ARTICLE

Postrelease Survival and Migration Behavior of Adult Walleye Following Intracoelomic Transmitter Implantation Using Two Methods of Electro-Immobilization

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Abstract

The use of electricity as a method of fish restraint (i.e., electro-immobilization) during field and hatchery operations has increased recently, and a need exists for field-based assessments of the effects of these techniques on the postrelease physiology, behavior, and survival of wild fish to develop best handling practices. Two common waveforms used in electro-immobilization are continuous and pulsed DC (cDC and pDC, respectively). With cDC, fish are immobilized through exposure to a continuous weak current and recover almost immediately once the current ceases. With pDC, fish are incapacitated via brief exposure to a strong current and often require several minutes to recover (i.e., regain equilibrium). Here, we present a comparison of cDC and pDC electro-immobilization techniques and their effects on the postrelease survival and spawning migration behavior of adult Walleye *Sander vitreus* in a Lake Erie tributary. Fish were intracoelomically implanted with acoustic transmitters and then tracked by a network of acoustic receivers throughout Lake Erie that provided extensive spatiotemporal coverage of posttagging movements. Survival

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did not differ between the two electro-immobilization treatments but was somewhat lower than in a control group consisting of fish tagged several years earlier (e.g., 50-d survival = 69% for the pDC group, 61% for the cDC group, and 90% for control fish). We did not find any plausible or biologically meaningful effects of treatment on downstream movement or migratory behavior over subsequent months postrelease. Our results suggest that the two electro-immobilization techniques did not differ in their effects on adult Walleye behavior, but more work is needed to elucidate the extent to which electro-immobilization in general contributes to potential decreases in survival versus other aspects of capture and handling associated with performing surgical procedures.

Advancements in the development and implementation of electronic tracking methods have revolutionized the study of behavior in fish (and other aquatic taxa), particularly as it pertains to acoustic telemetry whereby passive receiver arrays can provide a relatively cost-effective means of obtaining large-scale movement data for tagged fish (Hussey et al. 2015; Crossin et al. 2017). Acoustic telemetry has been used successfully in a variety of environments globally (e.g., Welch et al. 2009; Finn et al. 2014; Hayden et al. 2014; McAuley et al. 2017). Information gleaned from large-scale telemetry networks can be beneficial for conservation initiatives and for informing fisheries management policies (e.g., quota allocation; Cooke et al. 2011; Crossin et al. 2017; Krueger et al. 2018), and the development of these large-scale, collaborative research networks is becoming increasingly prevalent (e.g., Abecasis et al. 2018; Ellis et al. 2019). Collection of telemetry data across expansive geospatial scales provides researchers and resource managers with valuable insight related to the population dynamics, behavior, and movements of ecologically and economically relevant fish stocks.

Electronic transmitters are often surgically implanted in the coelom of fish, so researchers must capture the fish, perform a surgical procedure, and release the individual in a manner that is efficient and safe for both the fish and the handler. A broad range of general chemical anesthetics has been used to immobilize fish before implanting electronic transmitters, including tricaine methanesulfonate (MS-222; e.g., Topic Popovic et al. 2012), eugenol (e.g., Guénette et al. 2007), metomidate (e.g., Mattson and Riple 1989), and benzocaine (e.g., Gilderhus 1990). In recent decades, there has been a growing interest in using electricity to immobilize fish (henceforth, "electro-immobilization") as an alternative to traditional chemical approaches. While experiments involving electro-immobilization (as distinct from electrofishing) date back at least as far as the 1970s (e.g., Kynard and Lonsdale 1975), the 21st century has seen a considerable amount of attention given to the breadth and applications of available techniques, as well as comparisons with chemical anesthesia, in numerous fish species and aquatic systems (e.g., Chiba et al. 2006; Vandergoot et al. 2011; Balazik et al. 2013; Gao et al. 2014; Prystay et al. 2017).

Although electro-immobilization methods can vary in how they are administered and the degree of immobilization that is induced, they often result in faster induction and recovery times (Bowzer et al. 2012; Gause et al. 2012) as well as comparable or less severe adverse physiological responses (Trushenski et al. 2012) relative to chemical anesthetics. Furthermore, fish that undergo electro-immobilization may be released into the wild immediately upon recovery, whereas chemical anesthetics usually (depending on the substance and jurisdiction) have mandatory postexposure holding periods before the fish are safe for release into the wild due to the potential for capture and consumption by fishers; holding periods can range from 3 to 21 d in the USA (Trushenski et al. 2013). Such constraints have led a number of researchers and fisheries professionals to seek alternatives to currently accepted chemical anesthetics (particularly MS-222), whether these be other anesthetics, such as eugenol (clove oil), or electro-immobilization techniques (Zydlewski et al. 2008; Trushenski et al. 2013; Kim et al. 2017; Durhack et al. 2020). For this reason, electro-immobilization may be a more desirable and practical immobilization method for research conducted in field or hatchery settings. Many welfare-relevant knowledge gaps still remain, however, and adoption of electro-immobilization as a standard practice depends greatly on how this technology is perceived by the animal care and ethics committees in various jurisdictions.

A prototypical list of the stages of electro-immobilization was formulated by Reid et al. (2019) based on relevant knowledge garnered from previous experiments (e.g., Vandergoot et al. 2011) and mirroring the well-known stages of chemical anesthesia for fish as outlined by Summerfelt and Smith (1990). In general, two different current types—continuous DC (cDC) and pulsed DC (pDC)—have been used in fisheries research (e.g., see Abrams et al. 2018); the types differ in how the electrical waveform is administered. In brief, cDC is typically administered as a weak, low-voltage current that is run through a fish for the duration of the handling procedure to elicit a near-total loss of equilibrium and muscle relaxation, which subside upon removal of the current (Jennings and Looney 1998; Vandergoot et al. 2011). In contrast, pDC is typically administered through brief or pulsed

exposure (e.g., 3 s) to a strong, high-voltage current (often >50–100 V), resulting in total equilibrium loss, muscle relaxation, and a recovery period of several minutes after exposure to the current (Vandergoot et al. 2011; Faust et al. 2017). In this sense, the cDC and pDC approaches described here correspond with the "electroanesthesia" and "electrostunning" stages of electro-immobilization as described by Reid et al. (2019). Both cDC and pDC have been used in the field to immobilize fish prior to or while implanting acoustic transmitters (e.g., Hayden et al. 2014; Struthers et al. 2017; Raby et al. 2018; Faust et al. 2019; Matley et al. 2020; Harris et al. 2021) and also have been used in hatchery settings. Anecdotally, it appears that pDC may be used more commonly than cDC, especially in aquaculture, where stunning is much more desirable than lighter forms of immobilization (Robb and Roth 2003; Erikson et al. 2021), and commercial electro-immobilization units tend to be developed with this consideration in mind (e.g., Nguyen et al. 2018). However, we are unaware of any attempts to compare the effects of different electro-immobilization methods on the behavior and survival of fish once they have been released as part of a tracking study. Using a single pDC protocol, Wilson et al. (2017) found that the capture, tagging, and release process may elicit some differences in migration behavior among Walleye *Sander vitreus*, but these differences may not have been large enough to be ecologically relevant or meaningful.

The purpose of this experiment was to compare the effects of cDC and pDC on the postrelease survival and migratory behavior of adult Walleye implanted with acoustic transmitters in the Sandusky River, Ohio. Detection data provided by a large-scale passive receiver network maintained throughout Lake Erie were used to assess (1) survivorship following release (especially at 20, 50, 100, 200, and 365 d postrelease) and (2) the number of days required for Walleye to migrate out of the Sandusky River into Sandusky Bay, move to areas elsewhere in Lake Erie, and then return to Sandusky Bay and the Sandusky River in the following year (2019). We hypothesized that cDC fish would exhibit higher survival and faster migration rates than pDC fish, since cDC tends to be less likely to injure fish and allows for faster recovery (Reid et al. 2019). We also compared survival in both cDC and pDC treatments to that of Walleye tagged in 2014/2015 and observed in 2016, used as a form of "control" group for ambient survival rates. Our results are relevant for researchers developing best practices or simply trying to decide which of these immobilization methods is best for the purpose of performing surgery on or for use in sampling of Walleye or other (primarily freshwater) fishes.

