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ARTICLE

Acoustic telemetry as a potential tool for mixed-stock analysis of fishery harvest: a feasibility study using Lake Erie walleye[1]

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Abstract: Understanding stock composition is critical for sustainable management of mixed-stock fisheries. When natural markers routinely used for stock discrimination fail, alternative techniques are required. We investigated the feasibility of using acoustic telemetry to estimate spawning population contributions to a mixed-stock fishery using Lake Erie's summer walleye (*Sander vitreus*) recreational fishery as a case study. Postrelease survival was estimated after tagging and used to inform simulations to evaluate how contribution estimates could be affected by survival, sample size, and expected population contributions. Walleye experienced low short-term survival after tagging, but showed higher survival after 100 days, likely allowing fish to return to spawning areas the following spring. Based on simulations, accuracy and precision of population composition increased with an increase in the number of tagged fish released, and both appeared to stabilize when ≥200 tagged fish were released. Results supported the feasibility of using acoustic telemetry to estimate spawning population contributions to mixed-stock fisheries in Lake Erie.

Résumé : La compréhension de la composition des stocks est d'importance clé pour la gestion durable des pêches de stocks mélangés. Quand les marqueurs naturels couramment utilisés pour distinguer les stocks s'avèrent inefficaces, d'autres méthodes sont nécessaires. Nous avons étudié la faisabilité d'utiliser la télémétrie acoustique pour estimer les contributions de populations reproductrices à une pêche de stocks mélangés en utilisant la pêche sportive estivale au doré jaune (*Sander vitreus*) dans le lac Érié comme étude de cas. Le taux de survie après le lâcher a été estimé après l'étiquetage et utilisé dans des simulations pour évaluer l'incidence possible de la survie, de la taille de l'échantillon et des contributions de populations attendues sur les estimations des contributions. Les dorés jaunes présentaient une faible survie à court terme après l'étiquetage, mais une plus grande survie après 100 jours, ce qui a probablement permis aux poissons de retourner aux lieux de frai le printemps suivant. À la lumière des simulations, plus le nombre de poissons étiquetés relâchés est grand, plus l'exactitude et la précision de la composition des populations sont élevées, semblant toutes deux se stabiliser quand ≥200 poissons étiquetés sont relâchés. Les résultats appuient la faisabilité d'utiliser la télémétrie acoustique pour estimer les contributions de populations reproductrices aux pêches de stocks mélangés dans le lac Érié. [Traduit par la Rédaction]

Introduction

The ability to quantify population-specific harvest rates and identify source population(s) of harvested fish remains a challenging, yet important, issue for managing mixed-stock fisheries (Li et al. 2015). When harvest from a mixed-stock fishery is mistakenly assumed to be from a single population, unintended overexploitation can occur for small or less-productive populations and lead to inappropriate harvest regulations (Larkin 1979; Stephenson 1999; Li et al. 2015). For example, the collapse of Northwest Atlantic cod (*Gadus morhua*) may have been caused in part by failure to account for the existence of mixed-stock fisheries in assessment and management (Hutchinson 2008). Exploitation of mixed-stock fisheries has been most commonly investigated in marine and anadromous fish populations (e.g., Wood et al. 1989; Crozier et al. 2004; Jónsdóttir et al. 2007); however, the contribution of individual populations to mixed-stock fisheries are increasingly being evaluated in large freshwater systems, such as the Laurentian Great Lakes (e.g., Bott et al. 2009; Brenden et al. 2015; Andvik et al. 2016).

Previous attempts to identify source populations of some Great Lakes mixed-stock fisheries using natural markers have resulted in varied success. Mixed stock analyses using genetic markers successfully informed lake trout (*Salvelinus namaycush*) restoration efforts in Lake Ontario (Marsden et al. 1989) and provided an improved understanding of population-specific commercial harvest

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of lake whitefish (*Coregonus clupeaformis*) in Lake Michigan (Andvik et al. 2016). Stock discrimination analyses based on otolith chemistry were also able to resolve contributions of hatchery- and wild-origin salmonids to recreational fisheries in Lake Erie (steelhead, *Oncorhynchus mykiss*; Budnik et al. 2018) and Lake Huron (Chinook salmon, *Oncorhynchus tshawytscha*; Marklevitz et al. 2016). However, in other cases, low levels of differentiation in natural markers have made it difficult to use traditional stock-discrimination methods to identify populations contributing to fisheries. For example, Lake Erie's commercial and recreational walleye (*Sander vitreus*) fisheries are composed of fish from several discrete spawning populations (Strange and Stepien 2007; Einhouse and MacDougall 2010; DuFour et al. 2015), which intermix during nonspawning periods throughout the lake, notably when late spring and summer fisheries occur (Wang et al. 2007; Zhao et al. 2011; Vandergoot and Brenden 2014). Previous attempts to resolve the contributions of these populations to the lake-wide population and its fisheries using natural markers have had little success (scale shape: Riley and Carline 1982; allozyme and mitochondrial DNA: McParland et al. 1999; microsatellite: Strange and Stepien 2007; single nucleotide polymorphism: Chen 2016; otolith microchemistry: Chen et al. 2017). Integration of multiple natural markers (e.g., genetics and otolith chemistry) has been proposed to increase the ability to identify source populations (Begg and Waldman 1999; Kocovsky et al. 2013; Fraker et al. 2015), although uniformity of abiotic and biotic conditions in Lake Erie (Pangle et al. 2010) may also limit the potential discriminatory power of an integrated approach.

Acoustic telemetry, which has been widely used to study spatial and temporal ecology of fishes in recent years (e.g., Hussey et al. 2015; Crossin et al. 2017), may provide a novel approach by using behavior to directly estimate contributions of individual populations to a mixed-stock fishery. Such an approach would be particularly useful when natural markers are unable to differentiate between individual populations, such as the case for Lake Erie walleye. This approach would entail catching fish when populations are mixed, tagging and releasing them with acoustic transmitters, and in subsequent years deploying passive acoustic receivers at known or suspected spawning areas to determine which spawning populations tagged fish belong to. For such an approach to work, fish must be caught and tagged within the mixed-stock fishery, then released in sufficient numbers to compensate for immediate short-term mortality, and finally survive long enough to return to spawning locales so that population contributions can be estimated. The process of surgically implanting acoustic transmitters is an invasive surgical procedure, which can affect survival and behavior of tagged individuals, and thus must be assessed (e.g., Wagner et al. 2011; Schoonyan et al. 2017). However, relying on previous post-tagging survival estimates from other studies may be inappropriate if tagging fish is to be conducted under different conditions. For example, acoustic telemetry studies of walleye in the Great Lakes have tagged fish during spring spawning seasons (e.g., Hayden et al. 2014; Raby et al. 2018), when water temperatures were much cooler than during summer months when the recreational fishery occurs.

