Postrelease mortality of Lake Trout in Lakes Superior and Huron

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<A>Abstract

The effectiveness of fishing regulations that result in some angler-caught fish being released depends on accurate knowledge of postrelease (i.e., hooking) mortality of those individuals. In the Laurentian Great Lakes, Lake Trout are a major component of recreational fisheries, and across large regions of the lakes are managed with length-limit regulations 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 examined environmental and fishing factors that influence return rates of tagged fish. The basic study design was to compare tag return rates between two groups: 1) a treatment group comprising angler-caught and released fish; 2) a control group comprising trap net caught and released fish. Tag return rates for the angler group were evaluated by depth of capture, surface temperature at release (ST), fish length, fishing method, anatomical hook site, play time, handling time, and barotrauma. Tag return rates for angler-caught fish declined significantly with increasing ST. Effects from depth of capture, fish length, fishing method, anatomical hook site, play time, handling time, or barotrauma on tag return rates were generally small. AIC model-averaged postrelease mortality estimates incorporating ST were 15.0% (SE = 5.6%) (< 10 °C ST), 42.6% (SE = 3.0%) (10-16 °C ST), and 43.3% (SE = 3.6%) (> 16 °C ST) for Lake Superior, and 52.5% (SE = 26.8%) (< 10 °C ST), 45.2% (SE = 14.0%) (10-16 °C ST), and 76.4% (SE = 5.4%) (> 16 °C ST) for Lake Huron. 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 removed by recreational anglers.

<A>Introduction

Size and bag limits are widely used in regulation of fisheries (Paukert et al. 2001, 2007; Isermann and Paukert 2010) and often result in catch-release fishing and grading that can lead to a significant number of fish releases. An example in the Great Lakes is Lake Trout *Salvelinus namaycush*, which compose a major component of 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 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/hr. 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 in the Great Lakes by anglers, and each method may have different effects on caught fish. Great Lakes recreational Lake Trout harvest is managed with length-limits (Caroffino 2013) and daily quota regulations that have resulted in catch- release angling in some areas (Lockwood et al. 2001; Krueger et al. 2013). Between 2010 and 2015 in Michigan waters of the Upper Great Lakes, 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, personal communication). Most of the releases during this time period in Lakes Huron and Michigan were caused by 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.

Management of Lake Trout is a major focus of Great Lakes natural resources agencies and in many areas is supported by routine stock assessments using statistical catch-at-age models that use 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 fish that die postrelease (Quinn and Deriso 1999).

Numerous studies have indicated greater postrelease mortality from catch-release fishing practices during high water temperatures (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007). Given that Lake Trout are a cold- and deep-water species, a similar linkage between postrelease mortality rate and temperature would be expected. Indeed, studies conducted in inland lake recreational fisheries point to temperature being a major determinant of postrelease mortality rates. In 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 during cold temperatures, estimated Lake Trout postrelease mortality was 12%, whereas during the late summer postrelease mortality was as high as 87% (Lee and Bergersen 1995). 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 being an important determinant of resulting postrelease mortality rates, with Lake Trout hooked in vital areas such as 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% CI: 7.4-25.7%), although higher postrelease mortalities were reported for smaller fish and those hooked in vital areas. No effect of depth, temperature differential between surface and capture depth, lure type, and play time was found (Loftus et al. 1988).

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, there have been lingering concerns about the accuracy of the 15% estimate because of 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), limited depth range from which fish were caught (< 50 m), and short evaluation period (Modeling Subcommittee, Technical Fisheries Committee 2002). Furthermore, barotrauma has been a concern since most Lake Trout are brought up from deep water and many are observed with over-inflated gas bladders (Loftus et al. 1988; Ng et al. 2015).

The objective of our study was to conduct a tagging experiment and estimate postrelease mortality of Lake Trout from the upper Great Lakes and evaluate how return rates of tagged fish were affected by factors such as fish length, handling time, play time, surface temperature at time of release, fishing method, occurrence of barotrauma, and depth of capture. We conducted this study in Lakes Huron and Superior and assumed 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 is the form generally targeted by fisheries. All Lake Trout collected in this study were the lean morphotype.

<A>Methods

Lake Trout tagging.—For our research, postrelease mortality was evaluated by tagging two groups of Lake Trout: treatment (i.e., recreational 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, downrigger with no release, downrigger with release, and wire lining (Table 1). In Lake Huron, volunteer boat-anglers used three methods: surface fishing, downrigger with release, and wire lining/lead core fishing. The control group comprised fish 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 after release from this gear (Johnson et al. 2004b). Tagging was conducted off two recreational fishing ports of Michigan: Marquette in southern Lake Superior and Alpena in western Lake Huron (Figure 1). These two ports were chosen because of 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 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 from April through November between 2010 and 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, Washington). 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, and for postrelease mortality estimation data were used to the end of 2015

Volunteer boat-anglers were recruited at both study areas and trained on tagging technique, assessment of fish condition, and study protocols for the treatment group. Data collection and tagging techniques were developed such that treatment fish closely represented actual recreational catch and release practices. Data collected for treatment group fish included tag serial number, total length ($\pm$ 50 mm), date, location, depth of capture (m), play time, handling time, bloating (gas bladder inflated), presence of gulls *Larus spp* at release site (gulls), hook location, fishing method, and surface temperature (ST) on day of tagging. Descriptions for categorical data collected are listed in Table 1. We assessed only the overt symptom of barotrauma by counting fish that were bloated when released and did not document cryptic symptoms of barotrauma (Wilde 2009). To minimize handling time, digital cameras were used to record much of the data for post processing, and electronic chess game timers (Saitek Competition Game Clock, Saitek Industries) were used to record play and handling times (separately). Each captured fish was placed in a specialized measuring board that restrained the fish and displayed tag serial number and a digital photo was taken by the volunteer angler (which recorded date, tag serial number and total length). The measure board comprised a longitudinally-sectioned, 152-mm diameter 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 and handling times. 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 Lake Trout was calculated by averaging hourly ST between 0700 and1600 h (typical fishing times).