METHODS

Study site and experimental subjects.— The Walleye is an ecologically and economically important native fish species throughout North America, including the Laurentian Great Lakes basin (Hansen et al. 2019; Vandergoot et al. 2019; Cahill et al. 2020). Sexually mature adult Walleye migrate during early spring to spawn in tributaries or open-water reefs in lacustrine systems (Raabe and Bozek 2012; Dembkowski et al. 2018), sometimes undergoing significant longitudinal migrations in large bodies of water (Hayden et al. 2014; Matley et al. 2020). A coolwater and iteroparous species, Walleye spawn in the early spring and most often when water temperatures average approximately 7–9°C (Bowlby and Hoyle 2011), though spawning has been documented in water temperatures as low as 2.2°C and as high as 15.6°C (Hokanson 1977). After spawning, Great Lakes Walleye undertake complex inter- and intralake migrations (Hayden et al. 2014; Vandergoot and Brenden 2014; Raby et al. 2018). In the current study, all Walleye were collected from the Sandusky River, a tributary of Lake Erie (Figure 1) that contains a self-sustaining population (DuFour et al. 2015), on March 26 (day 1), March 30 (day 2), or April 2 (day 3), 2018. Walleye were captured during daylight hours via boat electrofishing gear (Smith-Root 5.0 Generator Powered Pulsator electrofisher; 60 pulses/s, 4–6 A; Smith-Root, Vancouver, Washington). This work was conducted in adherence to the American Fisheries Society's *Guidelines for the Use of Fishes in Research* (Jenkins et al. 2014).

Treatments and experimental protocol.— Prior to the process of implanting an acoustic transmitter, Walleye that were assigned to either the cDC or pDC treatment were handled in the same manner. Fish were randomly selected from holding tanks and alternately assigned to the cDC or pDC treatment. After capture, Walleye were transported to shore and held onshore in large holding tanks (378 L) supplied with aerated water. Each fish was measured, sexed, and tagged with an intramuscular external tag (FT-4 Lock-on; Floy Tag and Manufacturing, Inc., Seattle) located near the posterior edge of the secondary dorsal fin. Each fish's age was estimated using year- and sex-specific age–length keys via the methods described by Isermann and Knight (2005) and implemented in the FSA (Fisheries Stock Analysis) package (Ogle et al. 2021). For the cDC treatment, cDC was administered to Walleye via a transcutaneous electrical nerve stimulation (TENS) unit (MAXTENS 1000; Bio Protech, Chino, California) consisting of a power supply box and electrode leads. Prior to implanting the acoustic transmitters, Walleye were placed supine on a surgical board with two anode (+) electrodes placed toward the head and two cathode (−) electrodes near the tail of the fish; electrodes were held in place by the mass of the fish and a surgical assistant wearing latex gloves. Electrical intensity was increased incrementally until fish were immobilized and unresponsive to tactile stimulation, at which point surgery commenced. Electrical intensity is coarsely controlled on the
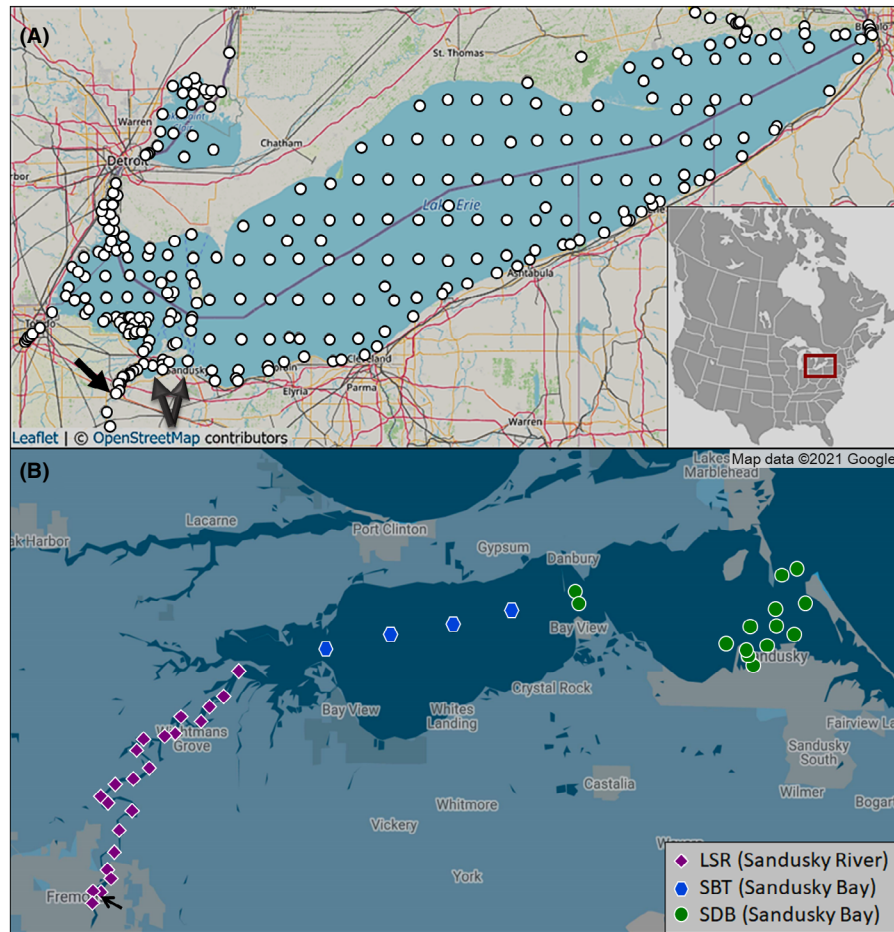
FIGURE 1. **(A)** Map of Lake Erie, with individual receiver stations active between January 1, 2018, and December 31, 2019, shown as white circles. The Sandusky River (black arrow) and Sandusky Bay (gray double-arrow) are visible near the bottom left corner of the map. Inset shows the lake's location within North America. **(B)** Receivers that were used to assess Walleye migration checkpoints within the Sandusky River and Sandusky Bay at which detections were recorded are shown; receivers in broader Lake Erie are not shown. Both the SBT array (blue hexagons) and the SDB array (green circles) were considered to represent Sandusky Bay, while the LSR array (purple diamonds) was considered to represent the Sandusky River. The black arrow near the southwest corner of the map denotes the release location.

TENS unit, where output ranges from 0 to 80 mA. Although the exact intensity varied by fish and was not recorded, in the current study the unit was typically set between 20 and 40 mA. A Smith-Root Portable Electrosedation System (PES) unit was used to immobilize Walleye with pDC. The PES unit consists of a battery-operated power supply box, which regulates the type, intensity, and duration of pDC administered, and an exposure chamber $(1.0 \times 0.4 \times 0.4 \, \text{m})$ with an anode and a cathode mounted on opposing ends. Walleye were placed in the exposure chamber, oriented toward the anode and perpendicular to the electrode plates. Fish were exposed to 3 s of pDC (30 V, 100 Hz, and 25% duty cycle) similar to the method described by Vandergoot et al. (2011). After being exposed to the pDC via the PES unit, fish were placed supine on a surgical board as previously described. For both electro-

immobilization treatments, fish received a constant supply of freshwater throughout the duration of the surgery.