The aim of this study was to evaluate the feasibility of using acoustic telemetry as a method for quantifying spawning-population contributions to mixed-stock fisheries using Lake Erie walleye as a test case. Because this approach would require tagging walleye during the summer when water temperatures are at or above their physiological optimum (i.e., 22 °C; Hokanson 1977), our first objective was to estimate how many tagged walleye, captured and tagged during the summer recreational fishery in western Lake Erie, would show immediate post-tagging mortality and how many might survive to the next spawning season (~9–10 months later). The second objective was to conduct a simulation analysis using the survival estimates from the first objective to determine how variables such as sample size (i.e., number of tags released) and population contribution levels affected accuracy and precision of stock composition estimates. Walleye in Lake Erie were captured with conventional fishing gear during summer 2015, implanted with acoustic transmitters, and released. Postrelease survival estimates were based on fishery recaptures (i.e., harvested fish) and tag detections observed by acoustic receivers deployed at known spawning locations and throughout Lake Erie. This study was intended to provide a proof-of-concept for using acoustic telemetry to quantify composition of mixed-stock fisheries and assist in designing future studies to estimate population contributions.

Materials and methods

Walleye collection and tagging occurred in western Lake Erie during July–August 2015 (Fig. 1). Lake Erie's most productive walleye populations are found in the western basin (DuFour et al. 2015), with an estimated 22 million age-2+ walleye in the lake during 2015 (WTG 2018). After spawning in rivers (e.g., Detroit, Maumee, and Sandusky rivers) and lake shoals (e.g., Ohio's reef complex) during March–May, these spawning populations intermix throughout the lake during nonspawning periods (Wang et al. 2007; Vandergoot and Brenden 2014; Raby et al. 2018). Most of the lake's recreational angling effort and harvest occurs in the western basin (WTG 2018). For instance, Ohio's recreational walleye fishery in the western basin averaged 61% of the lake-wide recreational harvest during 2000–2016 (WTG 2018).

To assess feasibility of our approach, 30 fish (mean total length = 469 mm, range 390–565 mm) were caught by trolling artificial lures in a manner consistent with methods used by Lake Erie's walleye anglers (Ohio Division of Wildlife 2017). All tagged fish were of legally harvestable size (>381 mm total length) and representative of the recreational fishery harvest during this period. Artificial lures were fished in the top 5–10 m of the water column to minimize incidence of barotrauma (Talmage and Staples 2011). After capture and hook removal, fish were visually assessed for signs of injury (e.g., bleeding) or barotrauma (e.g., inability to maintain equilibrium, stomach or anal eversion; Schreer et al. 2009), which generally assessed a fish's reflex action mortality predictors (Raby et al. 2012). Walleye that were deemed not impaired were transferred to shaded tanks containing lake water. Water in the tanks was circulated for 30 s every 5 min, and fresh water was pumped in from the lake at the same interval. Surface water temperatures were recorded at time of capture, along with surgery time and total holding time (Table 1).

Acoustic transmitters were surgically implanted using established methods for walleye (Cooke et al. 2011*b*; Hayden et al. 2014). Fish were sedated by a 3 s exposure to pulsed direct current (30 V, 100 Hz, and 25% duty cycle) from a Portable Electroanesthesia System unit (Smith-Root, Inc., Vancouver, Washington, USA; Vandergoot et al. 2011). Acoustic transmitters (V13-1H, 69 kHz, 180 s nominal delay, expected battery life = 904 days, Vemco, Halifax, Nova Scotia, Canada) were implanted into the coelom via a small (~3 cm) ventral incision, which was closed with two or three absorbable monofilament sutures (Schoonyan et al. 2017). After surgery, fish were transferred to tanks, allowed to regain equilibrium, and appeared normal before release. To assist with interpreting mortality estimates, we also inserted an external loop tag through the dorsal musculature underneath the posterior end of the first dorsal fin to alert fishers of a US$100 reward for returning the acoustic transmitter from a harvested fish.

After tagging, fish were released into a large-scale (≈780 km²) grid of 25 acoustic receivers (Vemco, Halifax, Nova Scotia, Canada) deployed in the western basin of Lake Erie during July–November 2015 (Fig. 1). Additional acoustic receiver coverage across Lake Erie encompassed the primary walleye spawning locations, with receivers deployed at open-water reef complexes and tributaries in the lake's western and eastern basins (Fig. 2) via ongoing projects supported by the Great Lakes Acoustic Telemetry Observation Sys-

Fig. 1. Number of unique walleye detected within the release array deployed in western Lake Erie during July–November 2015. Black dots indicate locations of acoustic receivers. Dashed ellipses A and B indicate locations where fish were released.

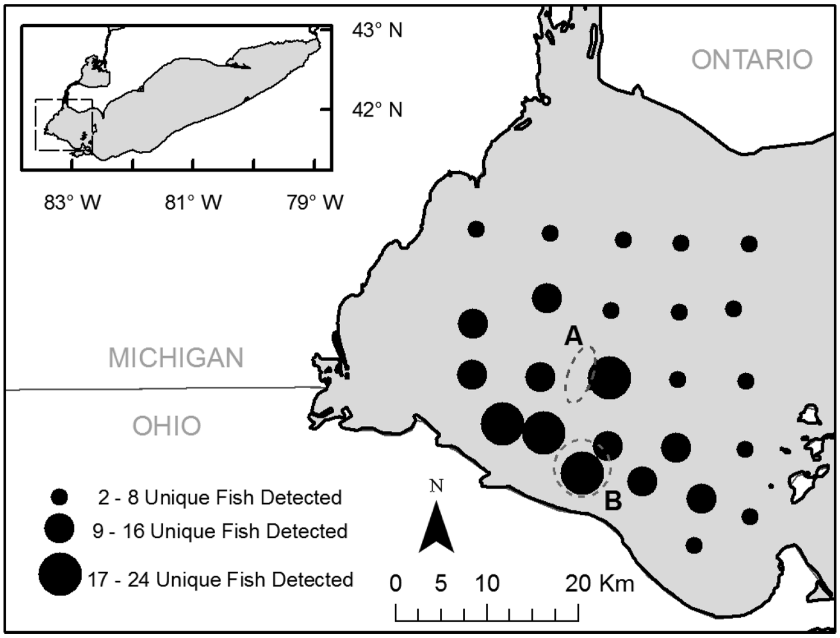


Table 1. Summary statistics (mean (standard error in parentheses)) for walleye tagged during July–August 2015 from Ohio waters of Lake Erie for determining the feasibility of using acoustic telemetry to monitor spawning population contributions to mixed-stock fisheries.