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

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

Statistical analysis of factors influencing tag return rates.—Individual or combination of treatment factors were evaluated by comparing angler group tag return rates with handling time, fishing method, play time, depth of capture, and barotrauma. Statistical tests and post-hoc comparisons used for these analyses are described in Table 2. Statistical significance was established at $\alpha = 0.05$. Although prior research indicated that postrelease mortality was greater for smaller Lake Trout (Loftus et al. 1985), we did not incorporate length in our analyses because the limited length range of tagged fish. Although this study did not measure temperature at depth of capture to estimate 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 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 depth at capture intervals. A significant negative slope for the greater depth intervals would suggest a potential temperature differential effect.

Relationships between tag return rates and surface temperature (ST) at time of release were evaluated using ANCOVA with group and year as factors and ST as the covariate (Table 2). In this case, both control and treatment groups were evaluated because it was important to assess whether any relationship between angler-group tag return and ST was also paralleled in the control group in order to isolate the treatment effect of recreational catch and release mortality.

Estimation of postrelease mortality.—Postrelease mortality for the factors identified as potentially important was estimated by fitting multi-group Brownie model (Brownie et al. 1985) to the 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 size differences between treatment and control fish. Models were fit separately for Lakes Huron and Superior. For Lake Superior, two separate Brownie models were fit to different length groups of fish (see below).

Following Hoenig et al. (1998), the probability of a treatment group fish being returned was specified as

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

where y = year of tagging, i = sampling gear from which a returned fish was caught, r = return year, θ = postrelease mortality rate, s_i = selectivity of the i-th fishing gear for treatment group fish relative to control group fish, $q_{i,r}$ = the catchability coefficient for the i-th fishing gear in the r-th return year, $E_{i,r}$ = amount of effort of the i-th fishing gear in the r-th return year, M_r = instantaneous natural mortality in the r-th return year, Δ_r = length of a period (expressed as a fraction of the year) of the r-th return year during which tagged fish were at large in the system. The Δ_r when 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 that recently tagged fish experienced in that year was different than what previously tagged fish experienced. Similarly, the amount of fishing effort that was specified when return year equaled the year of tagging was different than for other years to account for tagging operations not being completed until during the summer. The effort measures were angler-hours for the recreational fishery, meters of gill net for the commercial fishery and agency surveys, and the 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 regards to the selectivities assumed for recreational angling and trap net gear, we fit a separate Brownie model to return data for fish that were between 550 and 700 mm TL at time of tagging, which was the length range of greatest overlap between the treatment and control groups, to determine sensitivity of postrelease mortality estimates to differences in gear selectivity. When fitting the Brownie model to fish between 550 and 700 mm TL at time of tagging, we assumed equal selectivities for the sampling gears for treatment and control group fish. For tag returns from Lake Huron, equal selectivity were assumed for all sampling gears because the sizes of Lake Trout caught by recreational angling and trap nets were similar.

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

We implemented the tag-return models in AD Model Builder (Fournier et al. 2012). Tag returns of both treatment and control group fish were modeled through a multinomial likelihood. Gear catchabilities and natural mortalities 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 where postrelease mortalities, catchabilities, and natural mortalities 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 mortalities in 2014 and 2015 were assumed equal to the rate from 2013) and for catchabilities in the year of tagging to be different from other years to account for potential non-mixing of tagged fish with at-large populations. Candidate models were evaluated using Akaike information criteria (AIC) (Burnham and Anderson 2002). For each dataset, there was more than one model with ΔAIC values < 10. To account for model-selection uncertainty, model averaged postrelease mortality estimates and their standard errors were calculated from equations in Burnham and Anderson (2002) based on estimates and AIC weights for all models with ΔAIC values < 10.

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

<A>Results

<B>Mark-recapture of Lake Trout

Between 2010 and 2013, 2,329 Lake Trout were tagged in the angler group and 1,818 in the control group in Lake Superior. In Lake Huron, 934 Lake Trout were tagged in the angler group and 1,671 fish were tagged in the control group (Table 3). In Lake Superior, there were ten volunteer boat-anglers in 2010 and four in 2011, 2012, and 2013. In Lake Huron, there were nine volunteer boat-anglers during 2010-2012 and seven in 2013. Very few control group Lake Trout in Lake Superior were tagged in 2011 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.

<B>Factors influencing tag return rates

Angler handling times.—Handling time for the majority (> 65%) of Lake Trout tagged by anglers was less than 1 min 30 s in both Lakes Superior and Huron. We compared tag return rates for each fishing method according to five handling time categories: < 1 min 1-1.5 min, 1.5-2 min, 2-2.5 min, and > 2.5 min and found no significant differences in tag return rates for either Lake Superior or Lake Huron (Marascuilo procedure: $P > 0.05$, Tables A.1, A.2).

