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ARTICLE

Recreational Postrelease Mortality of Lake Trout in Lakes Superior and Huron

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Abstract
The effectiveness of fishing regulations that result in the release of some angler-caught fish depends on accurate knowledge of the postrelease mortality of those individuals. In the Laurentian Great Lakes, Lake Trout *Salvelinus namaycush* are a major component of recreational fisheries; across large regions of the lakes, they are managed with length limit and daily quota regulations assuming a 15% postrelease mortality rate. Due to concerns regarding the accuracy of that rate, we conducted a tagging study to estimate Lake Trout postrelease mortality in Lakes Superior and Huron, and we examined environmental and fishing factors that influenced the return rates of tagged fish. The basic study design was to compare tag return rates between two groups: (1) a treatment group comprising fish that were caught and released by anglers; and (2) a control group comprising fish that were caught via trap net and released. Tag return rates for the angler-caught group were evaluated in relation to depth of capture, surface temperature at release (ST), fishing method, anatomical hook site, play time, handling time, and barotrauma. Tag return rates for angler-caught fish declined significantly with increasing ST; the other factors' effects on tag return rates were generally small. For Lake Superior, model-averaged (Akaike's information criterion) postrelease mortality estimates incorporating ST were 15.0% (SE = 5.6%) at STs less than 10°C, 42.6% (SE = 3.0%) at STs of 10–16°C, and 43.3% (SE = 3.6%) at STs greater than 16°C. Model-averaged estimates for Lake Huron were 52.5% (SE = 26.8%) at STs less than 10°C, 45.2% (SE = 14.0%) at STs of 10–16°C, and 76.4% (SE = 5.4%) at STs greater than 16°C. Based on these findings, alternative fishery management regulations that limit recreational catch-and-release angling of Lake Trout in the Great Lakes may be prudent. Current management policies based on an assumed 15% postrelease mortality are likely underestimating the total numbers of Lake Trout that are removed by recreational anglers.

Size and bag limits are widely used in the regulation of fisheries (Paukert et al. 2001, 2007; Isermann and Paukert 2010) and often result in catch-and-release fishing and grading that can lead to a significant number of fish releases. An example in the Great Lakes is for Lake Trout *Salvelinus namaycush*, which are a major component of the recreational fisheries harvest. Great Lakes recreational anglers typically employ downriggers aboard small boats (<10 m) to catch Lake Trout because they inhabit deep water over

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large areas away from shore. A downrigger is an apparatus that clips to the fishing line above the lure and submerses it to deep water via a heavy weight attached to a cable on a reel (Dedual 1996). In the Great Lakes, downriggers are generally fished at depths between 25 and 60 m, with the vessel traveling less than 5 km/h. However, some Great Lakes boat anglers catch Lake Trout by trolling, stationary or drift fishing with a weighted line. There is little information on characteristics of the various fishing methods employed by anglers in the Great Lakes, and each method may have different effects on caught fish. Recreational harvest of Lake Trout in the Great Lakes is managed with length limits (Caroffino 2013) and daily quota regulations that have resulted in catch-and-release angling in some areas (Lockwood et al. 2001; Krueger et al. 2013). In Michigan waters of the upper Great Lakes between 2010 and 2015, total recreational fishery releases were 9,800 fish (7% of catch) in Lake Superior, 16,000 fish (18% of catch) in Lake Huron, and 96,000 fish (42% of catch) in Lake Michigan (T. Kolb, Michigan Department of Natural Resources [MDNR], personal communication). The MDNR angler survey program measures releases of both legal-sized and non-legal-sized Lake Trout, and most releases in Lakes Huron and Michigan during 2010–2015 were related to restrictive length limit regulations, whereas releases in Lake Superior were mostly due to high grading of catch (returning smaller fish when larger fish are caught) because length limits were unrestrictive (MDNR, unpublished data).

Management of Lake Trout is a major focus of Great Lakes natural resources agencies; in many areas, management is supported by routine stock assessments using statistical catch-at-age models that employ fishery harvest and fishery-independent survey data to estimate population abundances, recruitment levels, and mortality rates. These estimates in turn are used to determine annual harvest quotas based on agreed-upon harvest policies (Brenden et al. 2013). A key requirement of statistical catch-at-age analysis is an accurate estimate of total fishery kill, including both actual harvest and the fish that die after release (Quinn and Deriso 1999).

Numerous studies have indicated greater postrelease mortality from catch-and-release fishing practices during high water temperatures (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007). Given that the Lake Trout is a coldwater, deepwater species, a similar linkage between postrelease mortality rate and temperature would be expected. Indeed, studies of inland lake recreational fisheries point to temperature as a major determinant of postrelease mortality rates. For inland ice fisheries, estimates of postrelease mortality in Lake Trout have ranged from 9% to 32% (Dextrase and Ball 1991; Persons and Hirsch 1994). Similarly, in a Colorado reservoir, estimated Lake Trout postrelease mortality was 12% during cold temperatures, whereas it was as high as 87% during the late summer (Lee and Bergersen 1996). In Great Slave Lake, a large oligotrophic lake in northern Canada, 7% postrelease mortality was estimated for Lake Trout during the open-water fishery when the surface water temperature was 9°C or cooler (Falk et al. 1974). Studies have also pointed to hooking location as an important determinant of resulting postrelease mortality rates, with Lake Trout hooked in vital areas (e.g., gills or stomach) having greater mortality rates than fish hooked in the mouth (Dextrase and Ball 1991; Persons and Hirsch 1994).

Loftus et al. (1988) provided the only estimate of Lake Trout postrelease mortality in the Great Lakes. In that study, charter boat operators and sport boat anglers in Lakes Superior, Huron, and Michigan were employed to catch Lake Trout, and captured fish were tethered for up to 48 h to an anchor-buoy rig. The average postrelease mortality rate from the Loftus et al. (1988) study was 14.9% (95% confidence interval = 7.4–25.7%), although higher levels of postrelease mortality were reported for smaller fish and for fish hooked in vital areas. No effect of depth, temperature differential between the surface and capture depth, lure type, or play time was found in that study.

Based on the results of Loftus et al. (1988), a 15% postrelease mortality rate has been assumed in harvest policies and regulations enacted for Lake Trout across large areas of Lakes Superior, Huron, and Michigan (Modeling Subcommittee, Technical Fisheries Committee 2002). Nevertheless, concerns about the accuracy of the 15% estimate have lingered due to perceived limitations in the design of the Loftus et al. (1988) study, including small sample sizes (22 fish in year 1; 45 fish in year 2), the limited depth range from which fish were caught (<50 m), and the short evaluation period (Modeling Subcommittee, Technical Fisheries Committee 2002). Furthermore, barotrauma has been a concern, as most Lake Trout are brought up from deep water and many are observed with overinflated gas bladders (Loftus et al. 1988; Ng et al. 2015).

The objective of our study was to conduct a tagging experiment that allowed us to estimate the postrelease mortality of Lake Trout from the upper Great Lakes and to evaluate how the return rates of tagged fish were affected by factors such as fish length, handling time, play time, surface temperature at the time of release, fishing method, occurrence of barotrauma, and depth of capture. The study was conducted in Lakes Huron and Superior, and we assumed that the results from Lake Huron would be applicable to Lake Michigan because of similarity in limnology (Moll et al. 2013) and angling practices. Although four morphotypes of Lake Trout are extant in Lake Superior (Muir et al. 2014), only the lean morphotype is present in all of the Great Lakes, and it is the form generally targeted by fisheries. All Lake Trout collected in this study belonged to the lean morphotype.

METHODS

Lake Trout tagging.—For our research, postrelease mortality was evaluated by tagging two groups of Lake Trout: treatment fish (i.e., recreationally angled) and control fish (Pollock and Pine 2007). The treatment group comprised

Lake Trout caught by volunteer boat anglers. In Lake Superior, volunteer boat anglers employed four fishing methods: bobbing (BOB), downrigger with no release (DR-NR), downrigger with release (DR-REL), and wire lining (WIRE; Table 1). In Lake Huron, volunteer boat anglers used three methods: surface fishing (SURF), DR-REL, and WIRE/lead-core (LC) fishing. The control group comprised Lake Trout that were caught in Great Lakes trap nets (Westerman 1932: Brown et al. 1999; Brenden et al. 2013). Trap nets were selected for the control group because earlier research indicated minimal trauma and high survival rates after release from this gear type (Johnson et al. 2004b). Tagging was conducted off two recreational fishing ports of Michigan: Marquette on southern Lake Superior and Alpena on western Lake Huron (Figure 1). These two ports were chosen because of their proximity to research facilities, high levels of recreational harvest and effort for Lake Trout, availability of volunteer anglers, availability of commercial trap-net operators, and high tag return rates as indicated by prior studies. Tagging area boundaries were designated based on prior knowledge of Lake Trout movement and home range patterns (Schmalz et al. 2002; Kapuscinski et al. 2005; Adlerstein et al. 2007). Tagging of both treatment and control groups was restricted to each of the two study areas (Figure 1). Lake Trout were tagged throughout the fishing season (April–November) in 2010–2013. The target annual sample size was 600 fish per study group in each lake but was not achieved in some locations and years. Fish were tagged using serialized, lock-on loop tags (Floy FD-4; Floy Tag and Manufacturing, Inc., Seattle). Except for the unique identification numbers, tags were identical. A US$10 reward was offered to encourage tag returns. Tags were returned from the recreational fishery, commercial trap-net fishery, commercial gill-net fishery, and natural resource agency gill-net surveys. Tag returns summarized in this paper were collected through June 15, 2016; data used for postrelease mortality estimation were those collected through the end of 2015.

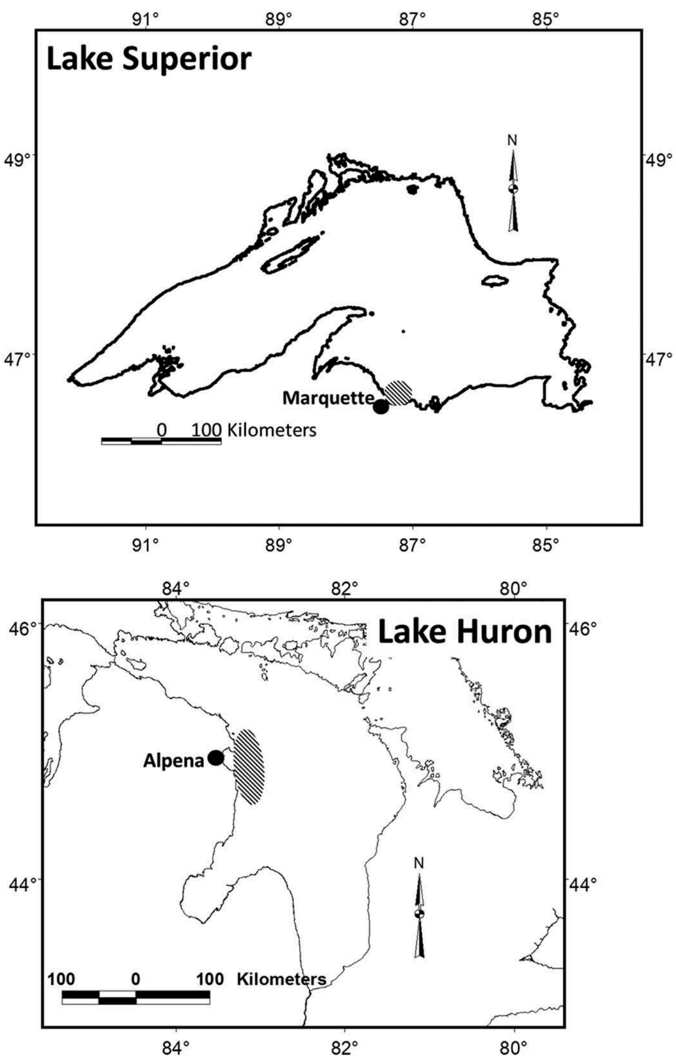


FIGURE 1. Study areas (shaded ellipses) where Lake Trout were tagged to assess postrelease mortality in Lakes Superior and Huron.