	Tagging date				
	10 July	29 July	5 August	17 August	Total
Number tagged	6	12	7	5	30
Mean length (mm)	491 (19.8)	476 (15.5)	476 (11.5)	414 (10.7)	469 (9.0)
Mean temperature (°C)	21.7 (0.6)	26.6 (0.5)	26.9 (0.5)	25.7 (1.2)	26.0 (0.4)
Mean surgery time (min)	3.0 (0.2)	2.7 (0.3)	3.3 (0.2)	2.9 (0.5)	2.9 (0.1)
Mean holding time (min)	54.5 (7.7)	54.5 (5.4)	40.5 (5.0)	36.0 (7.0)	48.3 (3.2)
Number harvested by fishery	2	3	3	0	8

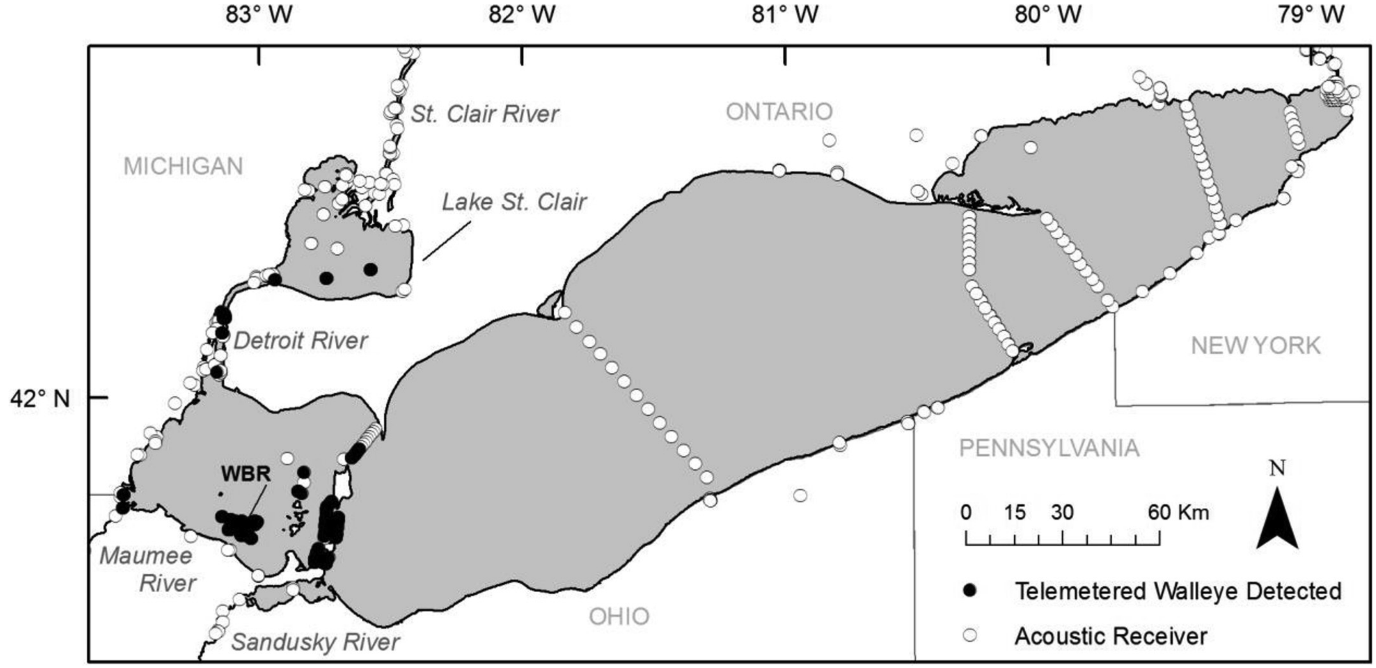
tem (http://glatos.glos.us/; Krueger et al. 2018) and Ocean Tracking Network (http://oceantrackingnetwork.org/; Cooke et al. 2011*a*). Spawning sites were monitored during the 2016 spawning period (i.e., March–June) for presence of tagged individuals. Although we were focused on estimating fish surviving to the 2016 spawning period, we have included detection data from fish still at-liberty through June 2017 in the survival estimates (described below). Use of acoustic telemetry to estimate survival may suffer from some level of bias if detection probabilities are reduced for extended periods of time or if tagged individuals do not encounter an acoustic receiver. However, acoustic receivers deployed in a grid across a given study area (versus deployed in a gate with limited spatial coverage), such as done here, provide improved spatial and temporal information about a tagged individual's fate across a range of conditions (e.g., detection probability, tag power; see Kraus et al. 2018). Potential false-positive detections due to code collision (Beeman and Perry 2012) were removed from the data using Pincock's (2012) criteria, resulting in a database of 178 358 detections comprising individual detection histories. Individual detection histories of tagged walleye were used to characterize status of each fish during the study (sensu: Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016). Each fish's status was classified as (*i*) harvested: reported by a fishery; (*ii*) alive: characterized by detections throughout Lake Erie; or (*iii*) deceased: characterized either by constant detection on a single acoustic receiver or by a lack of detections all together. For fish with a lack of detections or that were consistently detected but later were not detected, mortality was assumed to occur on the date of last detection. Logistic regression was used to estimate the possible influences of abiotic and biotic variables on post-tagging survival of walleye. Specifically, water temperature at capture (°C), surgery duration (minutes), holding time (i.e., total minutes elapsed between capture and release post-tagging), and fish length (total length, mm) were assessed. Each variable was considered alone because of the relatively small number of observations. Models were fit in R (R Core Team 2016; $\alpha = 0.05$).

Empirical survival of tagged walleye was estimated through Kaplan–Meier analysis based on time-at-large (i.e., post-tagging) observations:

$$\hat{S}(t) = \Pi_{t_j \leq t}(1 - d_j/r_j)$$

where $\hat{S}(t)$ is the probability of a given walleye surviving t units of time from the beginning of the study (i.e., date tagged), r_j is the number of tagged walleye at risk of dying at time t_j, and d_j is the number of deaths at time t_j (Kaplan and Meier 1958; Pollock et al. 1989). Mortality events were estimated based on either date of last detection or reported harvest dates. The Kaplan–Meier analysis was conducted using SAS 9.4 PROC LIFETEST (SAS Institute Inc., Cary, North Carolina). The maximum time-at-large considered

Fig. 2. Locations of walleye detections on acoustic receivers maintained by Great Lakes Acoustic Telemetry Observation System projects during November 2015 – June 2016. Suspected spawning populations contributing to the fishery include Detroit River, Maumee River, Sandusky River, and the western basin open-water reef complex (WBR).



was 696 days, which was the longest time-at-large observed in the data set.