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

Play time.—In Lake Superior, play time for most fish caught by bobbing, downrigger with no release, and downrigger with release was $\leq$ 4 min. Play time for wire line fishing was more variable with more than 50% of fish taking more than 5 min to land. In Lake Huron, the majority of fish caught by all fishing methods was ≤ 4 min. For Lake Superior, we compared tag return rates in six time intervals: < 1, 1-2, 2-3, 3-4, 4-5, and >5 min and did not detect significant differences in tag return rate by play time for any of the fishing methods (Marascuilo procedure: $P > 0.05$, Table A.5; Figure 3) except for fish caught < 1 min by the downrigger with release method, which had significantly lower tag return rate than all other play time intervals (Table A.5). There were no statistical differences in tag return rates according to play time for any of the fishing methods in Lake Huron (Marascuilo procedure: $P > 0.05$; Table A.6; Figure 3).

Depth of capture.— Overall mean depth of angler group tagged Lake Trout in Lake Superior was approximately 59 m. Among all Lake Superior angler group tagged Lake Trout, the shallowest depth fished was 1.5 m by wire lining and the maximum depth was 82.3 m fished by downrigger with release (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 depth of fish caught by downrigger without releases was 47.6 m and was the shallowest fishing method (Nemenyi post-hoc comparison versus: Bobbing, $\chi2$= 312.4, $P < 0.0001$; down rigger with release, $\chi2$= 16.8, $P = 0.0008$; wire line, $\chi2$= 13.0, $P = 0.005$; Figure 4). Mean depth for downrigger with releases (52.3 m) and wire lining (51.7 m) were intermediate among fishing methods and did not statistically differ (Nemenyi post-hoc test $\chi2$= 0.28, P =0.96). The deepest method of fishing was the bobbing method with an average depth of 78.6 m (Nemenyi post-hoc test, $P < 0.001$ for all comparisons). For Lake Superior, there was no significant relationship of tag return rate by depth of capture for any of the fishing methods (Figure 5). In Lake Huron, depth of capture ranged from < 1 m (surface) for wire lining to 61.6 m for downrigger with release method. In Lake Huron, overall mean depth of Lake Trout captured among all fishing methods was 27.3 m. Mean depth for downrigger with release method was 28.8 m and was different than both surface (Kruskal-Wallis Test χ^2= 144, df= 2, P <0.0001; Nemenyi post-hoc test χ^2= 46.5, P < 0.001) and wire lining methods (Nemenyi post-hoc test χ^2= 107.7, P < 0.001; Figure 4). Mean depth of Lake Trout caught by wire lining was 16.6 m and by surface fishing was 20.6 m but did not differ statistically (Nemenyi post-hoc test χ^2= 4.18, P = 0.12). There was no significant relationship of tag return rate by 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 rates by depth of capture for all fishing methods combined (Marascuilo procedure: P > 0.05; Tables 4, A.7, A.8).

Barotrauma.—Bloating of angler caught and released 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 depth of capture and was higher for Lake Trout caught at depths $\geq$ 50 m in Lake Superior (Z-test, Z=-3.15, P = 0.002) and was significantly greater at depths $\geq$ 40 m in Lake Huron (Z-test, Z=-4.83, P < 0.001). Gulls were present at time of release for 4.8% of fish in Lake Superior and 2.9% in Lake Huron. Overall tag return rates for bloated fish did not differ from non-bloated fish in both Lake Superior (Z-test, Z = 1.33, P = 0.184) and Lake Huron (Z-test, Z=0.541, P = 0.59; Figure 6). In Lake Superior, 4% of all tagged Lake Trout were bloated with gulls present at time of release. These fish had a significantly a lower tag return rate than bloated fish with no gulls present or non-bloated fish (2 x2 Contingency Table, $P \leq 0.05$; Figure 6). For Lake Huron, no statistical differences in tag return rates by barotrauma and gull status were detected.

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

Surface temperature at release.— Lake Trout in Lake Superior were tagged throughout the fishing season from April through November and were released in surface temperatures (ST) ranging from 3-23° C (Figure 7). In Lake Huron, the fishing season spanned April through October with a 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 that included year and group resulted in no significant interactions: 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), and 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 between ST and group was detected ($F_{1,62}$= 0.79, $P = 0.379$). For the angler 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 net 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 rates 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 40-60 m ($F_{1,18} = 5.89$, $P = 0.026$), 60-80 m ($F_{1,18} = 30.1$, $P < 0.0001$), and > 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 measured for Lake Superior Lake Trout caught at depths < 20 m ($F_{1,6} = 2.26$, $P = 0.183$) and at depths 20-40 m ($F_{1,9} = 0.21$, $P = 0.658$). Only 3.5% of angler group fish were caught at depths < 40 m in Lake Superior. For Lake Huron, no significant relationship between tag return rate and ST according to depth of capture was detected (< 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).

<B>Estimation of postrelease mortality

For Lake Superior, there were 12 models with ΔAICs < 10 for both the full and reduced (limited to fish between 550 and 700 mm TL at time of tagging) datasets (Table 6). The models with ΔAICs < 10 were the same for both datasets, although there were slight variations in model rankings between the datasets. Six of the 12 best performing models, including the model with the overall lowest AIC value, for both datasets estimated a unique postrelease mortality for the low ST group (< 10 °C) and a shared postrelease mortality for the medium (10-16 °C) and high ST groups (> 16 °C) (Table 6). The other six models with ΔAICs < 10 estimated a unique postrelease mortality for each ST group (Table 3). Across the different models, variation in postrelease mortality estimates was generally small, with absolute difference in postrelease mortality estimates between models within a particular ST level being no greater than 4.3% for both datasets (Table 3).