Volunteer boat anglers were recruited at both study areas and were trained on tagging technique, assessment of fish condition, and study protocols for the treatment group. Data collection and tagging techniques were developed such that the treatment fish closely represented actual recreational catch-and-release practices. Data collected for treatment group fish included tag serial number, TL (±50 mm), date, location, depth of capture (m), play time, handling time, bloating (gas bladder inflated), presence of gulls *Larus* spp. at the release site, hook location, fishing method, and surface temperature (ST) on the day of tagging. The categorical data collected are described in Table 1. We assessed only the overt symptom of barotrauma by counting fish that were bloated when released and did not document the cryptic symptoms of barotrauma (Wilde 2009). To minimize handling time, digital cameras were used to record much of the data for postprocessing, and electronic chess game timers (Saitek Competition Game Clock, Saitek Industries) were used to record play time and handling time (separately). Each captured fish was placed in a specialized measuring board that restrained the fish and displayed the tag serial number, and a digital photo was taken by the volunteer angler (i.e., the photo recorded the date, tag serial number, and TL). The measuring board comprised a longitudinally sectioned, 152-mm-diameter polyvinyl chloride (PVC) pipe that was painted with alternating black-and-white 50-mm bands so that length group could be measured from the photo. After the fish was tagged and released, a digital photo was also taken of the chess timer, which displayed both the play time and handling time. Hourly ST data were obtained from the online Great Lakes Coastal Forecasting System of the Great Lakes Observing System (2014). Daily mean ST for each tagged and released

TABLE 1. Categorical factors and levels recorded for Lake Trout that were tagged and released by anglers to assess postrelease mortality in Lakes Superior and Huron.

Factor	Levels	Description
Bloating	Yes or no	Barotrauma indicated by overinflated gas bladder
Gulls present	Yes or no	Gulls present in area when tagged fish was released
Hook location	Jaw/mouth	Hook embedded in the jaw or outer mouth region
	Eye	Hook embedded in the eye
	Stomach	Hook embedded in the esophagus to stomach region
	Gills	Hook embedded in the gills or gill rakers
	Throat	Hook embedded in the posterior region of the mouth
	Other	Hook embedded in other parts of the body
Fishing method	Bobbing (BOB)	Stationary or drift fishing with lure attached to handline or fishing pole (Lake Superior only)
	Downrigger with no release (DR-NR)	Lure on leader directly attached to a downrigger cable; vessel trolling
	Downrigger with release (DR-REL)	Lure fished from a fishing pole and attached to a downrigger cable with a release mechanism; vessel trolling
	Wire line/lead core (WIRE/LC)	Lure fished from a fishing pole with a heavy weight and wire line or lead core line; vessel trolling (lead core in Lake Huron only)
	Surface (SURF)	Lure fished from a fishing pole between surface and shallow depths with planer boards or dipsy divers and no weight; vessel trolling (Lake Huron only)

Lake Trout was calculated by averaging hourly STs between 0700 and 1600 hours (typical fishing times).

Great Lakes commercial trap nets fished by local commercial operators were used to collect and tag the control group of Lake Trout in the study areas (Figure 1). Tagging was performed by MDNR personnel. Data recorded for control fish included tag serial number, TL (mm), date, location, and depth of capture (m). Any fish collected in the trap net that was not in healthy condition (e.g., bloated) was not tagged and was omitted from the control group. Handling time for trap-net tagged fish was less than 1 min.

Background handling mortality associated with the tagging process was evaluated using hatchery Lake Trout broodstock from the Marquette State Fish Hatchery (Marquette, Michigan). Hatchery Lake Trout were tagged via the same procedures used for both the angler-caught group and the control group. Evaluations of handling mortality were conducted on three groups of fish. The first group, which comprised 20 hatchery Lake Trout selected to be greater than 500 mm TL, was tagged in a training session for volunteer boat anglers during spring 2010. The second group (n = 60 fish; mean TL = 359 mm; range = 251–436 mm) and third group (n = 60 fish; mean TL = 739 mm; range = 642–841 mm) were tagged by MDNR staff at the hatchery in January 2015. There were no mortalities among group 1 fish at 12 months, and a single mortality (1.7%) was observed in each of groups 2 and 3 at 6 months. Accordingly, we assumed that handling mortality was minimal and equivalent between the angler-caught group and the control group. Across groups 1–3, mean handling time was 52 s (range = 27–114 s).

Statistical analysis of factors influencing tag return rates.—Individual treatment factors or a combination of factors were evaluated by comparing tag return rates for the angler-caught group with handling time, fishing method, play time, depth of capture, and barotrauma. The statistical tests and post hoc comparisons used for these analyses are described in Table 2. Statistical significance was established at α = 0.05. Our preliminary analyses detected no differences in tag return rates according to Lake Trout TL due to low sample sizes for small fish (<450 mm) and large fish (>700 mm). Therefore, we did not incorporate length in our analyses because of the limited length range of tagged fish. Because we were unable to obtain measurements of temperature at the depth of capture (i.e., to estimate the temperature differential experienced by recreationally caught Lake Trout), we compared tag return rates between ST and depth of capture to gain insight into this effect. We assumed that the temperature differential was low for fish caught in shallower depths and would be greater for fish caught in deeper waters when the lakes were not isothermal. We evaluated simple linear relationships of tag return as a function of ST by 20-m capture depth intervals. A significant negative slope for the greater depth intervals would suggest a potential temperature differential effect.

Estimation of postrelease mortality.—Postrelease mortality for the factors identified as potentially important was

TABLE 2. Statistical tests and post hoc comparisons used to compare tag return rates and depth of capture for Lake Trout in Lakes Huron and Superior.

Dependent variable	Factor (effect)	Levels	Statistical/post hoc test used
Tag return rate	Barotrauma	2	*Z*-test for two proportions (Zar 1999)
	Barotrauma, gulls present	2	2 × 2 contingency table (Burnham et al. 1987)
	Fishing method	4	Marascuilo procedure for multiple proportions (Marascuilo 1966)
	Depth of capture	5	Marascuilo procedure for multiple proportions
	Play time	6	Marascuilo procedure for multiple proportions
	Handling time	3	Marascuilo procedure for multiple proportions
	Hook location	2	*Z*-test for two proportions
Depth of capture	Fishing method	4	Kruskal–Wallis test, Nemenyi post hoc test with chi-square approximation (Pairwise Multiple Comparison of Mean Ranks [PMCMR] package, R version 3.2.4; R Core Team 2016)
Tag return rate	Year, treatment group	Year (4), group (2)	ANCOVA with surface temperature at release as a covariate (R version 3.2.4; R Core Team 2016)

estimated by fitting a multigroup Brownie model (Brownie et al. 1985) to the tag returns of treatment and control fish. More specifically, we used the Hoenig et al. (1998) instantaneous formulation of a Brownie model, as this parameterization was necessary to account for different survival rates among treatment and control fish as a consequence of when tagging was completed during tagging years and the size differences between treatment and control fish. Models were fitted separately for Lakes Huron and Superior. For Lake Superior, two separate Brownie models were fitted to different length-groups of fish (see below).

Following Hoenig et al. (1998), the probability that a tag from the treatment group of Lake Trout would be returned was specified as

$$p_{i,r} = \begin{cases} \frac{(1.0-\theta)\, s_i q_{i,r} E_{i,r}}{\sum_i s_i q_{i,r} E_{i,r} + \Delta_r M_r}\left[1.0 - \exp\left(-\sum_i s_i q_{i,y} E_{i,r} - \Delta_r M_r\right)\right] & \text{for } r = y \\ \frac{(1.0-\theta)\, s_i q_{i,r} E_{i,r}}{\sum_i s_i q_{i,r} E_{i,r} + M_r}\left[1.0 - \exp\left(-\sum_i s_i q_{i,r} E_{i,r} - M_r\right)\right] \times & \\ \prod_{h=y+1}^{r-1} \exp\left(\sum_i s_i q_{i,h} E_{i,h} + M_h\right) \exp\left(\sum_i s_i q_{i,y} E_{i,y} + \Delta_y M_y\right) & \text{for } r > y \end{cases},$$

where y = year of tagging; i = sampling gear in which a returned fish was caught; r = tag return year; θ = postrelease mortality rate; s_i = selectivity of the ith fishing gear for treatment fish relative to control fish; $q_{i,r}$ = catchability coefficient for the ith fishing gear in the rth return year; $E_{i,r}$ = amount of effort of the ith fishing gear in the rth return year; M_r = instantaneous natural mortality in the rth return year; and Δ_r = length of a period (expressed as a fraction of the year) of the rth return year during which tagged fish were at large in the system. The Δ_r when the return year equaled the year of tagging was necessary because tagging operations frequently were not completed until sometime during the summer, meaning that the amount of natural mortality experienced by recently tagged fish in that year differed from the natural mortality experienced by previously tagged fish. Similarly, the amount of fishing effort that was specified when the return year equaled the year of tagging was different than for other years to account for the fact that tagging operations were not completed until the summer. The effort measures were angler-hours for the recreational fishery, meters of gill net for the commercial fishery and agency surveys, and number of lifts for commercial trap nets.

In Lake Superior, trap nets tended to catch larger Lake Trout than the volunteer boat anglers. Therefore, we assumed a relative selectivity of 1.25 for the treatment group relative to the control group for returns from recreational angling. Conversely, we assumed a relative selectivity of 0.67 for the treatment group relative to the control group for returns from trap-net gear. For all other fishing gear, equal selectivity was assumed for treatment and control groups. Because there was uncertainty with regard to the selectivities assumed for recreational angling and trap-net gear, we fitted a separate Brownie model to return data for fish that were between 550 and 700 mm TL at tagging—the length range of greatest overlap between the treatment and control groups—to determine the sensitivity of postrelease mortality estimates to differences in gear selectivity. When fitting the Brownie model to fish between 550 and 700 mm TL at the time of tagging, we assumed that selectivity was equal between the sampling gears for fish in the treatment and control groups. For tag returns from Lake Huron, equal selectivity was assumed for all sampling gears because the sizes of Lake

Trout caught by recreational angling and trap nets were similar.