An acoustic transmitter (Innovasea V16-4H; diameter = 16 mm, length = 68 mm, weight = 24 g, estimated battery life = 4.5 years, power output = 158 dB; Innovasea, Halifax, Nova Scotia) was surgically implanted into the coelom of each fish following the methods described by Hayden et al. (2014) and Schoonyan et al. (2017). Briefly, after an incision (~2–3 cm) was made with a scalpel along the midline of the abdomen in-line or slightly posterior of the pelvic fins, a sterilized transmitter was inserted into the coelom and the incision was closed with two or three interrupted sutures (Ethicon PDS II; Johnson and Johnson, New Brunswick, New Jersey; Schoonyan et al. 2017). After the surgery was completed (generally <180 s), fish were allowed to regain equilibrium in a container supplied

with fresh river water prior to release. After release, the movements of acoustically tagged fish were monitored by a large network of passive acoustic receivers maintained by the Great Lakes Acoustic Telemetry Observation System (GLATOS; Krueger et al. 2018; Matley et al. 2020) that were stationed throughout the Sandusky River (i.e., immediately downstream of the release location) and Lake Erie. Fish were released at approximately 41.351747°, 83.107060°.

Assessment of postrelease survival.—The number of days postrelease at which fish were considered dead was based on transmitter detections and evidence of movement from the GLATOS acoustic receiver network (Figure 1A). Fish were censored if they were either harvested during the observation period (with censoring occurring on the number of days postrelease at the time of harvesting) or if they survived beyond 365 d (at which point they were right-censored). For those that were not harvested, fish were assumed to be alive until one of the following events was observed and considered to be a mortality: (1) the total cessation of detections after clear evidence of movement; (2) the beginning of a gap in detection history spanning at least 4 months (the greatest gap we observed in detection data for fish that were still clearly alive after the gap), with no clear evidence of movement; or (3) the beginning of a long string of detections at one or very few adjacent receivers (e.g., ≥3 months; interpreted as a dead fish or a tag resting on the bottom near the receivers), with no subsequent evidence of movement.

To include an estimate of natural survivorship (of fish as a "control" group), the same criteria described above were applied to Walleye into which acoustic transmitters were implanted in 2014 or 2015 and recorded over a 1-year observation period beginning in spring 2016. We used detections between spring 2016 and spring 2017 because by 2018, there were too few of these fish remaining with functioning transmitters to allow for meaningful comparison. Similar to the process described earlier (i.e., with respect to collection and handling), control fish were immobilized with pDC in a similar fashion as the current study; therefore, the survival of individuals over subsequent years should be more reflective of natural and fishing mortality processes as opposed to the effects associated with being immobilized with cDC or pDC. Thus, we assumed that the postspawn movement and survival of fish released in 2014 and 2015 (i.e., 2 years and 1 year postsurgery, respectively) were not associated with electro-immobilization because enough time had passed for them to fully overcome any effects of capture, handling, and surgery (Wilson et al. 2017). Since these fish were "released" in 2014 or 2015, the second release day and month for cDC/pDC fish (March 30, which fell evenly between day 1 and day 3) was assigned as the "postrelease" date used to score the relative timing of any mortality events in the control group. Only fish that were considered alive in the Sandusky River during spring 2016 were included in the control group. Fish sizes by treatment and sex are listed in Table 1.

Fish in the cDC and pDC groups did not differ significantly in age at the time of tagging (2018; $P = 0.858$; Figure 2). However, control fish age estimates were significantly higher than those for fish in the cDC and pDC groups, both during the observation period (2016; $P < 0.0001$ [cDC and pDC]) and at the time of tagging (2014/2015; $P = 0.001$ [cDC] and $P = 0.0001$ [pDC]).

Egress times and 2019 migration checkpoints.—Downstream egress time was quantified as the number of days taken to reach certain "checkpoints" (or acoustic receiver stations) in the typical postspawn migration route (Figure 1B). We calculated the number of days postrelease for individuals to reach the following checkpoints along their postspawn migration route: the last detection within the lower Sandusky River, the first detection within Sandusky Bay, the last detection within Sandusky Bay, and the first detection within broader Lake Erie. In addition, checkpoints for the spring migration in the following year (2019) were also quantified to evaluate the possibility of long-term effects of the electro-immobilization treatments. This consisted of identifying each fish's last detection within Lake Erie, the first detection back in Sandusky Bay, the last detection within Sandusky Bay, and the first detection back in the lower Sandusky River. No values were assigned for 2019 checkpoints if the fish had previously died, and the number of days taken to enter and leave broader Lake Erie was likewise unquantifiable for a small number of fish that remained in Sandusky Bay until the 2019 spawning period.

Statistical analyses.—Analyses of all telemetry data were performed in RStudio version 1.2.5033 (RStudio Team 2020) with R version 3.6.2 (R Core Team 2019). Preliminary cleaning of the detection data was conducted using the package "glatos" version 0.3.1 (Holbrook et al. 2019). False detections were filtered out from the data by identifying and removing all detections that occurred at least 3,600 s (the mean nominal delay of each tag

TABLE 1. Walleye size distributions at the time of tagging for continuous-DC (cDC) and pulsed-DC (pDC) treatments (2018) and the control group (2014/2015), including sex-specific values.

Treatment	Initial n	Mean TL ± SE (mm)
cDC	44 (22 female; 22 male)	518 ± 7 (F: 538 ± 10; M: 499 ± 9)
pDC	48 (28 female; 20 male)	509 ± 6 (F: 519 ± 8; M: 495 ± 8)
Control	31 (24 female; 7 male)	578 ± 11 (F: 595 ± 12; M: 519 ± 12)

[120 s] × 30 signal transmission intervals) away from (before or after) any other detections of the same tag on the same receiver (Pincock 2012). This was conducted using the false_detections() function and resulted in the removal of 12,078 detections (0.37%) from a total of 3,272,026 detections within the data set containing the cDC and pDC fish detections. For the entire data set containing cDC and pDC detections and those from the control group fish, 31,503 detections (0.41%) were removed from a total of 7,613,229 detections.

Survival of cDC, pDC, and control group fish was analyzed by estimating Kaplan–Meier curves using the survfit() function from the "survival" package (Therneau 2021), with treatment included as the sole predictor variable. Due to sample imbalances and instances of perfect multicollinearity, sex was not included as a predictor variable. Treatment effects were analyzed using the survdiff() function from "survival," and survival curves were plotted using ggsurvplot() from the "survminer" package (Kassambara et al. 2021). Based on the plotted survival curves, logistic regressions were performed on survival at 20, 50, 100, 200, and 365 d postrelease for each treatment by using the base glm() function with a binomial error distribution and analyzed with the Anova() function from the "car" package (Fox and Weisberg 2019) and the emmeans() function from the "emmeans" package (Lenth 2020) for post hoc comparisons of differences in survival between treatments at specific time periods.

The times taken to reach each migration checkpoint (leave the Sandusky River, arrive in Sandusky Bay, arrive in Lake Erie, return to Sandusky Bay, and return to the Sandusky River) were fitted with generalized linear mixed models with a Poisson error distribution. Model selection using Akaike's information criterion corrected for small sample size (AIC_c) was performed with the dredge() function from the "MuMIn" package (Barton 2019) on a global model containing treatment, migration checkpoint, sex (plus the two- and three-way interactions of these three terms), and fish length as fixed effects and individual fish identity as a random effect. However, no model averaging was performed since only one model had an AIC_c difference (ΔAIC_c) of 2 or less (Table 2). This model was analyzed using the Anova()

function, and a likelihood ratio (LR) χ^2 test was used to evaluate the influence of random effects. A full list of models with AIC_c selection statistics is provided in Supplement 1 (available in the online version of this article). Post hoc analyses, asymptotic 95% confidence interval generation, and plotting for migration models and data were conducted using estimated marginal means via the emmeans() and emmip() functions from the "emmeans" package.