For Lake Huron, there were 34 models with ΔAICs < 10 (Table 6). The 6 best performing models, which all had ΔAICs < 4, estimated a unique postrelease mortality for each ST group. Compared to Lake Superior, there was greater variation in postrelease mortality estimates among models within the ST groups. The largest absolute difference in postrelease mortality estimates between models within the ST groups was 21.8 (< 10 °C), 30.9 (10-16 °C), and 12.9% (> 16°C) (Table 6).

The model-averaged postrelease mortality estimates for the ST groups based on the full Lake Superior dataset (with all lengths of fish) were 15.0 (SE=5.6%), 42.6 (SE=3.0%), and 43.3% (SE=3.6%) for the <10 °C, 10-16 °C, and >16 °C temperature levels, respectively. For the reduced Lake Superior dataset (550-700 mm fish), the model-averaged postrelease mortality estimates were 13.7 (SE=6.6%), 48.5 (SE=3.4%), and 48.4% (SE=3.9%) for the <10 °C, 10-16 °C, and >16 °C temperature levels, respectively. Lake Huron model-averaged postrelease mortality estimates were 52.4 (SE = 26.8%), 45.2 (SE = 14.0%), and 76.4% (SE = 5.4%) for the < 10 °C, 10-16 °C, and >16 °C temperature levels, respectively.

<A>Discussion

In this study, we measured postrelease mortality for Great Lakes Lake Trout to be greater than that estimated by Loftus et al. (1988). The key factor influencing postrelease mortality from recreational fishing was high ST at time of capture. Postrelease mortality estimates were generally consistent between Lakes Superior and Huron for angler-tagged fish released in ST between 10 and 16 °C. For fish released in ST < 10 °C, the postrelease mortality estimate in

Lake Huron was greater than in Lake Superior, but also had greater uncertainty due at least partly to the low number of recaptures (n=3 for angler-tagged fish) for this ST level (only 39 tagged fish were released in ST < 10 °C among all years). For high ST at capture and release (>16 °C), the greater postrelease mortality in Lake Huron may be driven by the difference in temperature distributions between lakes. For fish released in ST >16 °C in Lake Superior, the majority of fish were tagged and released between 17 and 19 °C whereas in Lake Huron, majority of fish were released in ST between 19-24 °C. In Lake Superior, postrelease mortality rates were more than 2.5 times greater at ST ≥ 10 °C compared to ST < 10 °C. In Lake Huron, postrelease mortality rates were approximately 1.5 times greater at ST ≥ 10 °C compared to ST < 10 °C.

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

An unexpected result in this study was that neither occurrence of bloating nor depth of capture had any effect on tag return rates. Depth of capture or occurrence of bloating have been found to affect survival of a variety of species including 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 why we did not observe an effect due to the occurrence of bloating or depth of capture are because depth effect was confounded with temperature as discussed above and Lake Trout are physostomous and some bloated fish were able to recover by decompressing their 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. This would suggest that there is little benefit of decompressing the gas bladder of bloated Lake Trout because even though they have the ability to recover on their own, the fish is already compromised from the overall trauma from recreational catch. The one caveat to this might be when bloating occurs in the presence of gulls because at least for Lake Superior there did appear to be some combined effect of bloating and gulls on return rates of Lake Trout, although a similar effect was not observed for Lake Huron.

Based on the results of this research, recreational catch and release of Great Lakes Lake Trout is a management dilemma. Most Lake Trout in the upper Great Lakes are harvested during the summer months when STs are well above their thermal optimum. For example, during this study period (2010-2015), 76% of total recreational harvest in Lake Superior occurred during the months when ST $\geq$ 10° C and in Lake Huron it was 97.5%. Regulations that require Great Lakes anglers to release Lake Trout will have a limited protective effect as anywhere from 40 to 76% of fish released may not survive with perhaps even higher mortality rates during warmer months. Recreational caught and released Lake Trout are physiologically compromised and the scope of return and survival is limited by release in suboptimal surface water temperatures. It is apparent that Lake Trout are generally not suitable for recreational catch-release fishing in the Great Lakes. Restrictive recreational length-limits for Lake Trout may not produce the desired management outcome and resource agencies may want 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 are likely underestimating the total numbers of fish harvested by recreational anglers, and we recommend updating assumed postrelease mortality rates based on the results of this study.

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Table 1. Categorical factors and levels recorded for angler group tagged and released Lake Trout to assess postrelease mortality in Lakes Superior and Huron.

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

Table 2. Statistical tests and post-hoc comparisons used to compare tag return rates, length, depth of capture.

Dependent variable	Factor (effect)	Levels	Statistical/post-hoc test used
Tag return rate	Barotrauma	2	Z-test for two proportions (Zar 1999)
Tag return rate	Barotrauma, gulls present	2	2 x 2 contingency table (Burnham et al. 1987)
Tag return rate	Fishing method	4	Marascuilo procedure for multiple proportions (Marascuilo 1966)
Tag return rate	Depth of capture	5	Marascuilo procedure for multiple proportions (Marascuilo 1966)
Tag return rate	Play time	6	Marascuilo procedure for multiple proportions (Marascuilo 1966)
Tag return rate	Handling time	3	Marascuilo procedure for multiple proportions (Marascuilo 1966)
Tag return rate	Hook location	2	Z-test for two proportions (Zar 1999)
Depth of capture	Fishing method	4	Mann-Whitney-Wilcoxon Test, Kruskal-Wallis Test, Nemenyi post-hoc test with Chi-squared approximation (Pairwise Multiple Comparison of Mean Ranks (PMCMR) Package, R version 3.2.4, Team 2016)
Tag return rate	Year, treatment group	Year (4), group (2)	ANCOVA with ST as covariate (R version 3.2.4, Team 2016)