Based on the empirical survival results, a piecewise exponential survival model was fit to the walleye time-at-large observations, which provided survival estimates for the simulations in objective 2. Based upon inspection of the raw data, breaks for the piecewise exponential survival model were assumed to occur at 1, 100, and 300 days post-tagging. The piecewise exponential survival model was selected over a simpler model (e.g., single exponential, Weibull, or gamma survival model) based on the survival pattern evident from the Kaplan–Meier results. The piecewise exponential survival model was fit by Bayesian inference using SAS 9.4 PROC PHREG (SAS Institute Inc., Cary, North Carolina). The rate parameters for the exponential pieces were estimated on a $\log_e$ scale and normal distributions with means of 0, and precisions of 1.0E-6 were assumed as prior distributions. Markov chain Monte Carlo (MCMC) simulations for deriving the posterior distributions for the parameters were based on an adaptive rejection Metropolis sampling algorithm (SAS Institute, Inc. 2013). Three parallel chains, each with 200 000 iterations, were run from overdispersed initialization values. The first 100 000 iterations were discarded as a burn-in and every 10th iteration was retained, resulting in a total of 30 000 saved samples across all chains. Chain convergence for each parameter was assessed through trace plots, Geweke (1992) diagnostic tests, and potential scale reduction factors (Gelman and Rubin 1992). Means of the saved MCMC chains were used as point estimates for parameters, and 95% highest posterior density (HPD) intervals were used as measures of uncertainty for the point estimates.

Tag-recovery data for evaluating the accuracy and precision of stock composition estimates across varying sample sizes and true spawning population contributions were generated from Dirichlet compound multinomial distributions. Simulated scenarios were defined by combinations of three stock compositions (one with equal proportions of five population (each population contributes 20% of the individuals in a mixed-stock fishery), a second with one disproportionately abundant population (one population contributes 60% of the individuals) relative to the others (four other populations each contribute 10% of the individuals), and a third with 10 populations with steadily declining contributions (36.64%, 23.36%, 14.90%, 9.50%, 6.06%, 3.86%, 2.46%, 1.57%, 1.01%, 0.064%)), six sample sizes (n = 30, 50, 100, 200, 400, and 800 tagged fish), and two survival rates (mean and 95th HPD survival curves from the piecewise exponential models). The disproportionate mixing scenario reflects the working hypothesis for the walleye fishery in western Lake Erie (i.e., a single population contributes a disproportionate amount to the fishery harvest and the remain-

Fig. 3. Estimated survival for walleye tagged during July–August 2015 in western Lake Erie's recreational fishery. Heavy dashed line indicates empirical survival estimates based on a Kaplan–Meier analysis. Solid black line indicates survival estimates based on a piecewise exponential survival model, with 95% credible intervals corresponding to the shaded area. Vertical dashed lines indicate range of time to survive postrelease to onset of spawning period (15 March 2016).

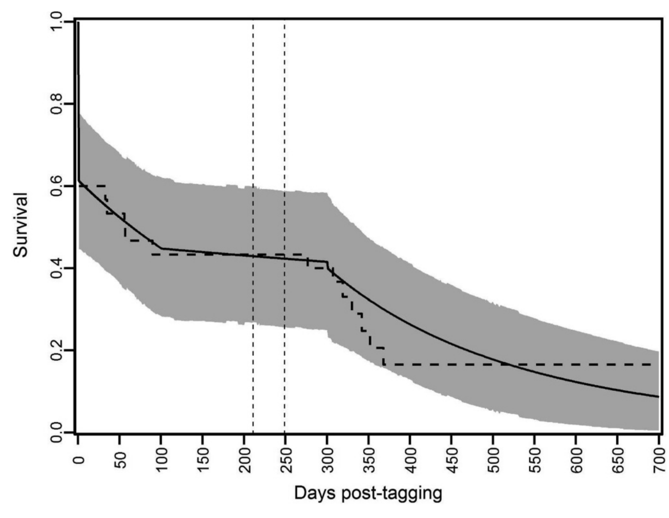
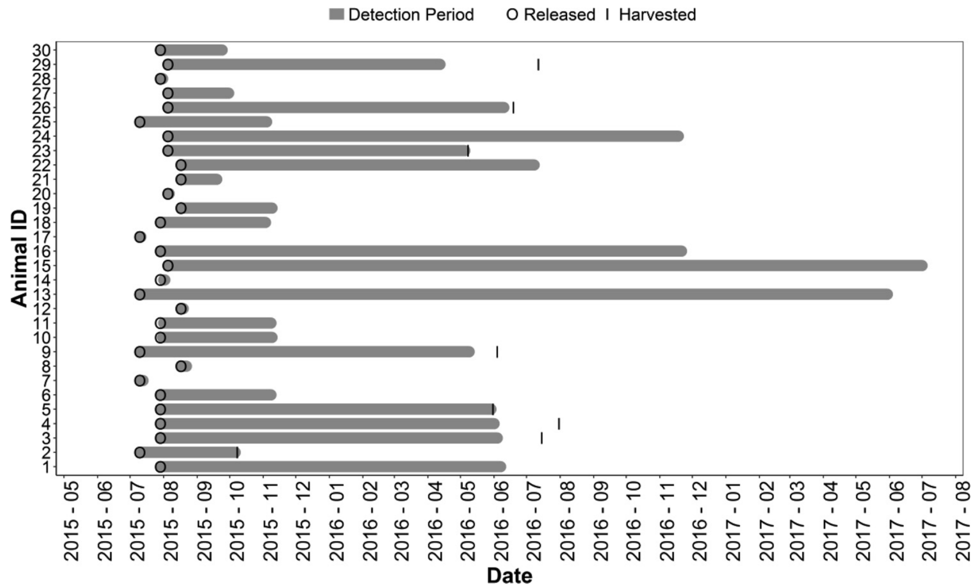


Fig. 4. Detection periods from all Great Lakes Acoustic Telemetry Observation System acoustic receivers for 30 walleye tagged during July–August 2015 in western Lake Erie.



ing populations contribute in lesser numbers; DuFour et al. 2015), whereas the equal mixing scenario reflects the opposite (all populations contribute equally). The third scenario evaluated how estimation performance would be influenced by increases in the number of possible spawning populations. Simulated sample sizes spanned a range of possibilities that researchers are likely to face when planning similar studies (e.g., small versus large budget).

To simulate tag-recovery data, the concentration parameters for the Dirichlet component of the distribution were set equal to the product of the expected contributions of the populations as described above and an effective sample size of 100. The probabilities resulting from the Dirichlet distribution were then used as inputs in a multinomial distribution to generate observed recoveries at each spawning locale where the number of trials for the multinomial distribution was the number of tagged fish alive on 15 March (assumed beginning of spawning period). Estimated spawning population contributions were simply the number of fish detected at each spawning locale divided by the total number of fish detected. A total of 100 000 iterations were conducted for each simulation scenario. Errors in stock composition estimates (estimated compositions – true compositions) were calculated for each iteration. Accuracy was evaluated using the median of the errors across all iterations, whereas precision was evaluated using the interquartile range of the errors. We primarily were interested in identifying the tagging level where accuracy and precision approached asymptotic levels (i.e., increasing sample size does not result in marked improvements in levels of accuracy and precision) across a range of population contribution levels.