The probability that a tag from a Lake Trout belonging to the control group would be returned was specified using the same equation as used for the treatment group except that (1) postrelease mortality was not included in the equation and (2) the selectivity was set equal to 1.0 for all fishing gears. An additional difference for the control group of fish (in both lakes) was that the return probability was multiplied by 0.984 to account for postrelease mortality based on the results of Johnson et al. (2004a). Reporting rates, handling mortality, and tag retention rates were assumed to be the same for the treatment and control groups. These rates were not factored into the return probabilities, which would lead to biased estimates of natural mortality and catchability from the tagging models but would not influence the estimate of postrelease mortality under the assumption that these rates were the same for the treatment and control groups.

We implemented the tag return models in AD Model Builder (Fournier et al. 2012). Tag returns from both treatment and control groups were modeled through a multinomial likelihood. Gear catchability and natural mortality rates were estimated on a logarithmic scale to constrain the estimates to positive values. Postrelease mortality rates were estimated through inverse logit functions, which constrained rates between 0.0 and 1.0 while allowing the estimated parameter to occur on the real number line. Diffuse upper and lower bounds were specified for all parameters to prevent the optimization algorithm from flat parts of the objective function surface. Models were considered to have converged on a solution when the maximum gradient of the parameters with respect to the objective function was less than 1.0×10^{-4}.

We used an information-theoretic approach for evaluating candidate models, which consisted of different combinations wherein postrelease mortality, catchability, and natural mortality varied among the different levels for the factors identified as being important. Evaluated candidate models also included the potential for natural mortality rates from 2010 to 2013 to vary annually (natural mortality rates in 2014 and 2015 were assumed equal to the rate from 2013) and for catchability in the year of tagging to be different from catchability values in other years to account for potential

TABLE 3. Number of Lake Trout tagged, number of tagged fish that were returned, and the tag return rate for the treatment group (caught and released by volunteer recreational anglers) and control group (captured by trap-netting and then released) in each tagging year and return year. Fish in Lake Superior were tagged near the port of Marquette, Michigan, with returns obtained from throughout the lake; fish in Lake Huron were tagged near the port of Alpena, Michigan, and returns were from throughout the lake. Results are based on tag returns recorded through June 15, 2016.

			Return year								
Group	Tagging year	Number tagged	2010	2011	2012	2013	2014	2015	2016	Number returned	Return rate
					Lake Superior						
Treatment	2010	535	32	76	32	27	13	8		188	0.351
	2011	595		50	76	61	32	9	2	230	0.387
	2012	590			52	67	55	24	7	205	0.347
	2013	609				29	64	35	11	139	0.228
	Total	2,329								762	0.327
Control	2010	601	90	100	66	36	11	7		310	0.516
	2011	38		7	6	5		1		19	0.500
	2012	576			110	129	51	28	1	319	0.554
	2013	603				171	99	60	3	333	0.552
	Total	1,818								981	0.540
					Lake Huron						
Treatment	2010	249	8	4	3	1	2			18	0.072
	2011	124		1	2	3	5			11	0.089
	2012	326			6	7	2	2		17	0.052
	2013	235				1	2	1	1	5	0.021
	Total	934								51	0.055
Control	2010	585	60	36	25	6	5	4		136	0.232
	2011	459		40	37	8	4			89	0.194
	2012	310			26	20	7	4		57	0.184
	2013	317				16	6	1	1	24	0.076
	Total	1,671								306	0.183

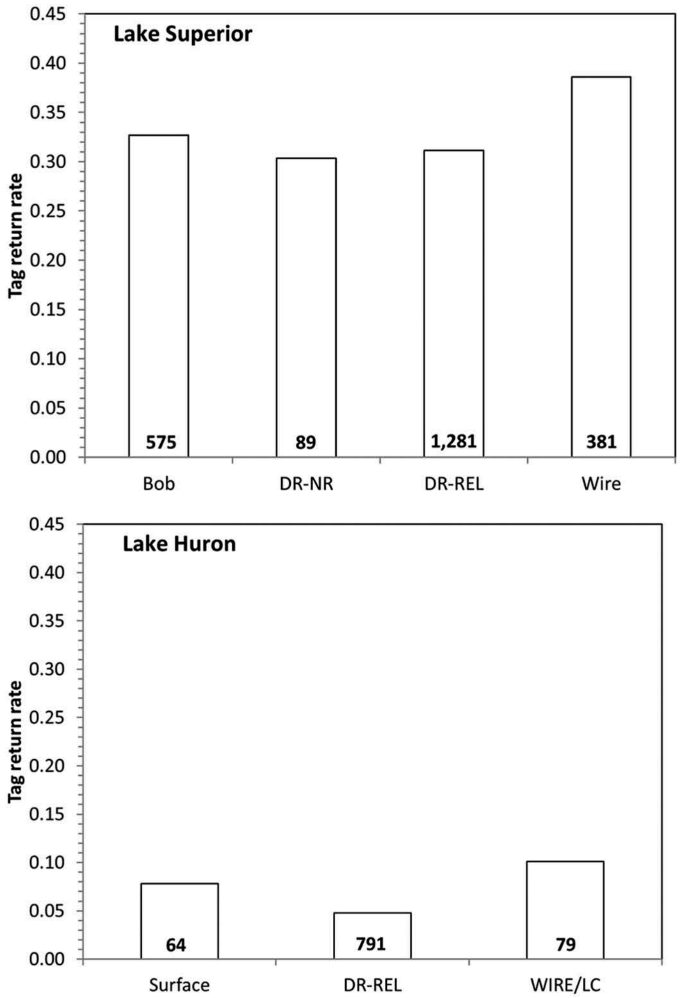


FIGURE 2. Tag return rates by fishing method (defined in Table 1) for Lake Trout tagged by volunteer recreational anglers in Lakes Superior and Huron (bold value within each column = number of tagged individuals from each fishing method). None of the return rates was statistically different within each lake (Marascuilo procedure: $P < 0.05$; Appendix Tables A.3, A.4).

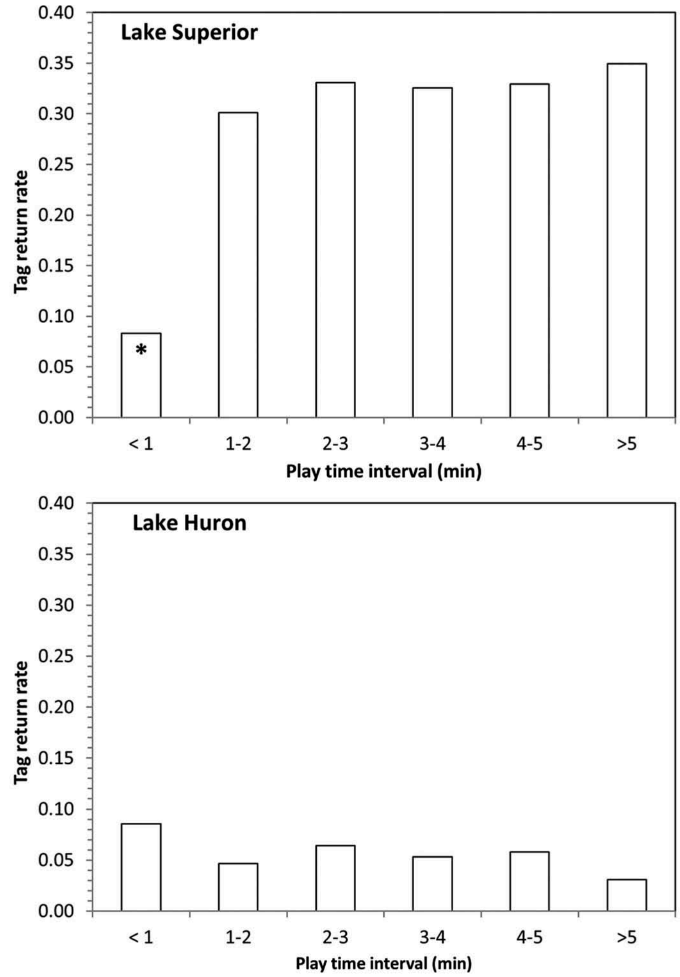


FIGURE 3. Tag return rate as a function of play time interval for Lake Trout that were caught and tagged by volunteer recreational anglers in Lakes Superior and Huron (asterisk = statistically different [$P < 0.05$] tag return rate relative to other play time intervals based on the Marascuilo procedure).

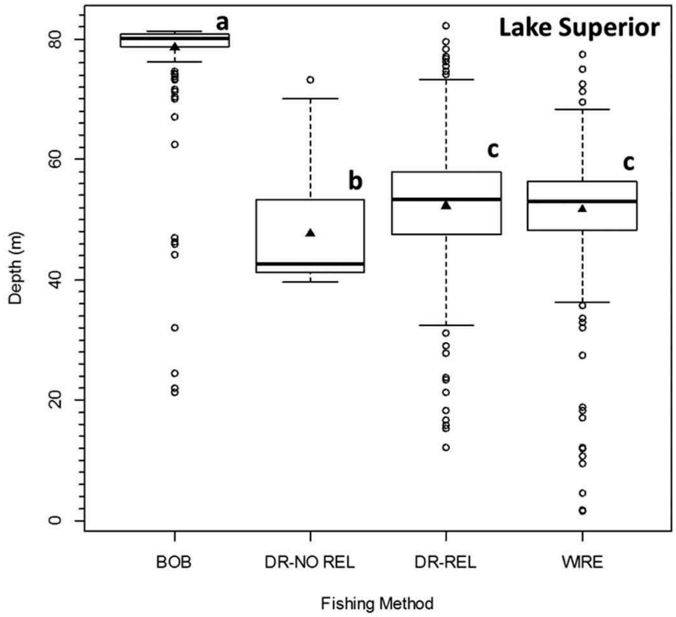
nonmixing of tagged fish with at-large populations. Candidate models were evaluated by using Akaike's information criterion (AIC; Burnham and Anderson 2002). For each data set, there was more than one model with AIC difference (ΔAIC) values less than 10. To account for model selection uncertainty, model-averaged postrelease mortality estimates and their SEs were calculated from equations given by Burnham and Anderson (2002) based on estimates and AIC weights for all models with ΔAIC values less than 10.

Based on analysis of key factors influencing tag return rates, grouped tag return models were fitted, incorporating ST at the time of release as an evaluated factor (see below). We divided ST into three levels (<10, 10–16, and >16°C) based on results from archival thermal tag studies (Bergstedt et al. 2003, 2016; Mattes 2004; R. Goetz, National Oceanic and Atmospheric Administration [NOAA], Seattle, Washington, personal communication). Candidate models allowed for postrelease mortality, catchability (potentially time varying), and natural mortality (potentially time varying) to be (1) unique for each ST level, (2) unique for the <10°C ST level but shared between the 10–16°C and >16°C ST levels, or (3) shared across all ST levels. In total, 108 models consisting of different combinations of parameters were fitted to the tag return data for each lake.