RESULTS

Postrelease Survival

Overall, the postrelease survival of control fish and Walleye that were immobilized with pDC and cDC (Figure 3) was significantly different (log rank $\chi^2 = 7.03$, df = 2, $P = 0.030$). Focusing on specific time points of interest (20, 50, 100, 200, and 365 d postrelease) also revealed significant differences in survival among treatment groups corresponding with visible trends in particular time windows (Figure 3). Survival was over 90% for control fish for the first ~130 d and decreased to roughly 75% for the remainder of the year (Figure 3). Within 50 d postrelease, survival rates for pDC and cDC fish declined rapidly before stabilizing for the remainder of the year (Figure 3). Survival was significantly different among treatments at 50 d (LR [likelihood ratio] $\chi^2 = 8.87$, df = 2, $P = 0.012$), 100 d (LR $\chi^2 = 15.99$, df = 2, $P < 0.001$), 200 d (LR $\chi^2 = 8.99$, df = 2, $P = 0.011$), and 365 d (LR $\chi^2 = 8.34$, df = 2, $P = 0.015$) postrelease but not at 20 d postrelease (LR $\chi^2 = 3.42$, df = 2, $P = 0.181$). At none of these times were the survival rates of cDC and pDC fish significantly different from one another (all $P \geq 0.192$). Rather, significantly lower survival rates were observed in the cDC treatment relative to the control group at 50 d ($P = 0.025$), 100 d ($P = 0.002$), 200 d ($P = 0.016$), and 365 d ($P = 0.020$) postrelease. Differences in survival between the pDC treatment and the control group were lesser and not statistically significant ($0.055 < P < 0.086$ at 50, 100, 200, and 365 d), yet the trend in survival for the pDC group remained more similar to that of the cDC group than to that of the control (Figure 3).

TABLE 2. Summary of model selection outputs for Walleye migration data analyses, showing models with Akaike weights (Akaike's information criterion corrected for small sample size [AIC_c]) greater than approximately zero. Full outputs are available in Table S1. The fixed effects included in each model are listed; all models included fish identity as a random effect. An asterisk denotes the inclusion of individual terms plus all two- and three-way interaction terms. Degrees of freedom, log likelihood (log[L]), AIC_c, AIC_c difference (ΔAIC_c), and Akaike weights are provided.

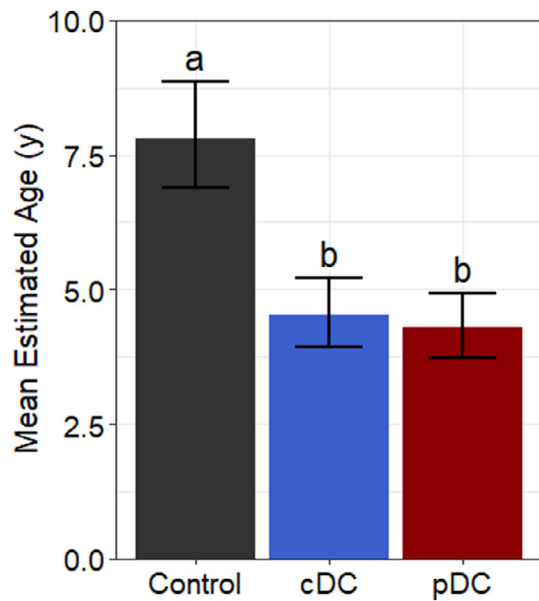| Model	Fixed effects	df	log(L)	AIC_c	ΔAIC_c	Akaike weight
M1	Checkpoint*Treatment*Sex, Length	22	−1,734.6	3,517.61	0.00	0.742
M2	Checkpoint*Treatment*Sex	21	−1,736.84	3,519.73	2.12	0.258
Other models				≥3,706.15	≥188.54	≤0.001

FIGURE 2. Mean estimated ages (years) for Walleye in each group during 2018, based on year- and sex-specific age–length keys (following methods described by Isermann and Knight [2005] and implemented in the FSA package [Ogle et al. 2021]). For fish in the continuous-DC (cDC) and pulsed-DC (pDC) treatments, values are estimated ages at the time of tagging (2018); for control fish, values are estimated ages at the time of tagging plus 1 or 2 years (for fish tagged in 2015 and 2014, respectively) for approximate age during the observation period in 2016. Lowercase letters denote significant differences between groups ($P < 0.0001$).
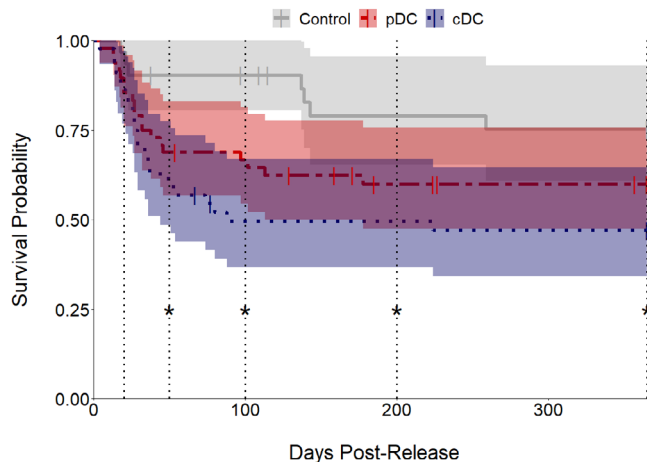

FIGURE 3. Kaplan–Meier survival curves for Walleye in the control group (solid line; 2016), pulsed-DC (pDC) group (dashed line; 2018), and continuous-DC (cDC) group (dotted line; 2018) after release. Vertical bars on each curve denote censoring, and 95% confidence intervals are shown as shaded areas surrounding each curve. Vertical dotted lines indicate points in time selected for logistic regression analyses (20, 50, 100, 200, and 365 d postrelease), with an asterisk placed on lines where significant differences ($P < 0.05$) were observed between treatments in logistic regression.

Downstream Movement and Movement during the Following Spawning Season

Significant one-way interactions existed among treatment, migration checkpoint, and sex ($P < 0.0001$; Table 3; Figure 4). Females in both treatments did not differ in the average time needed to leave the Sandusky River (pDC: 20.5 d; cDC: 20.7 d; $P = 0.942$) or to enter Sandusky Bay (pDC: 42.0 d; cDC: 42.8 d; $P = 0.867$). Females in the cDC treatment took longer than those in the pDC treatment to be detected outside of Sandusky Bay (pDC: 128.2 d; cDC: 161.1 d; $P = 0.020$); however, both treatments returned at around the same time to Sandusky Bay (pDC: 253.2 d; cDC: 239.3 d; $P = 0.557$) and the Sandusky River in 2019 (pDC: 325.2 d; cDC: 315.0 d; $P = 0.733$). Males tended to exhibit more pronounced differences between treatments in the time taken to reach later migration checkpoints. No significant differences were observed between the mean number of days at which males in either treatment left the Sandusky River (pDC: 28.5 d; cDC: 24.2 d; $P = 0.169$) or entered Sandusky Bay (pDC: 41.5 d; cDC: 35.6 d; $P = 0.179$). However, males in the cDC treatment typically migrated elsewhere in Lake Erie sooner than those in the pDC treatment (pDC: 99.3 d; cDC: 68.3 d; $P = 0.002$) and took longer to re-enter both Sandusky Bay (pDC: 253.4 d; cDC: 346.1 d; $P = 0.005$) and the Sandusky River (pDC: 265.2 d; cDC: 374.6 d; $P = 0.002$) in 2019. Return times in 2019 were more consistent between females of each treatment ($P > 0.55$), except that female fish in the cDC treatment took longer on average to be detected outside of Sandusky Bay than those in the pDC treatment ($P = 0.020$; Figure 4).