Table 3. Number of Lake Trout tagged, number of tagged lake trout returned, and tag return rate by tagging year and return year for treatment and control group fish. Lake Superior lake trout were tagged near the port of Marquette, Michigan with returns from throughout the lake; Lake Huron lake trout were tagged near the port of Alpena, Michigan with returns from throughout the lake. Results are based on tag returns through 15 June 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	0.08.9
	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

Table 4. Number of Lake Trout tagged, number of tagged lake trout returned, and tag return rate by depth of capture for fish tagged and released by volunteer recreational anglers in Lake Superior and Lake Huron. Results are based on tag returns through 15 June 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			

Table 5. Number of Lake Trout tagged, number of tagged lake trout returned, and tag return rate by anatomical hooking location for fish tagged and released by volunteer recreational anglers in Lake Superior and Lake Huron. Results are based on tag returns through 15 June 2016.

	Anatomical hooking location					
Statistic	Eye	Gills	Jaw	Stomach	Throat	Other
Lake Superior						
Number tagged	43	25	2180	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

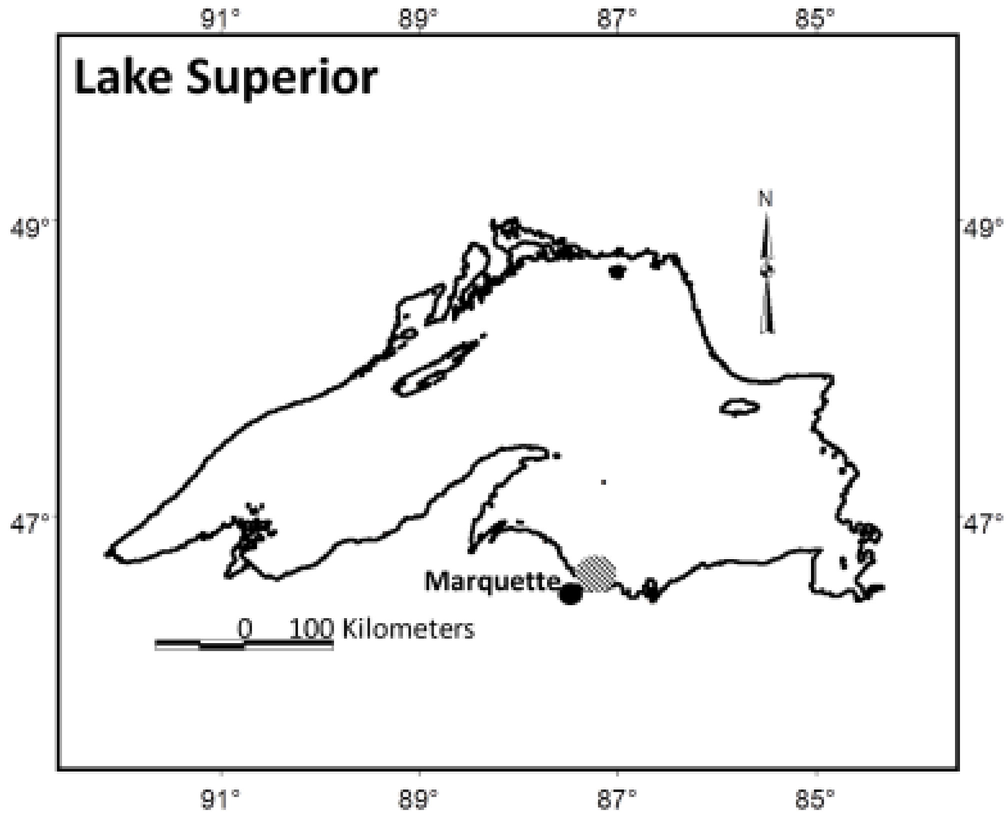
Table 6. AIC values, number of parameters (K), and postrelease mortality estimates by ST group (H: > 16 °C; M: 10-16 °C; L < 10 °C) by model for the tag-recovery models fit to each lake and dataset. Only models with ΔAICs < 10 are shown. Models are identified as to whether postrelease mortality rates (θ), recreational fishing gear catchabilities (q), and/or natural mortalities (M) differed by ST group or were time varying. For an individual parameter, if all ST group levels are indicated [e.g., θ(H,M,L)] than unique coefficients were estimated for each level. A • symbol indicates that common coefficients were assumed for at least some of the ST levels (the • symbol will replace the ST levels for which coefficients were shared). For q, TV indicates a model where fishing gear catchability in the tagging year differed from that of other recovery years. For M, TV indicates a model where natural mortalities in 2010-2013 differed annually but natural mortalities in 2014 and 2015 were set equal to that of 2013.