RESULTS

Mark–Recapture of Lake Trout

Between 2010 and 2013, 2,329 Lake Trout in the treatment (angler-caught) group and 1,818 in the control group were tagged in Lake Superior. In Lake Huron, 934 Lake



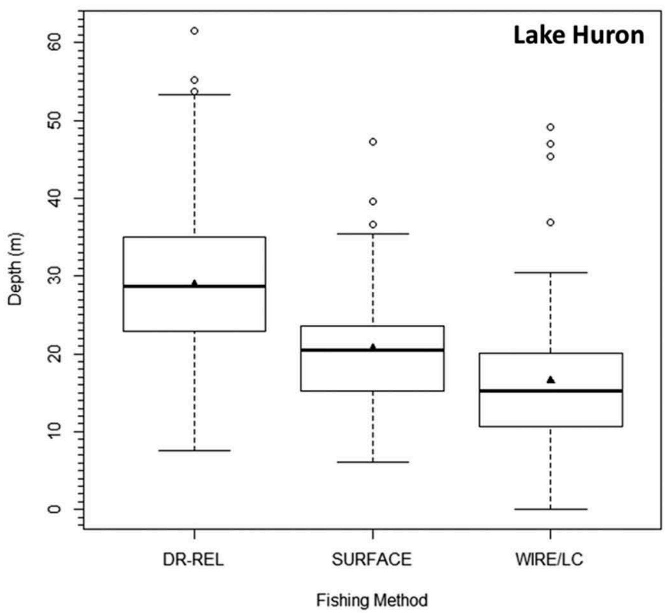


FIGURE 4. Box plots of capture depth for Lake Trout that were tagged by volunteer recreational anglers in Lakes Superior and Huron compared among different fishing methods (defined in Table 1). The horizontal line in each box indicates the median, the box dimensions represent the interquartile range (25th to 75th percentiles), the whiskers represent the highest and lowest values within 1.5× the interquartile range, and the open circles are outliers. Mean depth is indicated by solid triangles. Different letters indicate a statistical difference (P < 0.05) between fishing methods based on a Kruskal–Wallis test followed by multiple comparisons using a Nemenyi post hoc test.

Trout in the treatment group and 1,671 fish in the control group were tagged (Table 3). In Lake Superior, there were 10 volunteer boat anglers in 2010 and four volunteer boat anglers in 2011, 2012, and 2013. In Lake Huron, there were nine volunteer boat anglers during 2010–2012 and seven volunteer boat anglers in 2013. Very few control Lake Trout were tagged during 2011 in Lake Superior because the commercial trap-net operator was unavailable. Overall tag return rates in Lake Superior averaged 54.0% (range = 50–55.2%) for the control group and 32.7% (range = 22.8–38.7%) for the treatment group (Table 3). For Lake Huron, tag return rates averaged 18.3% (range = 7.6–23.2%) for the control group and 5.5% (range = 2.1–8.9%) for the treatment group. Approximately 4% of tags that were returned had unreadable serial numbers due to tag abrasion and were excluded from analyses.

Factors Influencing Tag Return Rates

Angler handling times.—Handling time for the majority (>65%) of Lake Trout tagged by anglers was less than 1.5 min in both Lake Superior and Lake Huron. We compared tag return rates for each fishing method according to five handling time categories (<1.0, 1.0–1.5, 1.5–2.0, 2.0–2.5, and >2.5 min) and found no significant difference in tag return rates for either Lake Superior or Lake Huron (Marascuilo procedure: P > 0.05; Appendix Tables A.1, A.2).

Fishing methods.—For Lake Superior, tag return rates did not differ between fishing methods (Marascuilo procedure: P > 0.05; Appendix Table A.3; Figure 2). Likewise, in Lake Huron, tag returns were not significantly different between fishing methods (Marascuilo procedure: P > 0.05; Appendix Table A.4).

Play time.—In Lake Superior, play time for most fish caught by the BOB, DR-NR, and DR-REL methods was 4 min or less. Play time for the WIRE method was more variable, with more than 50% of fish taking more than 5 min to land. In Lake Huron, play time was no more than 4 min for the majority of fish caught by all fishing methods. We compared tag return rates among six play time intervals (<1, 1–2, 2–3, 3–4, 4–5, and >5 min) and did not detect significant differences in tag return rate among intervals for any of the fishing methods used in Lake Superior (Marascuilo procedure: P > 0.05; Appendix Table A.5; Figure 3) except for fish that were caught in less than 1 min by the DR-REL method, which had a significantly lower tag return rate than all other play time intervals (Table A.5; Figure 3). There were no statistical differences in tag return rates according to play time for any of the fishing methods used in Lake Huron (Marascuilo procedure: P > 0.05; Appendix Table A.6; Figure 3).

Depth of capture.—Overall mean capture depth of tagged Lake Trout belonging to the angler-caught group in Lake Superior was approximately 59 m. Among all angler-caught Lake Superior Lake Trout, the shallowest capture depth was 1.5 m fished by WIRE and the maximum capture depth was 82.3 m fished by DR-REL (Figure 4). In Lake Superior, depth distributions were significantly different between fishing methods (Kruskal–Wallis test: χ^2 = 1,240, df = 3, P < 0.0001). Average capture depth of fish caught by DR-NR

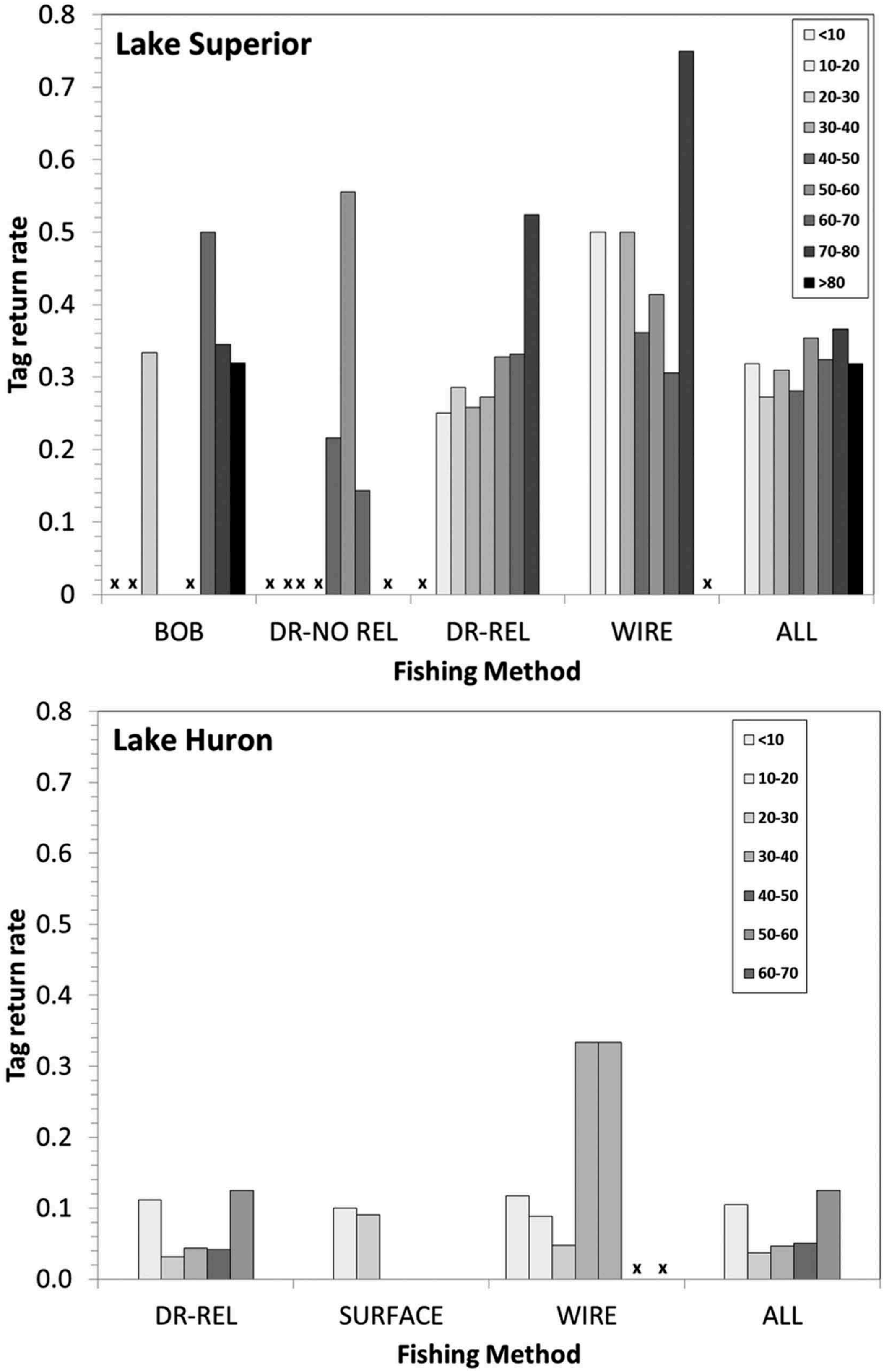


FIGURE 5. Tag return rate by capture depth (m) and fishing method (defined in Table 1) for Lake Trout that were caught and tagged by recreational anglers in Lakes Superior and Huron (X = no data for that depth interval).

TABLE 4. Number of Lake Trout tagged, number of tagged fish that were returned, and the tag return rate by depth of capture for fish that were tagged and released by volunteer recreational anglers in Lakes Superior and Huron. Results are based on tag returns recorded through June 15, 2016.

	Lake Superior			Lake Huron		
Depth (m)	Number tagged	Number returned	Return rate	Number tagged	Number returned	Return rate
<10	4	0	0.000	27	2	0.074
10–20	22	7	0.318	162	17	0.105
20–30	11	3	0.273	375	14	0.037
30–40	42	13	0.310	260	12	0.046
40–50	513	144	0.281	100	5	0.050
50–60	863	305	0.353	8	1	0.125
60–70	265	86	0.325	1	0	0.000
70–80	224	82	0.366			
>80	368	117	0.318			

was 47.6 m, and this was the shallowest fishing method (Nemenyi post hoc comparisons: DR-NR versus BOB, χ^2 = 312.4, P < 0.0001; DR-NR versus DR-REL, χ^2 = 16.8, P = 0.0008; DR-NR versus WIRE, χ^2 = 13.0, P = 0.005; Figure 4). Mean depths for DR-REL (52.3 m) and WIRE (51.7 m) were intermediate among fishing methods and did not statistically differ (Nemenyi post hoc test: χ^2 = 0.28, P = 0.96). The deepest method of fishing was BOB, with an average capture depth of 78.6 m (Nemenyi post hoc test: P < 0.001 for all comparisons). For Lake Superior, there was no significant relationship between tag return rate and depth of capture for any of the fishing methods (Figure 5).