DISCUSSION

Contrary to our hypothesis, postrelease survival did not differ between fish that were immobilized with cDC and those immobilized with pDC; however, relative to the control group, the lower survival rates observed for the cDC and pDC treatments, particularly over the first approximately 100 d (which did not occur nearly as drastically in the control group), indicate that a combination of capture, short-term captivity, electro-immobilization, and surgery decreased initial survivorship. During the first 7 d postrelease, overall survival was high (>96%), which was similar to the results of Vandergoot et al. (2011), who reported 100% survival of Walleye immobilized with pDC and cDC over a 5-d recovery period in captivity (i.e., discounting one individual that died during exposure to the electric current), although those fish did not undergo any surgical procedures. In many species, survival rates after electro-immobilization have most often been quantified over a 24-h period and are typically about 100% (e.g., Kim et al. 2017). A few laboratory investigations of survival rates over 2–3 weeks have observed 100% survival rates in some

TABLE 3. Results from analyses of the generalized linear mixed model used for Walleye migration behavior as shown in Table 2. For fixed effects, the coefficient for length (the only linear covariate) is shown, as are Wald's χ^2, df, and P-values. For random effects (fish identity), the variance is provided along with log likelihood (log[L]), likelihood ratio (LR) χ^2, df, and P-value from comparison with a generalized linear model (GLM) with the same fixed effects.

Model	Fixed or random effect	Coefficient (linear)	χ^2	Random effects variance	log(L)	LR χ^2	df	P
			Fixed effects					
M1	Treatment		0.13				1	0.716
	Checkpoint		3,655.22				4	<0.0001
	Sex		0.45				1	0.505
	Length	−1.781	4.65				1	0.031
	Treatment × Checkpoint		41.23				4	<0.0001
	Treatment × Sex		0.09				1	0.770
	Checkpoint × Sex		429.58				4	<0.0001
	Treatment × Checkpoint × Sex		195.81				4	<0.0001
			Random effects					
M1				0.072	−1,734.6			
Versus GLM					−2,109.0	748.76	1	<0.0001

fishes, such as the Striped Bass *Morone saxatilis* (Jennings and Looney 1998) and Lake Trout *Salvelinus namaycush* (Faust et al. 2017). A similar approach to the pDC method used in this study was used to immobilize Lake Whitefish *Coregonus clupeaformis* and Lake Trout in Lake Erie; 1-year postrelease survival was high (>82%) for both species (C.S.V., unpublished data). Any negative impacts on survival that could be attributed to treatment would seem most likely to manifest later within the first 50 d after electro-immobilization, when the sharpest decrease in survival was observed. However, we cannot fully separate the relative contributions of electro-immobilization treatments, handling stress, energy expenditure from spawning activities, and infection or disease at the surgery site to the gradual decrease in survival beyond this timeframe. Hayden et al. (2014) reported that about 64% of Walleye (i.e., immobilized with pDC, tagged, and released using a similar protocol) returned to the same spawning grounds the following year, although it is unknown exactly how many of the remaining 36% had actually died because of tagging rather than other factors or had simply not returned for other reasons (e.g., skipped spawning).

There are inherent challenges with using a control group in the manner we did here. Notably, even at the time of tagging, the mean size and age of fish in the control group were greater than those of fish in the cDC and pDC treatments. Natural mortality tends to decrease with size and age (i.e., larger and older fish may be more likely to survive a given year than smaller and younger fish;

Hansen et al. 2011; Vandergoot and Brenden 2014). For instance, Vandergoot and Brenden (2014) reported mean annual survival estimates of approximately 60–70% for age-4 and younger Walleye and about 73–87% for age-5 and older Walleye in Lake Erie, while in a data set spanning 1980–2015, estimated survival of age-2 and older Walleye varied between approximately 56% and 70% (Lake Erie Walleye Task Group 2015). Control fish were older at their times of tagging than the cDC and pDC fish tagged in 2018. Because we quantified survival in control fish 1–2 years after tagging (i.e., fish were tagged in 2014 and 2015), the fish in that group were therefore even larger and older on average than the cDC and pDC fish tagged in 2018, which might also have contributed to elevated survival rates in the control group. Indeed, 29 control fish (~93.5%) were age 5 or older during the 2016 observation period, while only 6 pDC fish (12.5%) and 7 cDC fish (~16%) were age 5 or older in 2018. Since the survival data for our control group had to be collected from a different year, we were likewise unable to account for variation in seasonal or year-to-year stressors, such as temperature, extreme weather events (e.g., river discharge), or fishing pressure, which may have influenced our treatment groups and the control group in different ways. Similar to other iteroparous species, Walleye have metabolic and bioenergetic adaptations that promote postspawn survival (McBride et al. 2015) but that are absent in semelparous migratory species (e.g., Sea Lamprey *Petromyzon marinus* and Pacific salmon *Oncorhynchus* spp.); however,
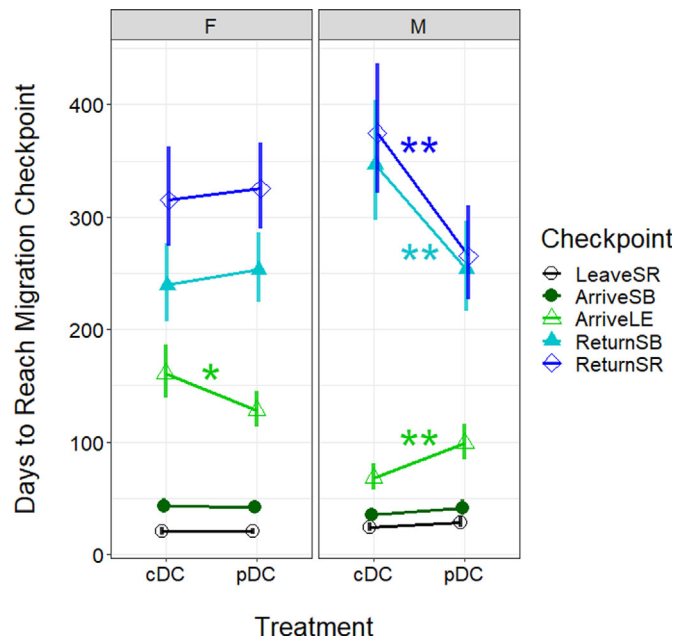
FIGURE 4. Estimated marginal mean numbers of days required for Walleye to reach each migration checkpoint following release, divided by sex and treatment, with asymptotic 95% confidence intervals. Treatments included weak continuous DC (cDC) provided by a transcutaneous electrical nerve stimulation unit and pulsed DC (pDC) provided by a Smith-Root Portable Electrosedation System unit. The checkpoints for each fish refer to the last detection within the Sandusky River in 2018 (LeaveSR), the first detection within Sandusky Bay (ArriveSB), the first detection elsewhere in Lake Erie (ArriveLE), the first detection in Sandusky Bay leading up to the spawning migration in the following year (ReturnSB), and the first detection in the Sandusky River during the spring of 2019 (ReturnSR). Significant differences are highlighted with asterisks ($*P < 0.05$; $**P < 0.005$).

we cannot rule out that any handling stressors (including electro-immobilization) may have had more severe effects during the spawning period than at other times of year since energy reserves had been depleted during the winter. The effects of electro-immobilization on immune function in fish remain poorly studied, but there is some evidence of impaired immune function lasting at least 24 h after electro-immobilization in Rainbow Trout *O. mykiss* (Mirzargar et al. 2011) and Common Carp *Cyprinus carpio* (Monsef Rad et al. 2016). Mortalities that occurred by 50 d postrelease might therefore be at least partially attributable to increased susceptibility to infection and disease. Additional research is needed to understand the long-term consequences of electro-immobilization given the uncertainty associated with the control group used here.

Without some form of immobilization, the acoustic transmitters necessary to track fish in the present study are impossible to humanely implant into fish in such a way as to maximize fish welfare. Although our control group provided an estimate for ambient survival after

spring spawning, there are still factors for which we could not account, such as year-to-year variation in environmental influences. In terms of survival, our results suggest that neither of the electro-immobilization methods applied here is more suitable than the other for carrying out intracoelomic tag implantation surgeries or similar procedures on adult Walleye. Likewise, the lack of differences in downstream egress time and other migratory behaviors in the summer and autumn of 2018 (residency in Sandusky Bay versus out-migration to broader Lake Erie, etc.) between cDC- and pDC-immobilized Walleye does not give reason to promote one method of electro-immobilization over the other in this context. However, researchers must consider which method is most appropriate for their study objectives and logistics in the field. For instance, Walleye in the pDC treatment required longer recovery periods than did individuals in the cDC treatment. Generally, fish need only a few seconds at most to regain equilibrium and behavioral control following immobilization with cDC, whereas pDC is associated with recovery times on the order of several minutes (Vandergoot et al. 2011; Prystay et al. 2017; Abrams et al. 2018). If tagging is to occur when the water temperature is low, as was the case here, holding fish for 15–30 min did not appear to lower their survival and either method is suitable. In contrast, if tagging is to occur in late spring or summer months, when water temperature has increased, holding fish for that same amount of time is likely to negatively impact survival (Schramm et al. 2010; Faust et al. 2019). From a practical perspective, longer recovery times may also reduce the number of fish that can be effectively tagged in a given period given the need for postoperative care.

