	1.04
6	0.8	0.6	2.10	1.02
	0.6	0.6	2.05*	1.00
	0.6	2	1.95	0.95
	0.8	0.6	2.08	1.01

*Parameter setting used for further analysis in 2012 (and used to standardize other density values).

Fig. A1. (a) Length–frequency histogram from gill net sampling, (b) TS–frequency histogram for fish tracks from stationary hydroacoustic sampling, and (c) TS–frequency histogram for fish tracks from mobile hydroacoustic sampling for 2011. Matching groups are circled, and the target strength threshold is denoted by the solid vertical line.

trough at 460 mm and the 2012 length–frequency had a trough at 500 mm. Based on three known TS–length equations (Love 1971; Frouzova et al. 2005; Borisenko et al. 2006), we determined that the mean TS for small walleye (<480 mm) was likely between -33 and -27 dB, and we began our search for a match to our length–frequency histograms in this range. By matching the gill net peaks and troughs with those from the mean TS–frequency histogram of stationary collections, we set mean TS threshold values at -30.0 dB for 2011 and -29.5 dB for 2012 (Figs. A1, A2). Only a small

Fig. A2. (a) Length–frequency histogram from gill net sampling, (b) TS–frequency histogram from fish tracks stationary hydroacoustic sampling, and (c) TS–frequency histogram for fish tracks from mobile hydroacoustic sampling for 2012. Matching groups are circled, and the target strength threshold is denoted by the solid vertical line.

fraction (about 5%) of walleye were smaller than the gill net trough values (460 mm in 2011 and 500 mm in 2012), however, the vast majority of fish larger than the trough values ($\sim 80\%$) were walleye. Assuming a perfect match between histograms, this could lead to a slight underestimate of walleye abundance. However, we chose thresholds to limit the contributions from non-walleye species that could potentially cause overestimation of walleye abundance. For example, white bass (*Morone chrysops*) are known to be very abundant in the Maumee River (ODW 2012) but are pelagic and likely less susceptible to our bottom-set gill net. Most white bass we observed were between 300 and 400 mm in total length, and based on a *Morone* sp. TS–length equation (Hartman and Nagy 2005), are expected to have target strengths of -33.5 to -31.5 dB. Thus, setting a threshold value less than -31 dB could lead to the misclassification of white bass in our walleye analysis.

In addition to the histogram analysis, we used a length–TS equation derived for multiple species, including Percidae (Frouzova et al. 2005), to approximate expected lengths from observed targets and determine threshold for potential walleye targets. The smallest mature walleye we observed was 430 mm which corresponds to a TS value of around -29.25 dB, based on Frouzova et al. (2005). This value is near the thresholds chosen from our paired histogram analysis. Of several possible TS–length equations for multiple species (Love 1971) and percids (Borisenko et al. 2006), Frouzova et al. (2005) appeared to best approximate our observed hydroacoustic data. For example, Love (1971) predicts we should have observed no fish with TS values greater than -28.0 dB, based on lengths from our gill net, whereas Borisenko et al. (2006) predicts we should have seen peaks in our TS histograms around

Table A2. Seasonal walleye abundance estimates for 2011 and 2012 for different mean TS thresholds.

Year	Value	-29.0	-29.5	-30.0	-30.5
2011	95% credible interval lower bound	254 800	358 600	431 000*	500 000
	Median	400 000	534 700	651 000*	758 500
	95% credible interval upper bound	856 200	1 115 000	1 446 000*	1 640 000
2012	95% credible interval lower bound	322 300	386 400*	468 900	569 500
	Median	451 900	543 000*	653 100	786 700
	95% credible interval upper bound	734 500	857 200*	1 022 000	1 228 000

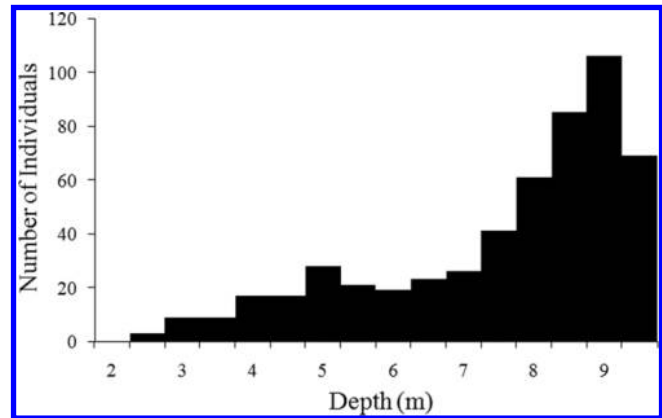
*Values based on histogram analysis.

-24.0 dB, corresponding to the high abundance of walleye of around 560–580 mm. In contrast to the predictions of Love (1971), we observed many fish with mean TS values exceeding -28 dB, and in contrast to the predictions of Borisenko et al. (2006) we observed peaks in mean TS-frequency histograms only at values less than -24 dB. The equation derived by Frouzova et al. (2005) predicted values intermediate to those of Love (1971) and Borisenko et al. (2006), as we observed in our data. The applicability of TS-length equations derived from captured, immobilized, or manipulated fish to observations made on wild, free-swimming fish has long been questioned (Simmonds and MacLennan 2005). Future work developing TS-length equations for walleye and other Lake Erie species, using methods that best mimic natural conditions, could lead to improved interpretation of the data used in this study and other hydroacoustic applications in the Great Lakes.

Because of the considerable uncertainty involved with selecting an appropriate threshold value, we estimated seasonal abundance for each year, using the Bayesian state-space model described above, with thresholds at -30.5, -30.0, -29.5, and -29.0 dB to understand how sensitive our estimates were to TS threshold. We found that a 1.0 dB change in the threshold used to classify fish as potential walleye caused a change of approximately 50% in fish abundance (Table A2). Thus, our estimates are highly sensitive to the choice of threshold used in echo-counting and potential misclassification of fish as potential walleye vs. other species could lead to inaccurate estimates.

Hydroacoustic data quality

The efficacy of a down-looking hydroacoustic approach in the Maumee River depended on several acoustic and behavioral characteristics of migrating fish. First, we assumed that fish did not migrate in the top 2 m of the water column and that density below the bottom dead zone was the same as density above the bottom dead zone. By plotting the number of potential walleye tracks observed by depth strata, we saw very few fish in the 2–4 m depth strata compared to the lower depth strata, indicating that few fish migrated at shallow depths (Fig. A3). The mean depth of potential walleye sized targets was 7.5 m and the mean distance above the bottom dead zone (0.2 m backstep from bottom) was 1.2 m. Thus, most fish migrated in the lower portion of the water column but were generally far enough above the bottom dead zone to be detected. Next, fish must not exhibit vertical movements (fish tracks must be flat) for accurate measurement of TS. We observed

Fig. A3. Distribution of potential walleye tracks by depth. Hydroacoustic sampling began at 2 m.

a mean change in range for our mobile fish tracks (i.e., the difference in minimum observed depth and maximum observed depth) to be only 0.03 m, and 97% of tracks had a change in range of less than 0.1 m, indicating that virtually all fish tracks were flat.

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