Results

Based on Kaplan–Meier analysis, the mean survival time for walleye tagged from the mixed-stock fishery in the summer was 213 days (standard error (SE) 47 days). Forty percent of tagged walleye (12/30) were assumed to have died within the first day of tagging (Figs. 3 and 4). A positive relationship existed between survival and water temperature, and a negative relationship existed between survival and surgery and holding times, although the estimated coefficients for these variables were not significantly different from zero (Table 2). After the initial tagging mortality period, mortality remained high for about 100 days post-tagging (i.e., 5/18 fish were assumed to have died during this period) due to a combination of harvest mortality and possibly delayed tagging mortality. Between 100 and 300 days post-tagging, survival of remaining fish was high (i.e., no fish died during this period; Fig. 3). After 300 days post-tagging, mortality increased primarily because of angler harvest during the spring and summer fishing season (Figs. 3 and 4). Of the 30 tagged walleye, four fish were detected more than 400 days after tagging. Despite the short-term mortality experienced by walleye tagged in this study, 72% (13/18) of fish that survived after 30 days postrelease were still alive during the 2016 spawning period (Figs. 2 and 4). Most of these fish (85%; 11/13) were detected within an open-water reef complex where spawning occurs in the western basin (Fig. 2). One walleye moved north through the Detroit River and remained within Lake St. Clair through May 2016, and the remaining fish was not detected at any spawning area. Eight walleye were harvested (two by commercial fishery and six by recreational fishery), seven of which were captured after the spawning season in 2016 (Fig. 4).

Table 2. Results of logistic regressions examining influence of fish length, water temperature, surgery time, and holding time on estimated survival of walleye tagged during July–August 2015.

	Length	Water temperature	Surgery time	Holding time
Slope	0.001 (±0.016)	0.306 (±0.459)	–0.750 (±1.247)	–0.052 (±0.053)
z	0.987	1.31	–1.18	–1.93
df	28	25	28	26
P	0.324	0.190	0.238	0.054

Note: Values in parentheses = 95% confidence interval.

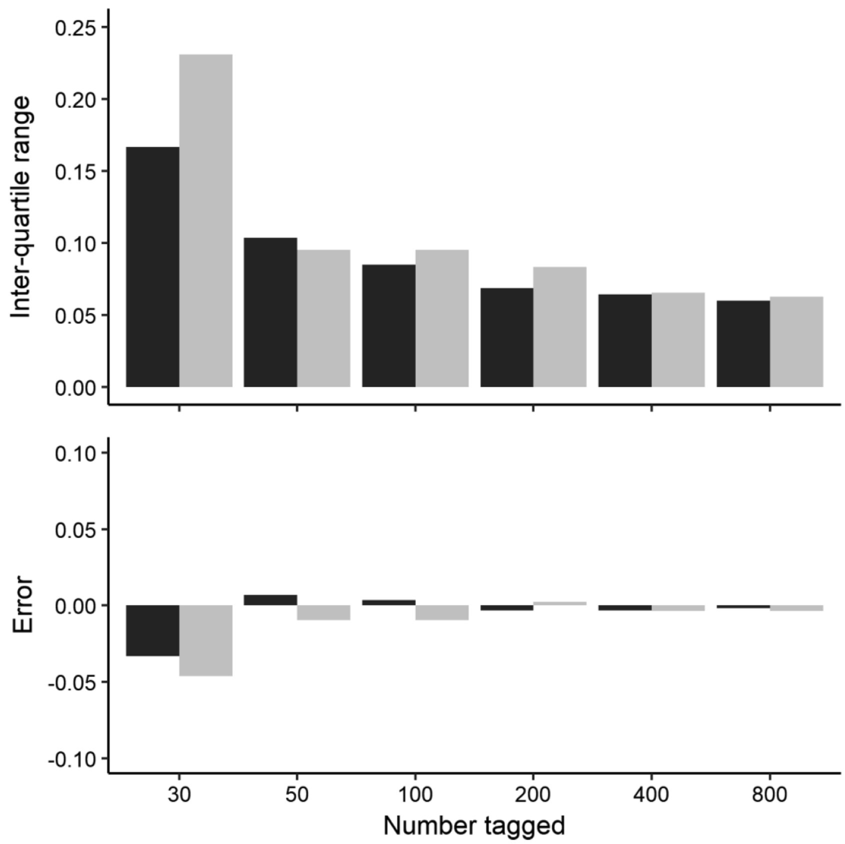
The parameter estimates for the exponential survival pieces, which correspond to daily instantaneous mortality rates, ranged from 2.240E-04 for days 100 to 300 to 0.479 for days 0 to 1 (Table 3). The parameter estimates for the exponential survival pieces were as follows: days 0 to 1: 0.479 (95% HPD interval: 0.266–0.837); days 1 to 100: 0.003 (95% HPD interval: 0.001–0.007); days 101 to 300: 2.240E-04 (95% HPD interval: 1.849E-05 – 1.875E-03); days 300+: 0.004 (95% HPD interval: 0.002–0.009). The predicted survival estimates from the piecewise exponential model agreed with the Kaplan–Meier survival rates well until around 300 days at large (Fig. 3). The predicted survival rates from the piecewise exponential model after 300 days at large diverged from the Kaplan–Meier estimates (Fig. 3), which was likely due to the length of this final

Table 3. Exponential survival rates and 95% highest posterior density (HPD) intervals from the piecewise exponential survival model fit to the walleye time-at-large data.

Statistic	Days 0 to 1	Days 1 to 100	Days 100 to 300	Days 300+
Survival rate	0.479	0.003	2.240E-04	0.004
95% HPD interval	0.266–0.837	0.001–0.007	1.849E-05–1.875E-03	0.002–0.009
Geweke diag. chain 1	1.447	–0.453	–1.324	–0.653
Geweke diag. chain 2	–0.559	0.737	–0.847	–0.698
Geweke diag. chain 3	0.069	0.791	1.221	0.991
Potential scale reduction	1.0	1.0	1.0	1.0
Effective sample size	30 319	30 000	28 763	30 000

Note: Also shown are the results from Bayesian diagnostic tests conducted on individual MCMC chains including Geweke (1992) *Z* scores for each MCMC chain, upper 95% confidence interval for the potential scale reduction factor calculated across the chains (Gelman and Rubin 1992), and effective sample size for the combined chains.