In Lake Huron, depth of capture ranged from less than 1 m (surface) for WIRE to 61.6 m for DR-REL. In Lake Huron, the overall mean depth of Lake Trout captured among all fishing methods was 27.3 m. Mean capture depth for the DR-REL method was 28.8 m and was different than that of both the SURF method (Kruskal–Wallis test: χ^2 = 144, df = 2, P < 0.0001; Nemenyi post hoc test: χ^2 = 46.5, P < 0.001) and the WIRE/LC method (Nemenyi post hoc test: χ^2 = 107.7, P < 0.001; Figure 4). Mean depth of Lake Trout caught by WIRE/LC was 16.6 m, and mean depth of fish caught by SURF was 20.6 m; these values did not differ statistically (Nemenyi post hoc test: χ^2 = 4.18, P = 0.12). There was no significant relationship between tag return rate and depth of capture for any of the fishing methods in Lake Huron (Figure 5). In both Lake Superior and Lake Huron, there were no statistical differences in tag return rate relative to depth of capture for all fishing methods combined (Marascuilo procedure: P > 0.05; Table 4; Appendix Tables A.7, A.8).

Barotrauma.—Bloating of angler-caught Lake Trout was observed in 32.3% of Lake Superior fish and only 5.6% of fish in Lake Huron. Incidence of barotrauma was related to the depth of capture: bloating was significantly more frequent for Lake Trout caught at 50-m or greater depths in Lake Superior (Z-test: Z = −3.15, P = 0.002) and for fish caught at

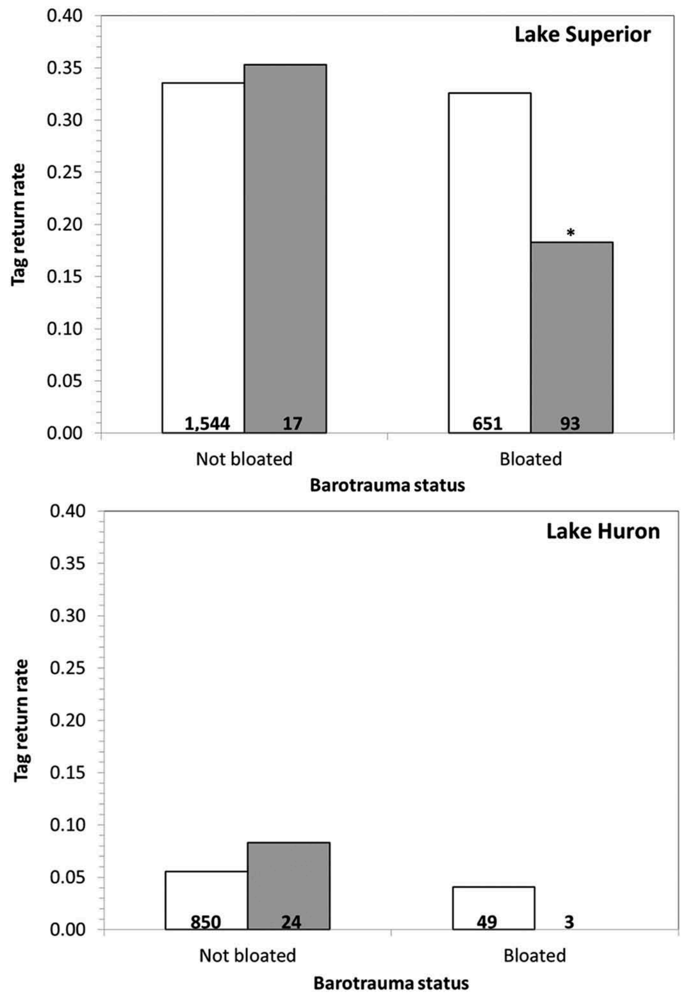


FIGURE 6. Influence of barotrauma (indicated by bloating) and the presence of gulls on the tag return rate for Lake Trout that were tagged by volunteer recreational anglers in Lakes Superior and Huron (bold value within each column = number of tagged individuals). White columns represent return rates for fish that were released without gulls present; gray columns represent return rates for fish that were released in the presence of gulls (asterisk = statistically different tag return rate for gull presence; 2 × 2 contingency table analysis: P < 0.05).

TABLE 5. Number of Lake Trout tagged, number of tagged fish that were returned, and the tag return rate by anatomical hooking location (defined in Table 1) for fish that were tagged and released by volunteer recreational anglers in Lakes Superior and Huron. Results are based on tag returns recorded through June 15, 2016.

	Anatomical hooking location					
Statistic	Eye	Gills	Jaw	Stomach	Throat	Other
			Lake Superior			
Number tagged	43	25	2,180	2	2	59
Number returned	10	3	716	1	1	24
Tag return rate	0.23	0.12	0.33	0.50	0.50	0.41
			Lake Huron			
Number tagged	1	3	923	1	2	3
Number returned	0	0	51	0	0	0
Tag return rate	0.00	0.00	0.06	0.00	0.00	0.00

40-m or greater depths in Lake Huron (Z = −4.83, P < 0.001). Gulls were present at the time of release for 4.8% of Lake Trout in Lake Superior and 2.9% of fish in Lake Huron. Overall tag return rates for bloated fish did not differ from those of non-bloated fish in both Lake Superior (Z-test: Z = 1.33, P = 0.184) and Lake Huron (Z = 0.541, P = 0.59; Figure 6). In Lake Superior, tagged Lake Trout that were bloated and that had gulls present at the time of release exhibited a significantly a lower tag return rate than bloated fish with no gulls present or non-bloated fish (2 × 2 contingency table: $P \leq 0.05$; Figure 6). For Lake Huron, no statistical differences in tag return rates based on barotrauma or gull presence/absence were detected.

Anatomical hook location.—Most of the angler-tagged fish (94.3% in Lake Superior; 98.9% in Lake Huron) were hooked in the jaw or mouth (Table 5). Fish in the "other" category were reported to be hooked on the non-vital parts of the outer body, such as the tail, head, fins, and musculature, and had a tag return rate that was not significantly different than that of fish hooked in the jaw or mouth (Z-test: Z = −1.29, P = 0.197). For all fishing methods combined in Lake Superior, the tag return rate for fish hooked in the eyes or gills (pooled data) was significantly lower than that of fish hooked in the jaw or mouth (Z = 2.43, P = 0.015). In Lake Huron, tag return rates were not significantly different between fish hooked in the jaw or mouth and those hooked in other body locations (Z = 0.799, P = 0.424).

Surface temperature at release.—Lake Trout in Lake Superior were tagged throughout the fishing season during April–November and were released in STs ranging from 3°C to 23°C (Figure 7). In Lake Huron, the fishing season spanned April–October, with an ST range of 7–24°C (Figure 7). Overall, Lake Trout were released in warmer temperatures in Lake Huron than in Lake Superior. For Lake Superior, the full ANCOVA model evaluating tag return rate as a function of ST and that included year and group resulted in no significant interactions of ST × group ($F_{1,\ 54}$ = 1.01, P = 0.32), ST × year ($F_{2,\ 54}$ = 0.23, P = 0.795), group × year ($F_{2,\ 54}$ = 1.18, P = 0.314), or ST × year × group ($F_{2,\ 54}$ = 0.19, P = 0.824). Furthermore, there was no significant year effect ($F_{2,\ 54}$ = 2.79, P = 0.07). In the reduced model, no significant interaction of ST × group was detected ($F_{1,\ 62}$ = 0.79, P = 0.379). For the angler-caught group, tag return rates declined significantly with increasing ST (intercept: t = 9.982, P < 0.001; slope: t = −3.83, P = 0.0003; Figure 8). There was no was significant relationship of tag return as a function of ST for the trap-netted group (intercept: t = 0.56, P = 0.577; slope: t = 0.89, P = 0.379; Figure 8). For Lake Huron, no significant relationship between ST and tag return rate was detected ($F_{1,\ 75}$ = 1.00, P = 0.321; Figure 8).

For Lake Superior, significant negative relationships between tag return rate and ST were found for Lake Trout caught at depths of 40–60 m ($F_{1,\ 18}$ = 5.89, P = 0.026), 60–80 m ($F_{1,\ 18}$ = 30.1, P < 0.0001), and over 80 m ($F_{1,\ 19}$ = 31.6, P < 0.0001; Table A.7; Figure 9). In shallower waters, no significant relationship between tag return rate and ST was detected for Lake Trout caught at depths less than 20 m ($F_{1,\ 6}$ = 2.26, P = 0.183) and 20–40 m ($F_{1,\ 9}$ = 0.21, P = 0.658). Only 3.5% of angler-caught fish were captured at depths less than 40 m in Lake Superior. For Lake Huron, no significant relationship was observed between tag return rate and ST according to depth of capture (<20 m: $F_{1,\ 14}$ = 0.006, P = 0.937; 20–40 m: $F_{1,\ 16}$ = 0.062, P = 0.806; 40–60 m: $F_{1,\ 8}$ = 0.764, P = 0.408; Table A.8).

Estimation of Postrelease Mortality

For Lake Superior, there were 12 models with ΔAIC values less than 10 for both the full data set and the reduced data set (i.e., limited to fish between 550 and 700 mm TL at the time of tagging; Table 6). The models with ΔAIC values less than 10 were the same for both data sets, although there

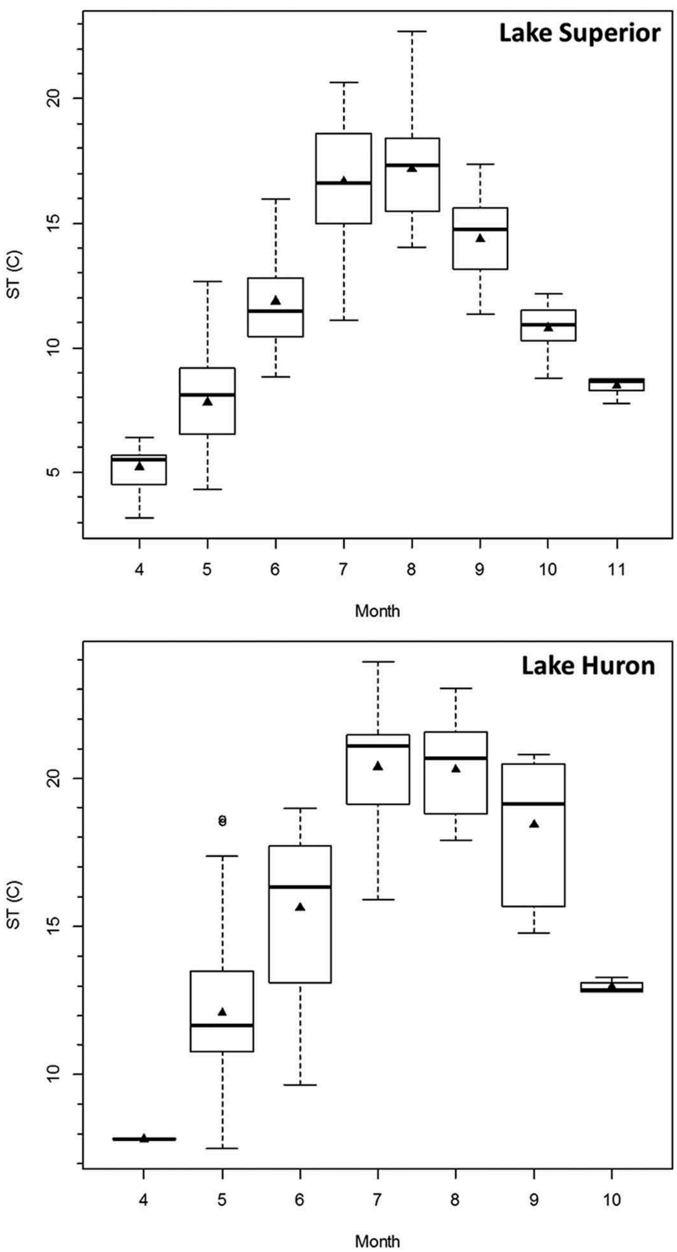


FIGURE 7. Box plot of surface temperature (ST; °C) at the time of release for Lake Trout that were tagged by volunteer recreational anglers in Lakes Superior and Huron during 2010–2013. The horizontal line in each box indicates the median, the box dimensions represent the interquartile range (25th to 75th percentiles), the whiskers represent the highest and lowest values within 1.5× the interquartile range, and the open circles are outliers. Mean monthly ST is represented by solid triangles.