Although our results imply potential effects of both treatment and tagging/release date on certain later migratory movements leading up to the 2019 spawning run, these are more likely attributable to the deteriorating and increasingly uneven sample sizes and variance in these groups over time (particularly males, as only 8 pDC and 7 cDC males returned to the Sandusky River in 2019). While estimated marginal means are much more suitable than arithmetic means for unbalanced designs (Searle and Speed 1980), they (and asymptotic confidence intervals such as those presented here) are still susceptible to issues arising from low sample size. Furthermore, no clear explanation exists as to how capture and handling stress could only begin to elicit differences in migratory behavior many months afterward. Following exposure to an acute stressor, changes in the primary stress response (i.e., corticosteroids) are most notable over a matter of minutes or hours postexposure (e.g., Barton 2002; Sopinka et al. 2016), although this varies with the severity and duration of the stressor (Wendelaar Bonga 1997). It was expected that had there been any biologically relevant effects of treatment or tagging/release date on these responses, they

would have been most apparent in the earliest tracking data, with migratory behavior approximating more natural/unimpacted behavior over time (Wilson et al. 2017). Since the generalized stress response in fish consists of cascading changes in primary, secondary (e.g., osmoregulatory and metabolic changes), and tertiary (e.g., long-term growth and survival) responses to stress, the possibility that migratory behavior is impacted by long-term sublethal effects of stress, such as cell and tissue damage, impaired growth, changes in immune function, and reduced general performance (Pulsford et al. 1994; Olsen et al. 2005; Nardocci et al. 2014; Sopinka et al. 2016), cannot be eliminated. It is possible that the long-term effects from injuries after electro-immobilization (e.g., vertebral fracture) might be associated with delayed migration timing, but this is improbable here because (1) injury rates tend to be higher in electrostunning rather than electroanesthesia due to the necessary production of strong muscle contractions (Reid et al. 2019), yet it was the electroanesthesia (cDC) treatment that generally exhibited delayed migration timing in males; and (2) previous work has found that similar electrostunning methods did not cause any visible injuries in the vertebrae of adult Walleye (Vandergoot et al. 2011) or Lake Trout (Faust et al. 2017). As with the survival analyses, we were unable to quantify the potential contributions of individual components of our experimental protocol (e.g., capture, handling) to the observed trends in migration behavior, as control groups for each of these stressors could not have been implemented in any reasonable manner.

Conclusions and Future Work

The results from this experiment suggest that cDC or pDC methods as described herein may be used on adult Walleye with no expected differences in relative survival of acoustically tagged fish over short-term (i.e., ≤7-d) periods and with no apparent impacts on their movements after spawning. Despite this, the root causes of decreasing survival (primarily >20 d after tagging) relative to unhandled fish in a previous year likely lie within interannual variation and age at time of sampling, as well as the process of capture, handling, tagging, and release, and such causes must be identified. We also observed an unexpected trend reversal in male versus female downstream egress and migration times relative to previous studies, emphasizing the need for more research about the factors contributing to the seasonal migration patterns of Walleye. In addition, similar work evaluating electro-immobilization and/or chemical anesthesia in this species and system may benefit from creative attempts at including different types of control groups to clarify the best means of quantifying ambient short- and long-term survivorship as well as migration behavior following an undisturbed spawning period. Clearly, additional research across a wider range of fish species and that compares electro-immobilization methods to other anesthetic methods is needed.

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REFERENCES

Abecasis, D., A. Steckenreuter, J. Reubens, K. Aarestrup, J. Alós, F. Badalamenti, L. Bajona, P. Boylan, K. Deneudt, L. Greenberg, and N. Brevé. 2018. A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. Animal Biotelemetry [online serial] 6(1):12.

Abrams, A. E. I., A. M. Rous, J. L. Brooks, M. J. Lawrence, J. D. Midwood, S. E. Doka, and S. J. Cooke. 2018. Comparing immobilization, recovery, and stress indicators associated with electric fish handling gloves and a portable electrosedation system. Transactions of the American Fisheries Society 147:390–399.

Balazik, M. T., B. C. Langford, G. C. Garman, M. L. Fine, J. K. Stewart, R. J. Latour, and S. P. McInich. 2013. Comparison of MS-222 and electronarcosis as anesthetics on cortisol levels in juvenile Atlantic Sturgeon. Transactions of the American Fisheries Society 142:1640–1643.

Barton, B. A. 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. Integrative and Comparative Biology 42:517–525.

Barton, K. 2019. MuMIn: multi-model inference. R package version 1.43.15. Available: https://cran.r-project.org/web/packages/MuMIn/index.html. (May 2021).

Bowlby, J. N., and J. A. Hoyle. 2011. Distribution and movement of Bay of Quinte Walleye in relation to temperature, prey availability and dreissenid colonization. Aquatic Ecosystem Health and Management 14:56–65.

Bowzer, J. C., J. T. Trushenski, B. R. Gause, and J. D. Bowker. 2012. Efficacy and physiological responses of Grass Carp to different sedation techniques: II. Effect of pulsed DC electricity voltage and exposure time on sedation and blood chemistry. North American Journal of Aquaculture 74:567–574.

Cahill, C. L., S. C. Anderson, A. J. Paul, L. MacPherson, M. G. Sullivan, B. T. van Poorten, C. J. Walters, and J. R. Post. 2020. A spatial-temporal approach to modeling somatic growth across inland recreational fisheries landscapes. Canadian Journal of Fisheries and Aquatic Sciences 77:1822–1835.

Chiba, H., T. Hattori, H. Yamada, and M. Iwata. 2006. Comparison of the effects of chemical anesthesia and electroanesthesia on plasma cortisol levels in the Japanese Eel Anguilla japonica. Fisheries Science 72:693–695.

Cooke, S. J., S. J. Iverson, M. J. W. Stokesbury, S. G. Hinch, A. T. Fisk, D. L. VanderZwaag, R. Apostle, and F. Whoriskey. 2011. Ocean Tracking Network Canada: a network approach to addressing critical issues in fisheries and resource management with implications for ocean governance. Fisheries 36:583–592.

Crossin, G. T., M. R. Heupel, C. M. Holbrook, N. E. Hussey, S. K. Lowerre-Barbieri, V. M. Nguyen, G. D. Raby, and S. J. Cooke. 2017. Acoustic telemetry and fisheries management. Ecological Applications 27:1031–1049.

Dembkowski, D. J., D. A. Isermann, S. R. Hogler, W. A. Larson, and K. N. Turnquist. 2018. Stock structure, dynamics, demographics, and movements of Walleyes spawning in four tributaries to Green Bay. Journal of Great Lakes Research 44:970–978.

DuFour, M. R., C. May, E. Roseman, C. M. Mayer, S. A. Ludsin, C. S. Vandergoot, J. J. Pritt, M. E. Fraker, J. T. Tyson, J. Miner, and E. A. Marschall. 2015. Portfolio theory as a management tool to guide conservation and restoration of multi-stock fish populations. Ecosphere [online serial] 6(12):article 296.

Durhack, T. C., J. D. Jeffrey, and E. C. Enders. 2020. In search of an anaesthesia alternative for field-based research. Aquaculture 525:735285.