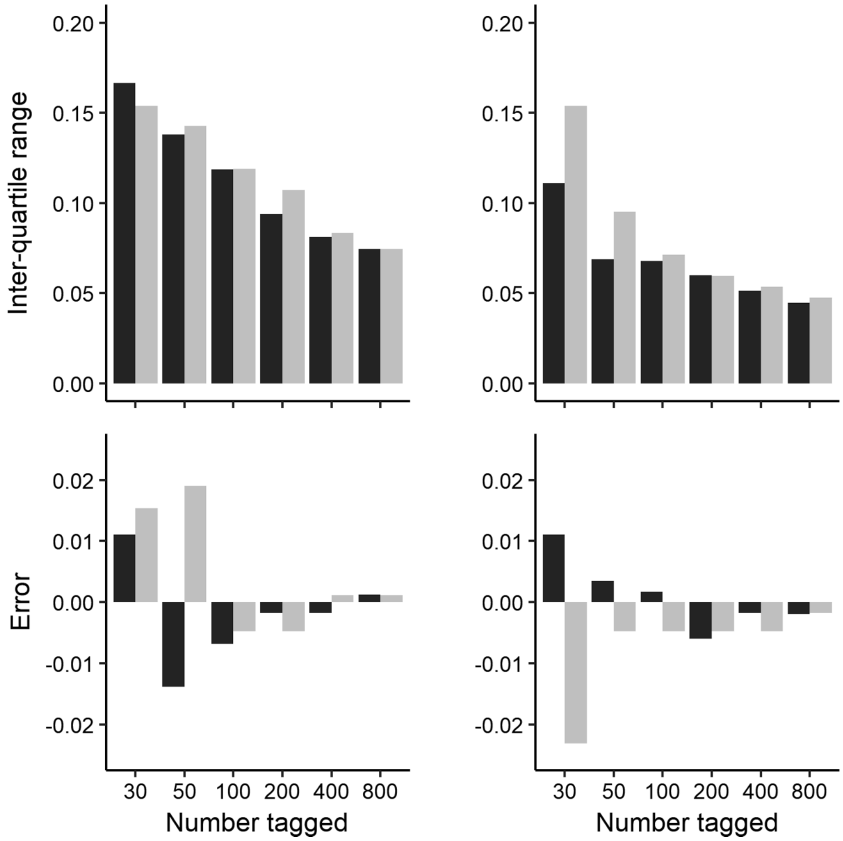
Fig. 5. Simulated precision (interquartile range of simulation results) and accuracy (error = median of simulation results – known value) of stock contribution estimates across varying numbers of fish tagged and survival probabilities (black bars = upper 95th highest posterior density (HPD); gray bars = mean) as estimated by a piecewise exponential model. Five populations were assumed to contribute equally (0.2) to a fishery.



period and that the last mortality event occurred on day 368. The saved MCMC chains for all parameters from the piecewise exponential survival model were judged to have converged on stable stationary distributions by all evaluated criteria (Table 3).

As expected, the simulations demonstrated how accuracy and precision of estimated population contributions to a fishery generally increased with the number of tagged fish and survival rate (Figs. 5–8). Of the scenarios evaluated, accuracy was generally lowest when fewer than 100 fish were tagged. For instance, when five spawning populations contributed equally to a fishery, median error ranged from –4.6% to –3.3% (across both survival assumptions) when 30 tagged fish were released, but accuracy improved (median error range = –0.9% to 0.3%) when 100 tagged fish were released (Fig. 5). Populations with low expected contributions tended to have less accurate estimates, with consistently negative median errors, even at sample sizes greater than 100 (Figs. 6 and 8). The interquartile range of simulation results declined as sample size increased, regardless of the assumed population contributions (Figs. 5–7). However, the resulting decrease of simulated results' interquartile range lessened at sample sizes greater than 100 (Figs. 5–7). For example, when one population contributed disproportionately relative to the four populations (i.e., population 1 = 60%, populations 2–5 each = 10%), increasing the sample size from 200 to 800 fish reduced the interquartile range of simulated results from 0.11 to 0.08 for the abundant population and from 0.06 to 0.05 for lesser populations (assuming mean survival rate; Fig. 6). Thus, tagging more than 200 fish would result in relatively small gains in accuracy and precision of stock composition estimates. The largest reductions in interquartile ranges were observed when sample sizes were increased from low (i.e., 30–50) to moderately high (i.e., 100–200) numbers across all population contribution levels (Figs. 5–7).

Fig. 6. Simulated precision (interquartile range of simulation results) and accuracy (error = median of simulation results – known value) of stock contribution estimates across varying numbers of fish tagged and survival probabilities (black bars = upper 95th HPD; gray bars = mean) as estimated by a piecewise exponential model. Five populations were assumed to contribute unequally to a fishery, with one population contributing disproportionately (0.6; left panels) and the remaining four contributing a less proportion (0.1; right panels).