		All Data				550-700 mm tagging length			
Model label	K	AIC	H	M	L	AIC	H	M	L
Lake Superior									
θ(•,L) q(TV,H,M,L) M(•)	27	13997.3	42.4%	42.4%	14.5%	10375.2	48.2%	48.2%	12.8%
θ(H,M,L) q(TV,H,M,L) M(•)	28	13999.1	44.2%	41.7%	14.5%	10377.2	48.2%	48.2%	12.8%
θ(•,L) q(TV,H,M,L) M(•,L)	28	13999.3	42.4%	42.4%	14.5%	10376.7	48.0%	48.0%	13.5%
θ(•,L) q(TV,H,M,L) M(TV,•,L)	37	14001.0	44.3%	44.3%	16.5%	10379.0	49.6%	49.6%	16.6%
θ(H,M,L) q(TV,H,M,L) M(•,L)	29	14001.1	44.2%	41.7%	14.5%	10378.7	47.8%	48.0%	13.5%
θ(•,L) q(TV,H,M,L) M(H,M,L)	29	14001.3	42.4%	42.4%	14.5%	10378.6	47.8%	47.8%	13.5%
θ(•,L) q(TV,H,M,L) M(TV,•)	36	14001.3	44.3%	44.3%	17.4%	10378.9	50.4%	50.4%	15.5%
θ(•,L) q(TV,H,M,L) M(TV,H,M,L)	38	14001.6	44.2%	44.2%	16.5%	10379.5	49.5%	49.5%	16.6%
θ(H,M,L) q(TV,H,M,L) M(TV,•,L)	38	14002.7	46.7%	43.3%	16.5%	10381.0	49.9%	49.5%	16.6%
θ(H,M,L) q(TV,H,M,L) M(TV,•)	37	14002.9	46.5%	43.3%	17.5%	10380.9	50.7%	50.3%	15.5%
θ(H,M,L) q(TV,H,M,L) M(H,M,L)	30	14003.1	44.2%	41.7%	14.5%	10380.5	46.9%	48.1%	13.5%

θ(H,M,L) q(TV,H,M,L) M(TV,H,M,L)	39	14003.6	44.4%	44.2%	16.5%	10381.4	48.2%	50.0%	16.6%
Lake Huron									
θ(H,M,L) q(TV,H,M,L) M(TV,•,L)	38	3571.7	77.3%	40.0%	46.1%	NA	NA	NA	NA
θ(H,M,L) q(•) M(H,M,L)	10	3572.1	77.4%	44.5%	59.0%	NA	NA	NA	NA
θ(H,M,L) q(•) M(TV,H,M,L)	19	3572.2	77.5%	46.6%	55.1%	NA	NA	NA	NA
θ(H,M,L) q(TV,H,M,L) M(TV,H,M,L)	39	3572.6	77.8%	39.4%	46.1%	NA	NA	NA	NA
θ(H,M,L) q(TV, •,L) M(TV,H,M,L)	35	3574.3	77.3%	44.5%	46.1%	NA	NA	NA	NA
θ(H,M,L) q(TV,H,M,L) M(•,L)	29	3575.5	77.3%	38.4%	51.7%	NA	NA	NA	NA
θ(•) q(•) M(TV,H,M,L)	17	3576.4	67.6%	67.6%	67.6%	NA	NA	NA	NA
θ(H,M,L) q(TV,H,M,L) M(H,M,L)	30	3576.6	77.7%	37.4%	51.7%	NA	NA	NA	NA
θ(H,M,L) q(•) M(TV,•,L)	18	3577.0	74.9%	52.8%	55.0%	NA	NA	NA	NA
θ(•) q(•) M(H,M,L)	8	3577.0	67.4%	67.4%	67.4%	NA	NA	NA	NA
θ(H,M,L) q(•,L) M(TV,H,M,L)	23	3577.8	77.7%	47.0%	51.6%	NA	NA	NA	NA
θ(H,M,L) q(TV,•,L) M(H,M,L)	26	3577.9	77.1%	42.1%	51.7%	NA	NA	NA	NA
θ(•,L) q(•) M(TV,H,M,L)	18	3578.1	68.2%	68.2%	55.1%	NA	NA	NA	NA
θ(•) q(•) M(TV,•,L)	16	3578.1	66.8%	66.8%	66.8%	NA	NA	NA	NA
θ(•) q(TV,H,M,L) M(TV,•,L)	36	3578.3	66.1%	66.1%	66.1%	NA	NA	NA	NA
θ(H,M,L) q(•,L) M(H,M,L)	14	3578.6	77.5%	44.8%	57.6%	NA	NA	NA	NA
θ(H,M,L) q(•) M(TV,•)	17	3578.8	75.8%	53.8%	52.0%	NA	NA	NA	NA