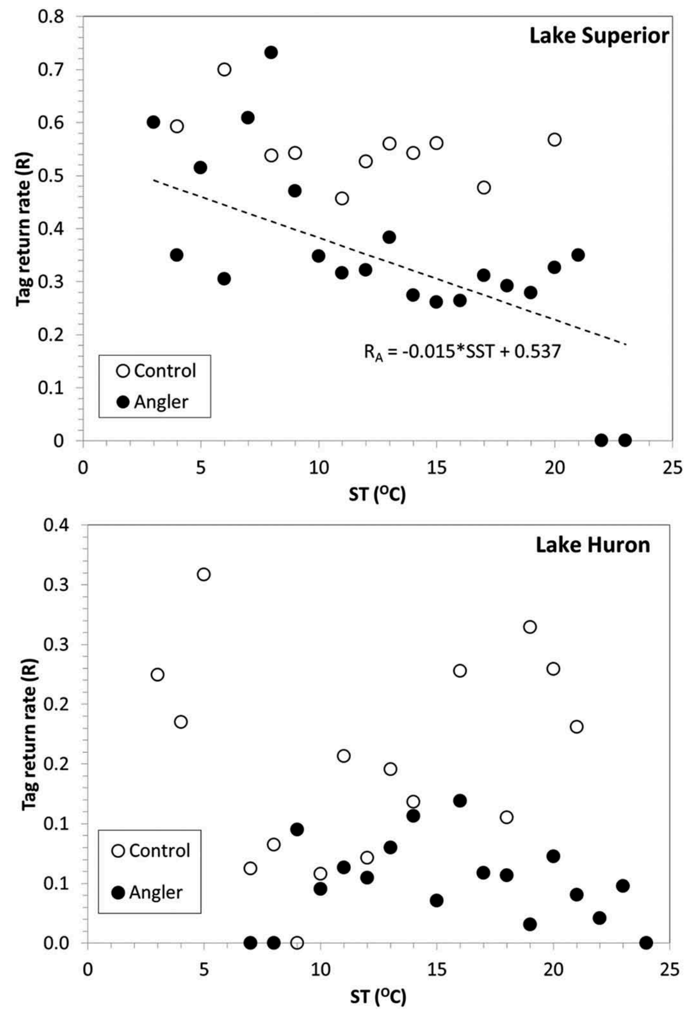


FIGURE 8. Relationship between tag return rate (R) and surface temperature (ST; °C) for angler-caught Lake Trout (tag return rate R_A) and control fish (captured via trap-netting) that were tagged in Lakes Superior and Huron during 2010–2013.

were slight variations in model rankings between the data sets. Six of the 12 best-performing models, including the model with the overall lowest AIC value, for both data sets estimated a unique postrelease mortality rate for the low-ST group (<10°C) and a shared postrelease mortality rate for the medium-ST (10–16°C) and high-ST (>16°C) groups (Table 6). The other six models with ΔAICs below 10 estimated a unique postrelease mortality for each ST group (Table 3). Across the different models, variation in postrelease mortality estimates was generally small, as the absolute difference in postrelease mortality estimates between models within a particular ST level was no greater than 4.3% for both data sets (Table 3).

For Lake Huron, there were 34 models with ΔAIC values less than 10 (Table 6). The six best-performing models, which all had ΔAICs less than 4, estimated a unique postrelease mortality rate for each ST group. Compared to Lake Superior, there was greater variation in postrelease mortality estimates among models within the ST groups for Lake Huron. The largest absolute difference in postrelease mortality estimates between models within the ST groups was 21.8%

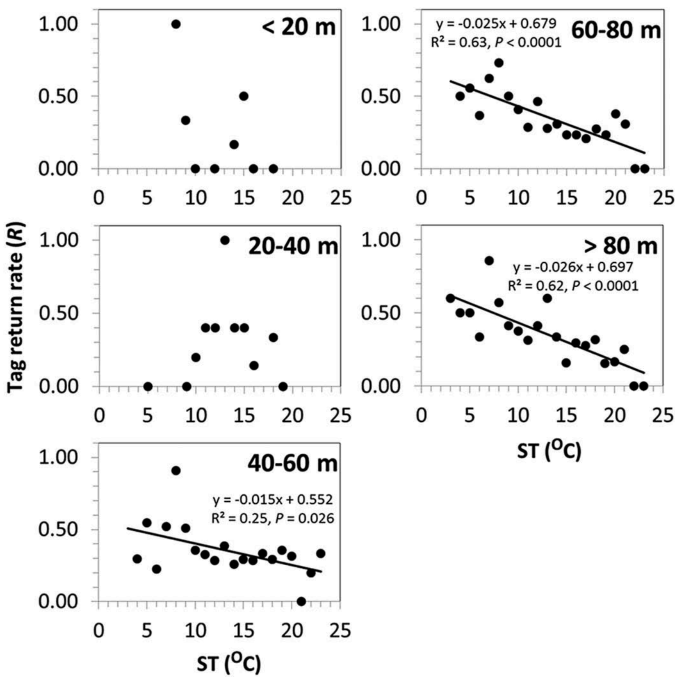


FIGURE 9. Relationship between the tag return rate (R) and surface temperature (ST; °C) by depth of capture for Lake Trout that were caught and released by volunteer recreational anglers in Lake Superior (R^2 = coefficient of determination).

(ST < 10°C), 30.9% (ST = 10–16°C), and 12.9% (ST > 16°C; Table 6).

The model-averaged postrelease mortality estimates for the ST groups based on the full Lake Superior data set (with all lengths of fish) were 15.0% (SE = 5.6%) for STs less than 10°C, 42.6% (SE = 3.0%) for STs of 10–16°C, and 43.3% (SE = 3.6%) for STs greater than 16°C. For the reduced Lake Superior data set (550–700-mm fish), the model-averaged postrelease mortality estimates were 13.7% (SE = 6.6%) for STs less than 10°C, 48.5% (SE = 3.4%) for STs of 10–16°C, and 48.4% (SE = 3.9%) for STs greater than 16°C. Model-averaged postrelease mortality estimates for Lake Huron were 52.4% (SE = 26.8%) for STs below 10°C, 45.2% (SE = 14.0%) for STs of 10–16°C, and 76.4% (SE = 5.4%) for STs exceeding 16°C.

DISCUSSION

The postrelease mortality we estimated for Lake Trout in the Great Lakes was greater than that estimated by Loftus et al. (1988). The key factor influencing postrelease mortality from recreational fishing was high ST at the time of capture. Postrelease mortality estimates were generally consistent between Lakes Superior and Huron for angler-tagged fish released in STs between 10°C and 16°C. For fish released in STs less than 10°C, the postrelease mortality estimate from Lake Huron was greater than that from Lake Superior but also had greater uncertainty, which was due at least partly to the low number of recaptures (n = 3 for angler-caught fish) at this ST level (only 39 tagged fish were released in STs < 10°C among all years). For fish captured and released at high STs (>16°C), the greater postrelease mortality in Lake Huron may have been driven by the difference in temperature distributions between lakes. Among Lake Trout that were released in STs over 16°C, the majority of fish were tagged and released between 17°C and 19°C in Lake Superior, whereas they were released in STs between 19°C and 24°C in Lake Huron. In Lake Superior, postrelease mortality rates at STs ≥ 10°C were more than 2.5 times the mortality rates observed at STs less than 10°C. In Lake Huron, postrelease mortality rates at STs ≥ 10°C were approximately 1.5 times those at STs less than 10°C.

From laboratory experiments, optimal thermal habitat for Lake Trout has been reported to be between 8°C and 12°C (Christie and Regier 1988; Magnuson et al. 1990; Mackenzie-Grieve and Post 2006). More recent archival thermal tagging studies for Lake Trout in Lake Huron (Bergstedt et al. 2003, 2016) and in Lake Superior (Mattes 2004; R. Goetz, NOAA, personal communication) indicate that Lake Trout may spend short periods in waters warmer than 10°C but spend the bulk of their time in water temperatures less than 10°C. The causative mechanism for greater postrelease mortality at high STs may be the compound effect of (1) the temperature differential experienced by Lake Trout when brought up from deep, cold waters to warm surface temperatures that are unsuitable for this species; combined with (2) the stress of being hooked, dragged, and reeled in by anglers. Angling is known to induce negative physiological effects in fish by elevating stress hormones and lactate levels (Lee and Bergersen 1996; Morrissey et al. 2005; Tracey et al. 2016). In our study, control Lake Trout (trap-netted group) released in warm temperatures were able to survive better than angler-caught fish because minimal trauma was experienced by trap-netted fish.

An unexpected result in this study was that neither the occurrence of bloating nor the depth of capture had any effect on tag return rates. Capture depth and bloating have been found to affect survival in a variety of species, including the Walleye *Sander vitreus* (Talmage and Staples 2011), Largemouth Bass *Micropterus salmoides* (Feathers and Knable 1983), and Striped Bass *Morone saxatilis* (Bettoli and Osborne 1998). Possible explanations for the lack of observed effect from bloating or depth of capture are that (1) the depth effect was confounded with temperature (as discussed above) and (2) Lake Trout are physostomous, and some bloated fish were able to recover by decompression of the gas bladder, which allowed them to return to deeper waters after release (Ng et al. 2015). This was observed by Loftus et al. (1988) and by volunteer anglers in this study,

TABLE 6. Akaike's information criterion (AIC) values, number of parameters (K), and postrelease mortality estimates (%) for Lake Trout released at three surface temperature (ST) levels (high [H], >16°C; medium [M], 10–16°C; low [L], <10°C) based on tag return models fitted to each lake and data set. Only models with AIC difference (ΔAIC) values less than 10 are shown. Models are identified based on whether the postrelease mortality rate (j), recreational fishing gear catchability (q), and/or natural mortality rate (M) differed by ST group or were time varying (TV). For an individual parameter, if all ST levels are indicated (e.g., j[H, M, L]), then unique coefficients were estimated for each level. The dot (· symbol) indicates that common coefficients were assumed for at least some of the ST levels (i.e., the dot replaces the ST levels for which coefficients were shared). For q, "TV" indicates a model for which q in the year of tagging differed from that in other tag return years. For M, "TV" indicates a model in which M values during 2010–2013 differed annually but M values in 2014 and 2015 were set equal to the 2013 level. Blank cells for Lake Huron indicate that models were not fitted to a reduced data set (i.e., 550–700-mm fish).