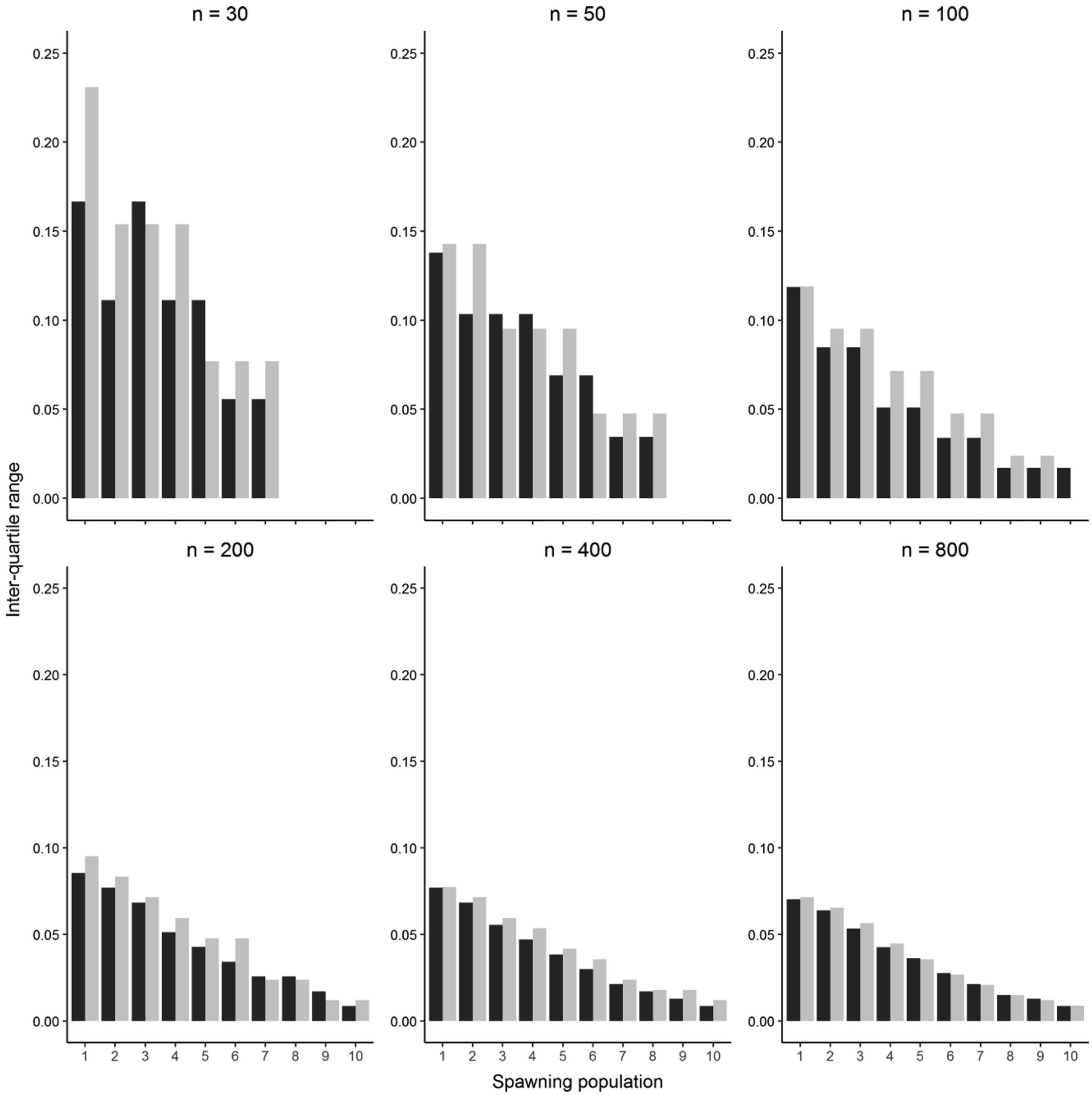


Discussion

This study was a proof-of-concept for using acoustic telemetry to assess contributions to mixed-stock fisheries for freshwater and marine systems using Lake Erie's recreational walleye fishery as a test case. The ability to estimate accurately spawning population contributions to mixed-stock fisheries is in part determined by whether enough fish can be tagged such that suitable numbers will survive to subsequent spawning periods. Here, walleye captured and tagged from Ohio's summer recreational fishery experienced high initial mortality (~40%), with delayed mortality occurring to 100 days postrelease, but those that survived this initial period had relatively high survival rates (i.e., of the 13 fish that survived beyond 100 days postrelease, all were likely alive during the 2016 spawning period). High tagging mortality may be overcome by releasing more tagged fish to achieve a desired sample size during subsequent spawning periods. For instance, if a population was large enough to support tagging high numbers of fish (e.g., 200+) and budgetary (i.e., does the project budget afford the purchase of hundreds of acoustic transmitters?) and field constraints (e.g., ability to capture large numbers of fish) could also be overcome, this approach would allow sufficient numbers of tagged individuals to survive to be detected on spawning grounds. Lake Erie's walleye population fits this description, with an estimated 41.4 million age-2+ fish in 2018 and a mean recreational harvest rate of 0.46 fish per angler hour in the western basin (WTG 2018). Thus, by tagging a large enough number of fish (~200 individuals), this approach would be feasible to estimate contributions for Lake Erie's fisheries. However, compensation for mortality issues at tagging could not only focus on tagging more fish, but also focus on reducing stress associated with capture and handling to improve survival.

The combined effects of capture and handling methods may be just as important as the tagging procedure to fish survival and ultimate success or failure of a study (Jepsen et al. 2015). Although surgery and holding times were not statistically significant predictors of postrelease survival, estimated coefficients suggested negative relationships with these variables. Clearly, taking steps to reduce surgery and holding times to expedite the return of tagged individuals to their ambient environment are desired. Alternative tagging methods, such as external attachment, can be used to reduce surgery and holding times (Jepsen et al. 2015). However, studies that successfully used externally attached electronic transmitters typically focused on research questions that did not require long-term retention (e.g., Raby et al. 2015; Breine et al. 2017), and tag loss is commonly reported (Jepsen et al. 2015). Further, when external tag retention was high, biofouling (Thorstad et al. 2001) and an increased vulnerability to capture (Rikardsen and Thorstad 2006) may introduce bias or reduce the number of tagged fish at large with negative impacts on study objectives. Development of external electronic transmitters that minimize these negative issues is possible (e.g., Deng et al. 2012), but Jepsen et al. (2015) ultimately recommended surgically implanting electronic transmitters for long-term studies. Other sedation techniques, such as use of direct current to immobilize fish during surgery rather than pulsed direct current (Vandergoot et al. 2011), may decrease recovery times and allow fish to be released more quickly. If fish must be held in tanks pre- and postsurgery, dissolved oxygen levels at or near

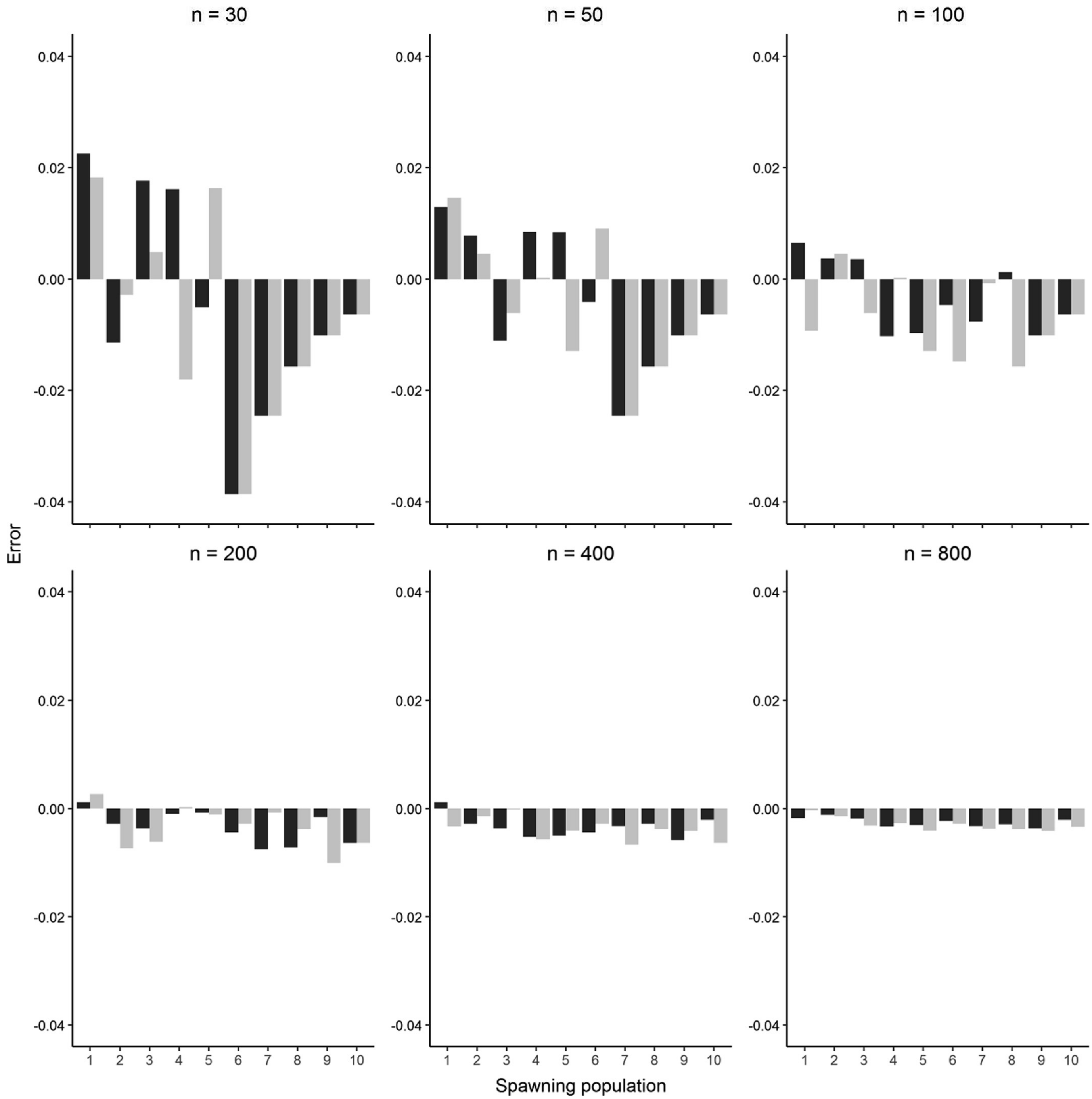
Fig. 7. Simulated precision (interquartile range of simulation results) of stock contribution estimates across varying numbers of fish tagged and survival probabilities (black bars = upper 95th HPD; gray bars = mean) as estimated by a piecewise exponential model. Ten populations were assumed to contribute in declining proportions (36.64%, 23.36%, 14.90%, 9.50%, 6.06%, 3.86%, 2.46%, 1.57%, 1.01%, 0.064%).