θ(•,L) *q*(•) *M*(H,M,L)	9	3578.9	67.9%	67.9%	59.0%	NA	NA	NA	NA
θ(•) *q*(TV, •,L) *M*(TV,H,M,L)	33	3579.4	66.7%	66.7%	66.7%	NA	NA	NA	NA
θ(H,M,L) q(TV, •,L) *M*(TV,•,L)	34	3579.5	74.2%	51.0%	46.1%	NA	NA	NA	NA
θ(•) q(TV,H,M,L) *M*(TV,H,M,L)	37	3579.7	66.1%	66.1%	66.1%	NA	NA	NA	NA
θ(•,L) q(TV,H,M,L) *M*(TV,•,L)	37	3579.7	67.0%	67.0%	46.1%	NA	NA	NA	NA
θ(•,L) q(•) *M*(TV,•,L)	17	3579.8	67.4%	67.4%	55.0%	NA	NA	NA	NA
θ(H,M,L) q(H,M,L) *M*(TV,•,L)	26	3580.2	77.4%	40.5%	51.6%	NA	NA	NA	NA
θ(•) q(•) *M*(TV,•)	15	3580.3	67.9%	67.9%	67.9%	NA	NA	NA	NA
θ(H,M,L) q(TV,H,M,L) *M*(TV,•)	37	3580.5	78.1%	39.4%	47.7%	NA	NA	NA	NA
θ(H,M,L) q(H,M,L) *M*(TV,H,M,L)	27	3580.5	78.2%	40.1%	51.6%	NA	NA	NA	NA
θ(•,L) q(TV, •,L) *M*(TV,H,M,L)	34	3580.8	67.7%	67.7%	46.1%	NA	NA	NA	NA
θ(H,M,L) q(TV,H,M,L) *M*(TV,•)	28	3581.0	78.4%	39.0%	51.7%	NA	NA	NA	NA
θ(•,L) q(TV,H,M,L) *M*(TV,H,M,L)	38	3581.0	67.0%	67.0%	46.1%	NA	NA	NA	NA
θ(•) q(TV, •,L) *M*(TV,•,L)	32	3581.1	65.5%	65.5%	65.5%	NA	NA	NA	NA
θ(H,M,L) *q*(•) *M*(TV,•,L)	9	3581.3	74.1%	53.6%	58.8%	NA	NA	NA	NA
θ(H,M,L) *q*(TV, •) *M*(TV,H,M,L)	31	3581.5	75.7%	43.5%	52.6%	NA	NA	NA	NA
θ(•) *q*(•) *M*(TV,•,L)	7	3581.5	66.5%	66.5%	66.5%	NA	NA	NA	NA