		All data				550–700-mm tagging length			
Model label	K	AIC	H	M	L	AIC	H	M	L
Lake Superior									
j(·, L), *q*(TV, H, M, L), *M*(·)	27	13,997.3	42.4	42.4	14.5	10,375.2	48.2	48.2	12.8
j(H, M, L), *q*(TV, H, M, L), *M*(·)	28	13,999.1	44.2	41.7	14.5	10,377.2	48.2	48.2	12.8
j(·, L), *q*(TV, H, M, L), *M*(·, L)	28	13,999.3	42.4	42.4	14.5	10,376.7	48.0	48.0	13.5
j(·, L), *q*(TV, H, M, L), *M*(TV, ·, L)	37	14,001.0	44.3	44.3	16.5	10,379.0	49.6	49.6	16.6
j(H, M, L), *q*(TV, H, M, L), *M*(·, L)	29	14,001.1	44.2	41.7	14.5	10,378.7	47.8	48.0	13.5
j(·, L), *q*(TV, H, M, L), *M*(H, M, L)	29	14,001.3	42.4	42.4	14.5	10,378.6	47.8	47.8	13.5
j(·, L), *q*(TV, H, M, L), *M*(TV, ·)	36	14,001.3	44.3	44.3	17.4	10,378.9	50.4	50.4	15.5
j(·, L), *q*(TV, H, M, L), *M*(TV, H, M, L)	38	14,001.6	44.2	44.2	16.5	10,379.5	49.5	49.5	16.6
j(H, M, L), *q*(TV, H, M, L), *M*(TV, ·, L)	38	14,002.7	46.7	43.3	16.5	10,381.0	49.9	49.5	16.6
j(H, M, L), *q*(TV, H, M, L), *M*(TV, ·)	37	14,002.9	46.5	43.3	17.5	10,380.9	50.7	50.3	15.5
j(H, M, L), *q*(TV, H, M, L), *M*(H, M, L)	30	14,003.1	44.2	41.7	14.5	10,380.5	46.9	48.1	13.5
j(H, M, L), *q*(TV, H, M, L), *M*(TV, H, M, L)	39	14,003.6	44.4	44.2	16.5	10,381.4	48.2	50.0	16.6
Lake Huron									
j(H, M, L), *q*(TV, H, M, L), *M*(TV, ·, L)	38	3,571.7	77.3	40.0	46.1				
j(H, M, L), *q*(·), *M*(H, M, L)	10	3,572.1	77.4	44.5	59.0				
j(H, M, L), *q*(·), *M*(TV, H, M, L)	19	3,572.2	77.5	46.6	55.1				
j(H, M, L), *q*(TV, H, M, L), *M*(TV, H, M, L)	39	3,572.6	77.8	39.4	46.1				
j(H, M, L), *q*(TV, ·, L), *M*(TV, H, M, L)	35	3,574.3	77.3	44.5	46.1				
j(H, M, L), *q*(TV, H, M, L), *M*(·, L)	29	3,575.5	77.3	38.4	51.7				
j(·), *q*(·), *M*(TV, H, M, L)	17	3,576.4	67.6	67.6	67.6				
j(H, M, L), *q*(TV, H, M, L), *M*(H, M, L)	30	3,576.6	77.7	37.4	51.7				
j(H, M, L), *q*(·), *M*(TV, ·, L)	18	3,577.0	74.9	52.8	55.0				
j(·), *q*(·), *M*(H, M, L)	8	3,577.0	67.4	67.4	67.4				
j(H, M, L), *q*(·, L), *M*(TV, H, M, L)	23	3,577.8	77.7	47.0	51.6				
j(H, M, L), *q*(TV, ·, L), *M*(H, M, L)	26	3,577.9	77.1	42.1	51.7				
j(·, L), *q*(·), *M*(TV, H, M, L)	18	3,578.1	68.2	68.2	55.1				
j(·), *q*(·), *M*(TV, ·, L)	16	3,578.1	66.8	66.8	66.8				
j(·), *q*(TV, H, M, L), *M*(TV, ·, L)	36	3,578.3	66.1	66.1	66.1				
j(H, M, L), *q*(·, L), *M*(H, M, L)	14	3,578.6	77.5	44.8	57.6				
j(H, M, L), *q*(·), *M*(TV, ·)	17	3,578.8	75.8	53.8	52.0				
j(·, L), *q*(·), *M*(H, M, L)	9	3,578.9	67.9	67.9	59.0				

TABLE 6. Continued.

Model label	K	All data				550–700-mm tagging length			
		AIC	H	M	L	AIC	H	M	L
$j(\cdot)$, $q(\mathrm{TV}, \cdot, \mathrm{L})$, $M(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$	33	3,579.4	66.7	66.7	66.7				
$j(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $q(\mathrm{TV}, \cdot, \mathrm{L})$, $M(\mathrm{TV}, \cdot, \mathrm{L})$	34	3,579.5	74.2	51.0	46.1				
$j(\cdot)$, $q(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$, $M(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$	37	3,579.7	66.1	66.1	66.1				
$j(\cdot, \mathrm{L})$, $q(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$, $M(\mathrm{TV}, \cdot, \mathrm{L})$	37	3,579.7	67.0	67.0	46.1				
$j(\cdot, \mathrm{L})$, $q(\cdot)$, $M(\mathrm{TV}, \cdot, \mathrm{L})$	17	3,579.8	67.4	67.4	55.0				
$j(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $q(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $M(\mathrm{TV}, \cdot, \mathrm{L})$	26	3,580.2	77.4	40.5	51.6				
$j(\cdot)$, $q(\cdot)$, $M(\mathrm{TV}, \cdot)$	15	3,580.3	67.9	67.9	67.9				
$j(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $q(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$, $M(\mathrm{TV}, \cdot)$	37	3,580.5	78.1	39.4	47.7				
$j(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $q(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $M(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$	27	3,580.5	78.2	40.1	51.6				
$j(\cdot, \mathrm{L})$, $q(\mathrm{TV}, \cdot, \mathrm{L})$, $M(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$	34	3,580.8	67.7	67.7	46.1				
$j(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $q(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$, $M(\mathrm{TV}, \cdot)$	28	3,581.0	78.4	39.0	51.7				
$j(\cdot, \mathrm{L})$, $q(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$, $M(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$	38	3,581.0	67.0	67.0	46.1				
$j(\cdot)$, $q(\mathrm{TV}, \cdot, \mathrm{L})$, $M(\mathrm{TV}, \cdot, \mathrm{L})$	32	3,581.1	65.5	65.5	65.5				
$j(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $q(\cdot)$, $M(\mathrm{TV}, \cdot, \mathrm{L})$	9	3,581.3	74.1	53.6	58.8				
$j(\mathrm{H}, \mathrm{M}, \mathrm{L})$, $q(\mathrm{TV}, \cdot)$, $M(\mathrm{TV}, \mathrm{H}, \mathrm{M}, \mathrm{L})$	31	3,581.5	75.7	43.5	52.6				
$j(\cdot)$, $q(\cdot)$, $M(\mathrm{TV}, \cdot, \mathrm{L})$	7	3,581.5	66.5	66.5	66.5				

suggesting that there is little benefit of decompressing the gas bladders of bloated Lake Trout because even though they have the ability to recover on their own, the fish are already compromised from the overall trauma associated with recreational catch. The one potential exception is when bloating occurs in the presence of gulls, because there did appear to be some combined effect of bloating and gulls on tag return rates of Lake Trout in Lake Superior, although a similar effect was not observed for fish in Lake Huron.

Prior research has indicated significantly higher postrelease mortality for Lake Trout smaller than 509 mm (57.1%; Loftus et al. 1988). Unfortunately, our study lacked a sufficient sample size of smaller Lake Trout to assess this. Since size limit regulations are important tools for managing Lake Trout, an examination of postrelease mortality according to size would be valuable for future research.

Based on the results of this research, the use of recreational catch-and-release practices with Lake Trout in the Great Lakes poses a management dilemma. Most Lake Trout in the upper Great Lakes are harvested during the summer months, when STs are well above the species' thermal optimum. For example, during our study period (2010–2015), 76% of total recreational harvest in Lake Superior and 97.5% of recreational harvest in Lake Huron occurred during months when STs were 10°C or higher. Regulations that require Great Lakes anglers to release Lake Trout will have a limited protective effect, as 40–76% of released fish may not survive and perhaps even higher mortality rates will occur during warmer months. Lake Trout that are subject to recreational catch and release are physiologically compromised, and the scope for recovery and survival is limited by release into suboptimal STs. It is apparent that Lake Trout may not be suitable for recreational catch-and-release fishing in the Great Lakes. Restrictive recreational length limits for Lake Trout may not produce the desired management outcome; therefore, it would be prudent for resource agencies to consider alternatives that would minimize overall catch, such as season or area restrictions or limiting daily quotas. Current management policies based on an assumed 15% postrelease mortality rate are likely underestimating the total numbers of fish harvested by recreational anglers, and we recommend updating the assumed postrelease mortality rates based on the present results.

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Appendix: Detailed Data

TABLE A.1. Marascuilo procedure for all pairwise comparisons of tag return rates according to angler handling times (<1.0, 1.0–1.5, 1.5–2.0, 2.0–2.5, and >2.5 min) for Lake Trout tagged in Lake Superior. Marascuilo test statistics include absolute difference in proportions (*a*), critical value (*r*), and statistical significance at $\alpha = 0.05$ (yes or no).

Comparison pair	*a*	*r*	*a* − *r*	Significance
<1.0 min versus 1.0–1.5 min	0.011	0.102	−0.091	No
<1.0 min versus 1.5–2.0 min	0.013	0.117	−0.104	No
<1.0 min versus 2.0–2.5 min	0.045	0.166	−0.121	No
<1.0 min versus >2.5 min	0.035	0.210	−0.175	No
1.0–1.5 min versus 1.5–2.0 min	0.002	0.098	−0.096	No
1.0–1.5 min versus 2.0–2.5 min	0.034	0.153	−0.119	No
1.0–1.5 min versus >2.5 min	0.046	0.098	−0.052	No
1.5–2.0 min versus 2.0–2.5 min	0.032	0.163	−0.130	No
2.0–2.5 min versus >2.5 min	0.080	0.230	−0.150	No

TABLE A.2. Marascuilo procedure for all pairwise comparisons of tag return rates according to angler handling times (<1.0, 1.0–1.5, 1.5–2.0, 2.0–2.5, and >2.5 min) for Lake Trout tagged in Lake Huron. Marascuilo test statistics include absolute difference in proportions (*a*), critical value (*r*), and statistical significance at $\alpha = 0.05$ (yes or no).