Ellis, R. D., K. E. Flaherty-Walia, A. B. Collins, J. W. Bickford, S. Boucek, S. L. Walters Burnsed, and S. K. Lowerre-Barbieri. 2019. Acoustic telemetry array evolution: from species- and project-specific designs to large-scale, multispecies, cooperative networks. Fisheries Research 209:186–195.

Erikson, U., L. Grimsmo, and H. Digre. 2021. Establishing a method for electrical immobilization of whitefish on board fishing vessels. Journal of Aquatic Food Product Technology 30:694–705.

Faust, M. D., C. S. Vandergoot, T. O. Brenden, R. T. Kraus, T. Hartman, and C. C. Krueger. 2019. Acoustic telemetry as a potential tool for mixed-stock analysis of fishery harvest: a feasibility study using Lake Erie Walleye. Canadian Journal of Fisheries and Aquatic Sciences 76:1019–1030.

Faust, M. D., C. S. Vandergoot, E. T. Hostnik, T. R. Binder, J. L. Mida Hinderer, J. T. Ives, and C. C. Krueger. 2017. Use of electricity to sedate Lake Trout for intracoelomic implantation of electronic transmitters. North American Journal of Fisheries Management 37:768–777.

Finn, J. T., J. W. Brownscombe, C. R. Haak, S. J. Cooke, R. Cormier, T. Gagne, and A. J. Danylchuk. 2014. Applying network methods to acoustic telemetry data: modelling the movements of tropical marine fishes. Ecological Modelling 293:139–149.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression, 3rd edition. Sage Publications, Thousand Oaks, California.

Gao, Y., D. Li, X. Peng, and R. Tang. 2014. Effects of low-voltage constant direct current on plasma biochemical profiles and gene expression levels in Crucian Carp Carassius carassius. Fisheries Science 80:993–1000.

Gause, B. R., J. T. Trushenski, J. C. Bowzer, and J. D. Bowker. 2012. Efficacy and physiological responses of Grass Carp to different sedation techniques: I. Effects of various chemicals on sedation and blood chemistry. North American Journal of Aquaculture 74:560–566.

Gilderhus, P. A. 1990. Benzocaine as a fish anesthetic: efficacy and safety for spawning-phase salmon. Progressive Fish-Culturist 52:189–191.

Guénette, S. A., F. C. Uhland, P. Hélie, F. Beaudry, and P. Vachon. 2007. Pharmacokinetics of eugenol in Rainbow Trout (Oncorhynchus mykiss). Aquaculture 266:262–265.

Hansen, G. J. A., L. A. Winslow, J. S. Read, M. Treml, P. J. Schmalz, and S. R. Carpenter. 2019. Water clarity and temperature effects on Walleye safe harvest: an empirical test of the safe operating space concept. Ecosphere [online serial] 10(5):e02737.

Hansen, M. J., A. H. Fayram, and S. P. Newman. 2011. Natural mortality in relation to age and fishing mortality on Walleyes in Escanaba Lake, Wisconsin, during 1956–2009. North American Journal of Fisheries Management 31:506–514.

Harris, C., T. O. Brenden, C. V. Vandergoot, M. D. Faust, S. J. Herbst, and C. C. Krueger. 2021. Tributary use and large-scale movements of Grass Carp in Lake Erie. Journal of Great Lakes Research 47:48–58.

Hayden, T. A., C. M. Holbrook, D. G. Fielder, C. S. Vandergoot, R. A. Bergstedt, J. M. Dettmers, C. C. Krueger, and S. J. Cooke. 2014. Acoustic telemetry reveals large-scale migration patterns of Walleye in Lake Huron. PLoS (Public Library of Science) One [online serial] 9 (12):e114833.

Hokanson, K. E. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada 34:1524–1550.

Holbrook, C., T. Hayden, T. Binder, J. Pye, and A. Nunes. 2019. glatos: a package for the Great Lakes Acoustic Telemetry Observation System. R package version 0.3.1. Available: https://gitlab.oceantrack.org/GreatLakes/glatos. (October 2019).

Hussey, N. E., S. T. Kessel, K. Aarestrup, S. J. Cooke, P. D. Cowley, A. T. Fisk, R. G. Harcourt, K. N. Holland, S. J. Iverson, J. F. Kocik, J. F. Mills Flemming, and F. G. Whoriskey. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science 348:1255642.

Isermann, D. A., and C. T. Knight. 2005. A computer program for age–length keys incorporating age assignment to individual fish. North American Journal of Fisheries Management 25:1153–1160.

Jenkins, J. A., H. L. Bart Jr., J. D. Bowker, P. R. Bowser, J. R. MacMillan, J. G. Nickum, J. D. Rose, P. W. Sorensen, G. W. Whitledge, J. W. Rachlin, and B. E. Warkentine. 2014. Guidelines for the use of fishes in research. American Fisheries Society, Bethesda, Maryland.

Jennings, C. A., and G. L. Looney. 1998. Evaluation of two types of anesthesia for performing surgery on Striped Bass. North American Journal of Fisheries Management 18:187–190.

Kassambara, A., M. Kosinski, and P. Biecek. 2021. survminer: drawing survival curves using 'ggplot2'. R package version 0.4.9. Available: https://cran.r-project.org/web/packages/survminer/index.html. (May 2021).

Kim, J., B. Doyle, and N. E. Mandrak. 2017. Electrosedation of freshwater fishes for the surgical implantation of transmitters. Canadian Journal of Zoology 95:575–580.

Krueger, C. C., C. M. Holbrook, T. R. Binder, C. S. Vandergoot, T. A. Hayden, D. W. Hondorp, N. Nate, K. Paige, S. C. Riley, A. T. Fisk, and S. J. Cooke. 2018. Acoustic telemetry observation systems: challenges encountered and overcome in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 75:1755–1763.

Kynard, B., and E. Lonsdale. 1975. Experimental study of galvanonarcosis for Rainbow Trout (Salmo gairdneri) immobilization. Journal of the Fisheries Research Board of Canada 32:300–302.

Lake Erie Walleye Task Group. 2015. Report for 2014 by the Lake Erie Walleye Task Group. Great Lakes Fishery Commission, Ann Arbor, Michigan.

Lenth, R. 2020. emmeans: estimated marginal means, aka least-squares means. R package version 1.4.5. Available: https://cran.r-project.org/web/packages/emmeans/index.html. (May 2021).

Matley, J. K., M. D. Faust, G. D. Raby, Y. Zhao, J. Robinson, T. MacDougall, T. A. Hayden, A. T. Fisk, C. S. Vandergoot, and C. C. Krueger. 2020. Seasonal habitat-use differences among Lake Erie's Walleye stocks. Journal of Great Lakes Research 46:609–621.

Mattson, N. S., and T. H. Riple. 1989. Metomidate, a better anesthetic for cod (Gadus morhua) in comparison with benzocaine, MS-222, chlorobutanol, and phenoxyethanol. Aquaculture 83:89–94.

McAuley, R. B., B. D. Bruce, I. S. Keay, S. Mountford, T. Pinnell, and F. G. Whoriskey. 2017. Broad-scale coastal movements of White Sharks off Western Australia described by passive acoustic telemetry data. Marine and Freshwater Research 68:1518–1531.

McBride, R. S., S. Somarakis, G. R. Fitzhugh, A. Albert, N. A. Yaragina, M. J. Wuenschel, A. Alonso-Fernández, and G. Basilone. 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish and Fisheries 16:23–57.

Mirzargar, S. S., M. Soltani, M. Ahmadi, A. Abrishamifar, A. Bahonar, and P. Yousefi. 2011. Anesthetic effect of tricaine methanesulfonate, clove oil and electroanesthesia on lysozyme activity of *Oncorhynchus mykiss*. Iranian Journal of Fisheries Sciences 10:393–402.

Monsef Rad, S. F., S. Y. Paighambari, A. Haji Moradlou, F. Mashayekhi, and R. Qorbani. 2016. Evaluation of electronarcosis and clove oil for short-term anesthesia in Common Carp, *Cyprinus carpio* L. 1758. Caspian Journal of Environmental Sciences 14:299–310.