saturation should be maintained (Oldenburg et al. 2011; Loomis et al. 2013).

High water temperatures can contribute substantially to sublethal and lethal effects for fishes released after capture (Gale et al. 2013). For instance, when walleye were tagged with acoustic telemetry transmitters using the same process as described here but at temperatures less than 10 °C, the survival rate to 21 days was estimated to be 95% (Hayden et al. 2014). In our study, water temperature had a nonsignificant, positive relationship with postrelease survival, which was likely caused by a combination of low sample size (n = 30) and relatively low variation in water temperatures during tagging. Although Oldenburg et al. (2011) recommended that fish be held and surgeries performed at ambient water temperatures from which fish were sampled, brief exposure to elevated water temperatures after capture may negatively impact survival (Schramm et al. 2010). Thus, taking steps to maintain water temperatures at ambient levels (e.g., use of covered recirculating tanks, use of ice to cool water if temperatures become elevated) may improve postrelease survival.

Fig. 8. Simulated accuracy (error = median of simulation results − known value) of stock contribution estimates across varying numbers of fish tagged and survival probabilities (black bars = upper 95th HPD; gray bars = mean) as estimated by a piecewise exponential model. Ten populations were assumed to contribute in declining proportions (36.64%, 23.36%, 14.90%, 9.50%, 6.06%, 3.86%, 2.46%, 1.57%, 1.01%, 0.064%).



The results from our simulations, informed by survival estimates for Lake Erie walleye tagged during summer months, suggested that tagging more than 200 fish would result in relatively small gains in accuracy and precision of stock composition estimates. Ultimately, selection of an appropriate tagging level must strike a balance among factors such as the level of accuracy and precision in estimates required for them to be useful in informing management decision-making, logistical constraints (e.g., time, personnel, budget) required to achieve such a sample size, and knowledge about expected population contributions. If a study's purpose is to identify only which populations contribute a substantial fraction of individuals to a fishery, then lower tagging levels may suffice. Conversely, if a concern exists that exploitation of mixed-stock fisheries may overexploit small, less productive populations, then higher tagging levels will likely be needed. Despite the marked increase in use of electronic transmitters during the last decade (Hussey et al. 2015), the evaluation of study design through simulation such as conducted here appears to be uncommon (for exceptions see Powell et al. 2000; Nations and Anderson-Sprecher 2006; Rudd et al. 2014) when compared with conventional mark–recapture studies (e.g., Pine et al. 2003; Vandergoot and Brenden 2015; Sackett and Catalano 2017). Before initiating an acoustic telemetry study for assessing stock composition, we strongly recommend using simulations similar to what we have done in this study for evaluating whether a target tagging level is sufficient for meeting a study's objectives.

A variety of assumptions were made in our simulations, which if not met in empirical studies could lead to larger inaccuracies or poorer precision in population contribution estimates than what our results suggest. A Dirichlet compound multinomial distribution was used for the simulations because this distribution allows for greater variability in results than other distributions that might have been used for similar purposes, such as the multinomial distribution. However, even greater variability in results with empirical studies could stem from spatial and (or) temporal variability in mortality rates, nonreporting of harvested fish, transmitter malfunction, transmitter detection efficiencies, and other factors. Additionally, our simulations assumed that the spawning grounds of all populations were known. In situations where population membership for some individuals is unknown (e.g., if a subset of spawning locations is unknown or unmonitored), accuracy and precision of population contributions estimates will degrade.

Various factors can cause traditional methods for identifying contributions to mixed-stock fisheries, such as otolith chemistry or genetic markers, to have low discriminatory power. For instance, lack of spatial variation or high levels of temporal (i.e., interannual) variation in water chemistry can limit success in determining origins of long-lived fish using otolith chemistry unless a long-term (i.e., multidecadal) library of chemical signatures existed (Pangle et al. 2010). Further, advection of larval fish by currents from natal sites may result in considerable mixing of fish during early life stages, which if unaccounted for can make population delineation challenging (Spangler et al. 1981; Fraker et al. 2015). The use of genetic markers to identify spawning populations can have low discriminatory power depending on the level of straying that occurs between populations or historical stocking practices that have been conducted in the system. For example, walleye in Lake Erie have been identified as showing spawning site fidelity (Chen et al. 2017; Hayden et al. 2018); however, the level of genetic differentiation in some Lake Erie walleye populations has been found to be low, regardless of the marker used (allozyme and mitochondrial DNA: McParland et al. 1999; microsatellite: Strange and Stepien 2007; Stepien et al. 2010; Brenden et al. 2015; single nucleotide polymorphism: Chen 2016), likely because of straying among populations (Chen et al. 2017; Hayden et al. 2018). Additionally, low genetic differentiation may result if fish establish fidelity to spawning sites via learning as adults and return to sites of first spawning experience rather than via natal homing (Olson et al. 1978). Based on field trials tagging walleye during the summer season and simulation results, use of acoustic telemetry is a viable alternative to natural markers to estimate spawning population contributions to a mixed-stock fishery. To our knowledge, this study is one of the first attempts to propose the use of acoustic telemetry to estimate population contributions to a mixed-stock fishery, despite previous applications to understand population structure using fish captured and implanted with electronic tags when populations are mixed (e.g., Block et al. 2005; D'Amelio et al. 2008). Acoustic telemetry would provide a direct estimate of contributions of populations to harvest that occurred in a previous fishing season, which means this approach could not be used for estimating stock composition for in-season harvest analysis and management (e.g., Dahle et al. 2018). Nevertheless, postseason stock composition estimates of harvest can provide valuable information regarding differing fishing mortality experienced among populations and potentially prevent overharvest.

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