Comparison pair	*a*	*r*	*a* − *r*	Significance
<1.0 min versus 1.0–1.5 min	0.003	0.063	−0.060	No
<1.0 min versus 1.5–2.0 min	0.016	0.097	−0.081	No
<1.0 min versus 2.0–2.5 min	0.054	0.161	−0.107	No
<1.0 min versus >2.5 min	0.038	0.152	−0.113	No
1.0–1.5 min versus 1.5–2.0 min	0.019	0.098	−0.079	No
1.0–1.5 min versus 2.0–2.5 min	0.057	0.162	−0.105	No
1.0–1.5 min versus >2.5 min	0.041	0.098	−0.056	No
1.5–2.0 min versus 2.0–2.5 min	0.038	0.177	−0.140	No
2.0–2.5 min versus >2.5 min	0.015	0.212	−0.197	No

TABLE A.3. Marascuilo procedure for all pairwise comparisons of tag return rates by angler fishing method for Lake Trout tagged in Lake Superior. Fishing methods are described in Table 1. Marascuilo test statistics include absolute difference in proportions (*a*), critical value (*r*), and statistical significance at $\alpha = 0.05$ (yes or no).

Comparison pair	*a*	*r*	*a* − *r*	Significance
BOB versus DR-NR	0.024	0.147	−0.123	No
BOB versus DR-REL	0.015	0.066	−0.050	No
BOB versus WIRE	0.059	0.089	−0.030	No
DR-NR versus DR-REL	0.008	0.141	−0.133	No
DR-NR versus WIRE	0.082	0.153	−0.071	No
DR-REL versus WIRE	0.074	0.079	−0.004	No

TABLE A.4. Marascuilo procedure for all pairwise comparisons of tag return rates by angler fishing method for Lake Trout tagged in Lake Huron. Fishing methods are described in Table 1. Marascuilo test statistics include absolute difference in proportions (*a*), critical value (*r*), and statistical significance at $\alpha = 0.05$ (yes or no).

Comparison pair	*a*	*r*	*a* − *r*	Significance
SURF versus DR-REL	0.030	0.084	−0.054	No
SURF versus WIRE/LC	0.023	0.117	−0.094	No
DR-REL versus WIRE/LC	0.053	0.085	−0.032	No

TABLE A.5. Marascuilo procedure for all pairwise comparisons of tag return rates by play time interval (p1 = <1 min; p2 = 1–2 min; p3 = 2–3 min; p4 = 3–4 min; p5 = 4–5 min; p6 = >5 min) for each fishing method for Lake Trout tagged in Lake Superior. Fishing methods are described in Table 1. Marascuilo test statistics include absolute difference in proportions (*a*), critical value (*r*), and statistical significance (Sig) at α = 0.05 (yes or no). No fish were caught by the BOB method with play times greater than 4 min or by DR-NR and WIRE with play times less than 1 min.

	BOB				DR-NR				DR-REL				WIRE			
Comparison pair	*a*	*r*	*a* − *r*	Sig	*a*	*r*	*a* − *r*	Sig	*a*	*r*	*a* − *r*	Sig	*a*	*r*	*a* − *r*	Sig
p1 versus p2	0.19	0.41	−0.22	No					0.30	0.16	0.14	Yes				
p1 versus p3	0.18	0.37	−0.19	No					0.34	0.08	0.25	Yes				
p1 versus p4	0.31	0.56	−0.25	No					0.32	0.08	0.24	Yes				
p1 versus p5									0.30	0.12	0.18	Yes				
p1 versus p6									0.30	0.11	0.19	Yes				
p2 versus p3	0.01	0.19	−0.18	No	0.05	0.37	−0.33	No	0.04	0.18	−0.13	No	0.03	0.73	−0.70	No
p2 versus p4	0.12	0.46	−0.34	No	0.09	0.43	−0.34	No	0.02	0.17	−0.15	No	0.03	0.70	−0.67	No
p2 versus p5					0.20	0.64	−0.44	No	0.01	0.20	−0.19	No	0.03	0.69	−0.66	No
p2 versus p6					0.52	0.72	−0.20	No	0.00	0.19	−0.19	No	0.00	0.68	−0.68	No
p3 versus p4	0.13	0.42	−0.30	No	0.13	0.42	−0.28	No	0.02	0.11	−0.09	No	0.07	0.34	−0.27	No
p3 versus p5					0.25	0.63	−0.38	No	0.04	0.15	−0.11	No	0.06	0.32	−0.26	No
p3 versus p6					0.57	0.71	−0.15	No	0.04	0.14	−0.10	No	0.04	0.30	−0.26	No
p4 versus p5					0.11	0.66	−0.55	No	0.01	0.14	−0.13	No	0.00	0.25	−0.24	No
p4 versus p6					0.43	0.74	−0.31	No	0.02	0.13	−0.11	No	0.03	0.22	−0.19	No
p5 versus p6					0.32	0.88	−0.56	No	0.01	0.16	−0.16	No	0.03	0.19	−0.17	No

TABLE A.6. Marascuilo procedure for all pairwise comparisons of tag return rates by play time interval (p1 = <1 min; p2 = 1–2 min; p3 = 2–3 min; p4 = 3–4 min; p5 = 4–5 min; p6 = >5 min) for each fishing method for Lake Trout tagged in Lake Huron. Fishing methods are described in Table 1. Marascuilo test statistics include absolute difference in proportions (*a*), critical value (*r*), and statistical significance (Sig) at α = 0.05 (yes or no).

	SURF				DR-REL				WIRE/LC			
Pair	*a*	*r*	*a* − *r*	Sig	*a*	*r*	*a* − *r*	Sig	*a*	*r*	*a* − *r*	Sig
p1 versus p2	0.05	0.17	−0.12	No	0.04	0.11	−0.07	No	0.07	0.23	−0.16	No
p1 versus p3	0.17	0.36	−0.19	No	0.03	0.12	−0.09	No	0.06	0.19	−0.13	No
p1 versus p4	0.05	0.16	−0.11	No	0.06	0.12	−0.06	No	0.27	0.38	−0.11	No
p1 versus p5	0.11	0.35	−0.24	No	0.04	0.15	−0.11	No	0.06	0.20	−0.14	No
p1 versus p6	0.00	0.00	0.00	No	0.07	0.13	−0.06	No	0.06	0.20	−0.14	No
p2 versus p3	0.11	0.40	−0.28	No	0.01	0.07	−0.06	No	0.01	0.30	−0.29	No
p2 versus p4	0.01	0.23	−0.23	No	0.02	0.06	−0.04	No	0.20	0.44	−0.25	No
p2 versus p5	0.06	0.39	−0.33	No	0.00	0.11	−0.11	No	0.01	0.31	−0.30	No
p2 versus p6	0.05	0.17	−0.12	No	0.02	0.08	−0.06	No	0.01	0.31	−0.30	No
p3 versus p4	0.12	0.39	−0.27	No	0.03	0.08	−0.04	No	0.21	0.43	−0.22	No
p3 versus p5	0.06	0.50	−0.44	No	0.01	0.12	−0.11	No	0.00	0.28	−0.27	No
p3 versus p6	0.17	0.36	−0.19	No	0.04	0.09	−0.05	No	0.00	0.28	−0.27	No
p4 versus p5	0.06	0.38	−0.32	No	0.02	0.12	−0.10	No	0.20	0.43	−0.23	No
p4 versus p6	0.05	0.16	−0.11	No	0.01	0.09	−0.08	No	0.20	0.43	−0.23	No
p5 versus p6	0.11	0.35	−0.24	No	0.02	0.13	−0.10	No	0.00	0.29	−0.29	No

TABLE A.7. Marascuilo procedure for all pairwise comparisons of tag return rates by capture depth interval (m) for all fishing methods combined for Lake Trout tagged in Lake Superior. Fishing methods are described in Table 1. Marascuilo test statistics include absolute difference in proportions (*a*), critical value (*r*), and statistical significance at α = 0.05 (yes or no).

Comparison pair	*a*	*r*	*a* − *r*	Significance
<20 m versus 20–30 m	0.003	0.6	−0.597	No
<20 m versus 30–40 m	0.04	0.422	−0.382	No
<20 m versus 40–50 m	0.011	0.335	−0.323	No
<20 m versus 50–60 m	0.084	0.332	−0.248	No
<20 m versus 60–70 m	0.055	0.344	−0.288	No
<20 m versus 70–80 m	0.097	0.348	−0.251	No
<20 m versus >80 m	0.049	0.339	−0.29	No
20–30 m versus 30–40 m	0.037	0.57	−0.533	No
20–30 m versus 40–50 m	0.008	0.509	−0.501	No
20–30 m versus 50–60 m	0.081	0.507	−0.427	No
20–30 m versus 60–70 m	0.052	0.515	−0.463	No
20–30 m versus 70–80 m	0.093	0.518	−0.425	No
20–30 m versus >80 m	0.045	0.512	−0.467	No
30–40 m versus 40–50 m	0.029	0.278	−0.249	No
30–40 m versus 50–60 m	0.044	0.274	−0.231	No
30–40 m versus 60–70 m	0.015	0.288	−0.273	No
30–40 m versus 70–80 m	0.057	0.294	−0.237	No
30–40 m versus >80 m	0.008	0.283	−0.274	No
40–50 m versus 50–60 m	0.073	0.096	−0.024	No
40–50 m versus 60–70 m	0.044	0.131	−0.087	No
40–50 m versus 70–80 m	0.085	0.142	−0.056	No
40–50 m versus >80 m	0.037	0.118	−0.08	No
50–60 m versus 60–70 m	0.029	0.124	−0.095	No
50–60 m versus 70–80 m	0.013	0.135	−0.123	No
50–60 m versus >80 m	0.035	0.11	−0.074	No
60–70 m versus 70–80 m	0.042	0.162	−0.12	No
60–70 m versus >80 m	0.007	0.141	−0.135	No
70–80 m versus >80 m	0.048	0.151	−0.103	No

TABLE A.8. Marascuilo procedure for all pairwise comparisons of tag return rates by capture depth interval (m) for all fishing methods combined for Lake Trout tagged in Lake Huron. Fishing methods are described in Table 1. Marascuilo test statistics include absolute difference in proportions (*a*), critical value (*r*), and statistical significance at α = 0.05 (yes or no).

Comparison pair	*a*	*r*	*a* − *r*	Significance
<10 m versus 10–20 m	0.031	0.186	−0.155	No
<10 m versus 20–30 m	0.037	0.171	−0.134	No
<10 m versus 30–40 m	0.028	0.173	−0.145	No
<10 m versus 40–50 m	0.024	0.183	−0.159	No
<10 m versus >50 m	0.037	0.387	−0.35	No
10–20 m versus 20–30 m	0.068	0.086	−0.019	No
10–20 m versus 30–40 m	0.059	0.091	−0.032	No
10–20 m versus 40–50 m	0.055	0.108	−0.053	No
10–20 m versus >50 m	0.006	0.358	−0.351	No
20–30 m versus 30–40 m	0.009	0.054	−0.045	No
20–30 m versus 40–50 m	0.013	0.079	−0.067	No
20–30 m versus >50 m	0.074	0.35	−0.276	No
30–40 m versus 40–50 m	0.004	0.084	−0.081	No
30–40 m versus >50 m	0.065	0.351	−0.286	No
40–50 m versus >50 m	0.061	0.356	−0.295	No