Nardocci, G., C. Navarro, P. P. Cortés, M. Imarai, M. Montoya, B. Valenzuela, P. Jara, C. Acuña-Castillo, and R. Fernández. 2014. Neuroendocrine mechanisms for immune system regulation during stress in fish. Fish and Shellfish Immunology 40:531–538.

Nguyen, P. L., K. Haman, L. Carstensen, T. McKlveen, P. Cooney, and S. Gibson. 2018. Evaluation of three electrical outputs in an electro-immobilization system to reduce induction time during routine handling of fish at a hatchery. North American Journal of Aquaculture 80:239–248.

Ogle, D. H., P. Wheeler, and A. Dinno. 2021. FSA: Fisheries Stock Analysis. R package version 0.9.0. Available: https://github.com/droglenc/FSA. (May 2021).

Olsen, R. E., K. Sundell, T. M. Mayhew, R. Myklebust, and E. Ringø. 2005. Acute stress alters intestinal function of Rainbow Trout, *Oncorhynchus mykiss* (Walbaum). Aquaculture 250:480–495.

Pincock, D. G. 2012. False detections: what they are and how to remove them from detection data. Vemco, Application Note 902, Halifax, Nova Scotia.

Prystay, T. S., C. K. Elvidge, W. M. Twardek, J. M. Logan, C. H. Reid, S. H. Clarke, J. G. Foster, E. L. L. Cooke, and S. J. Cooke. 2017. Comparison of the behavioral consequences and recovery patterns of Largemouth Bass exposed to MS-222 or electrosedation. Transactions of the American Fisheries Society 146:556–566.

Pulsford, A. L., S. Lemaire-Gony, M. Tomlinson, N. Collingwood, and P. J. Glynn. 1994. Effects of acute stress on the immune system of the Dab, *Limanda limanda*. Comparative Biochemistry and Physiology Part C: Pharmacology, Toxicology and Endocrinology 109:129–139.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raabe, J. K., and M. A. Bozek. 2012. Quantity, structure, and habitat selection of natural spawning reefs by Walleyes in a north temperate lake: a multiscale analysis. Transactions of the American Fisheries Society 141:1097–1108.

Raby, G. D., C. S. Vandergoot, T. A. Hayden, M. D. Faust, R. T. Kraus, J. M. Dettmers, S. J. Cooke, Y. Zhao, A. T. Fisk, and C. C. Krueger. 2018. Does behavioural thermoregulation underlie seasonal movements in Lake Erie Walleye? Canadian Journal of Fisheries and Aquatic Sciences 75:488–496.

Reid, C. H., C. S. Vandergoot, J. D. Midwood, E. D. Stevens, J. Bowker, and S. J. Cooke. 2019. On the electroimmobilization of fishes for research and practice: opportunities, challenges, and research needs. Fisheries 44:576–585.

Robb, D. H., and B. Roth. 2003. Brain activity of Atlantic Salmon (*Salmo salar*) following electrical stunning using various field strengths and pulse durations. Aquaculture 216:363–369.

RStudio Team. 2020. RStudio: integrated development for R. RStudio, Boston.

Schoonyan, A., R. T. Kraus, M. D. Faust, C. S. Vandergoot, S. J. Cooke, H. A. Cook, T. A. Hayden, and C. C. Krueger. 2017. Estimating incision healing rate for surgically implanted acoustic transmitters from recaptured fish. Animal Biotelemetry [online serial] 5(1):15.

Schramm, H. L., B. Vondracek, W. E. French, and P. D. Gerard. 2010. Factors associated with mortality of Walleyes and Saugers caught in live-release tournaments. North American Journal of Fisheries Management 30:238–253.

Searle, S. R., F. M. Speed, and G. A. Milliken. 1980. Population marginal means in the linear model: an alternative to least-squares means. American Statistician 34:216–221.

Sopinka, N. M., M. R. Donaldson, C. M. O'Connor, C. D. Suski, and S. J. Cooke. 2016. Stress indicators in fish. Pages 405–462 *in* C. B. Schreck, L. Tort, A. P. Farrell, and C. J. Brauner, editors. Fish physiology, volume 35. Academic Press, Cambridge, Massachusetts.

Struthers, D. P., L. F. Gutowsky, E. C. Enders, K. E. Smokorowski, D. A. Watkinson, A. T. Silva, M. Cvetkovic, E. Bibeau, and S. J. Cooke. 2017. Factors influencing the spatial ecology of Lake Sturgeon and Walleye within an impounded reach of the Winnipeg River. Environmental Biology of Fishes 100:1085–1103.

Summerfelt, R. C., and L. S. Smith. 1990. Anaesthesia, surgery and related techniques. Pages 213–272 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Therneau, T. 2021. Survival: a package for survival analysis in R. R package version 3.2-11. Available: https://cran.r-project.org/web/packages/survival/index.html. (May 2021).

Topic Popovic, N., I. Strunjak-Perovic, R. Coz-Rakovac, J. Barisic, M. Jadan, A. Persin Berakovic, and R. Sauerborn Klobucar. 2012. Tricaine methane-sulfonate (MS-222) application in fish anaesthesia. Journal of Applied Ichthyology 28:553–564.

Trushenski, J. T., J. D. Bowker, S. J. Cooke, D. Erdahl, T. Bell, J. R. MacMillan, R. P. Yanong, J. E. Hill, M. C. Fabrizio, J. E. Garvey, and S. Sharon. 2013. Issues regarding the use of sedatives in fisheries and the need for immediate-release options. Transactions of the American Fisheries Society 142:156–170.

Trushenski, J. T., J. D. Bowker, B. L. Mulligan, and B. R. Gause. 2012. Induction, recovery, and hematological responses of Largemouth Bass to chemo- and electrosedation. North American Journal of Aquaculture 74:214–223.

Vandergoot, C. S., and T. O. Brenden. 2014. Spatially-varying population demographics and fishery characteristics of Lake Erie Walleye (*Sander vitreus*) inferred from a long-term tag-recovery study. Transactions of the American Fisheries Society 143:188–204.

Vandergoot, C. S., M. D. Faust, J. T. Francis, D. W. Einhouse, R. Drouin, C. Murray, and R. L. Knight. 2019. Back from the brink: sustainable management of the Lake Erie Walleye fishery. Pages 431–466 *in* C. C. Krueger, W. W. Taylor, and S. J. Youn, editors. From catastrophe to recovery: stories of fishery management success. American Fisheries Society, Bethesda, Maryland.

Vandergoot, C. S., K. J. Murchie, S. J. Cooke, J. M. Dettmers, R. A. Bergstedt, and D. G. Fielder. 2011. Evaluation of two forms of electroanesthesia and carbon dioxide for short-term anesthesia in Walleye. North American Journal of Fisheries Management 31:914–922.

Welch, D. W., M. C. Melnychuk, E. R. Rechisky, A. D. Porter, M. C. Jacobs, A. Ladouceur, R. S. McKinley, and G. D. Jackson. 2009. Freshwater and marine migration and survival of endangered Cultus Lake Sockeye Salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. Canadian Journal of Fisheries and Aquatic Sciences 66:736–750.

Wendelaar Bonga, S. E. 1997. The stress response in fish. Physiological Reviews 77:591–625.

Wilson, A. D. M., T. A. Hayden, C. S. Vandergoot, J. M. Dettmers, S. J. Cooke, and C. C. Krueger. 2017. Do intracoelomic telemetry transmitters alter the post-release behaviour of migratory fish? Ecology of Freshwater Fish 26:292–300.

Zydlewski, G. B., W. Gale, J. Holmes, J. Johnson, T. Brigham, and W. Thorson. 2008. Use of electroshock for euthanizing and immobilizing adult spring Chinook Salmon in a hatchery. North American Journal of Aquaculture 70:415–424.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.