NA = models were not fit to this dataset and lake combination


91°
89°
87°
85°
Lake Superior
49°
47°
N
Marquette
0 100 Kilometers

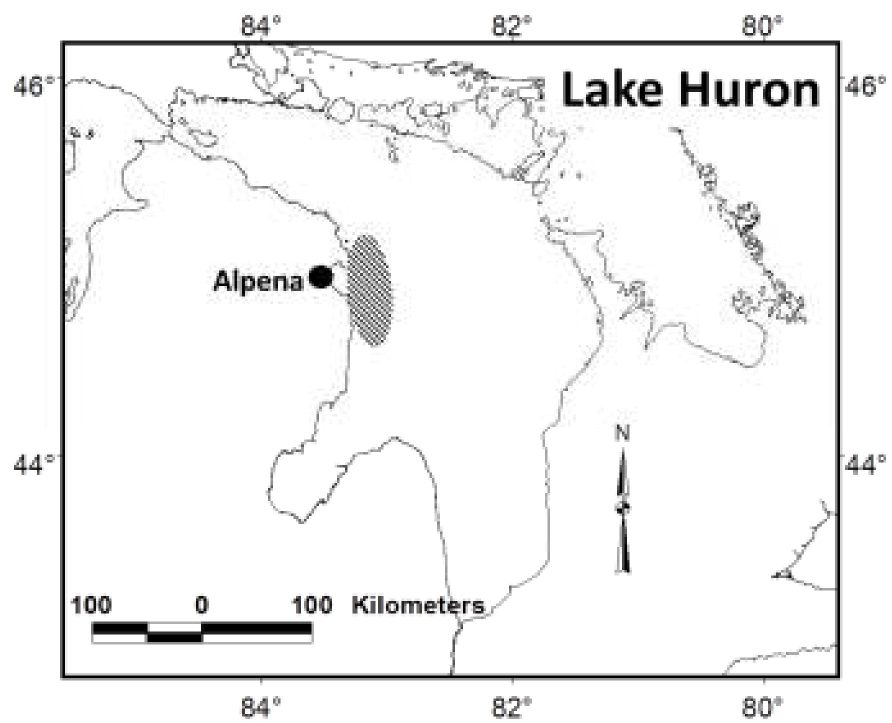

84°
82°
80°
Lake Huron
46°
44°
Alpena
N
100 0 100 Kilometers

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

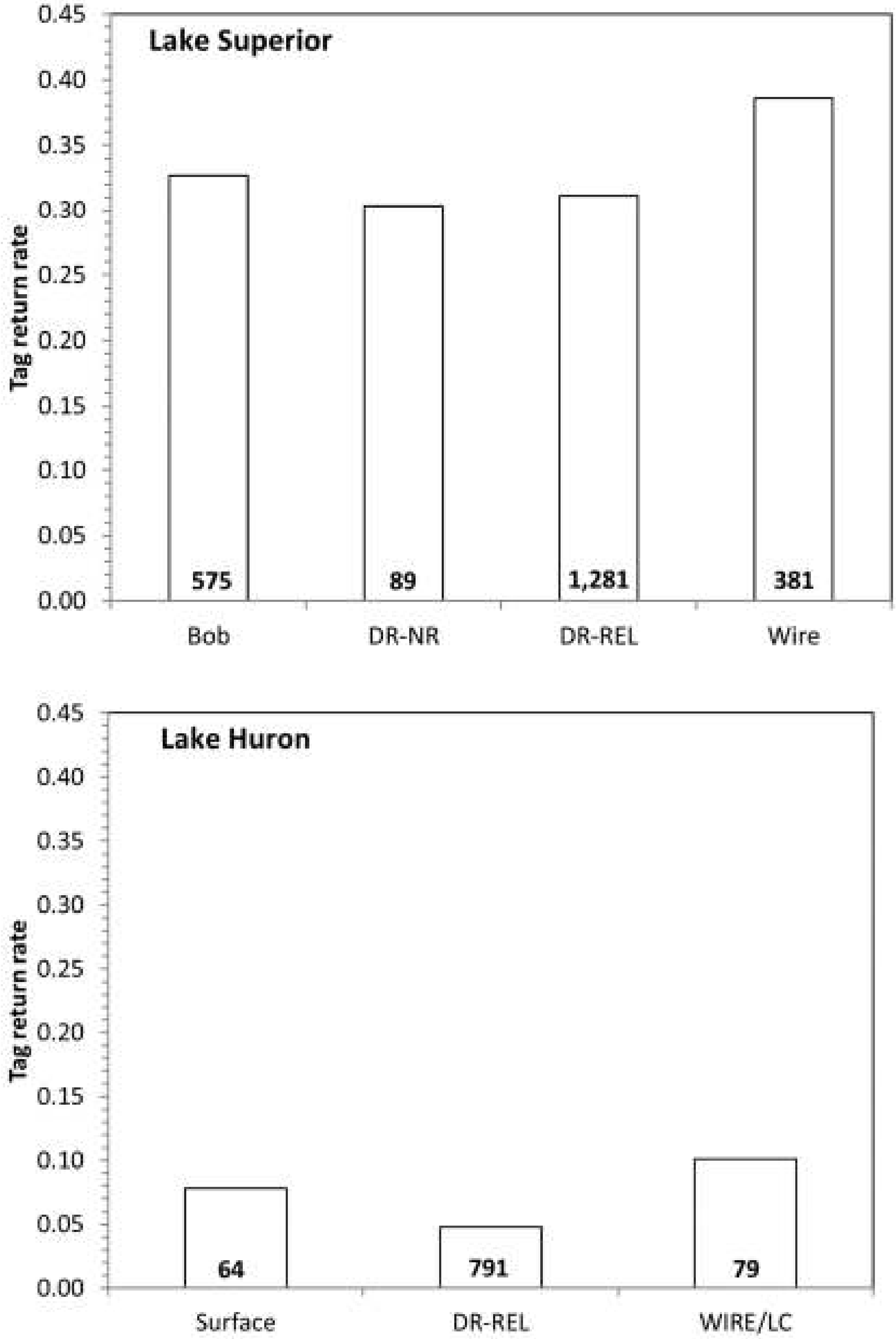
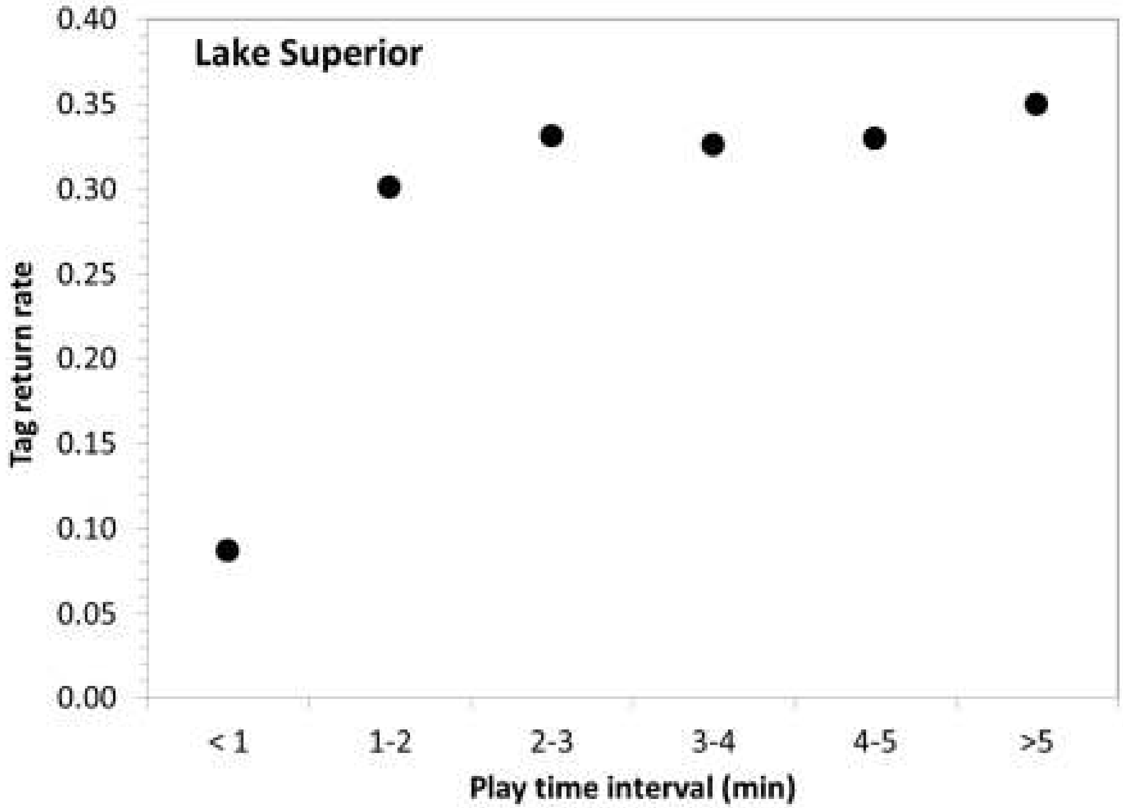


Figure 2. Tag return rates by fishing method (Table 1) for Lake Trout tagged by volunteer anglers in Lake Superior and Lake Huron. None of the return rates

were statistically different within each lake (Marascuilo procedure: $P < 0.05$, Tables A.3, A.4). At bottom center of each column is the number of fish tagged by fishing method.


Lake Superior
Tag return rate
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
< 1
1-2
2-3
3-4
4-5
>5
Play time interval (min)

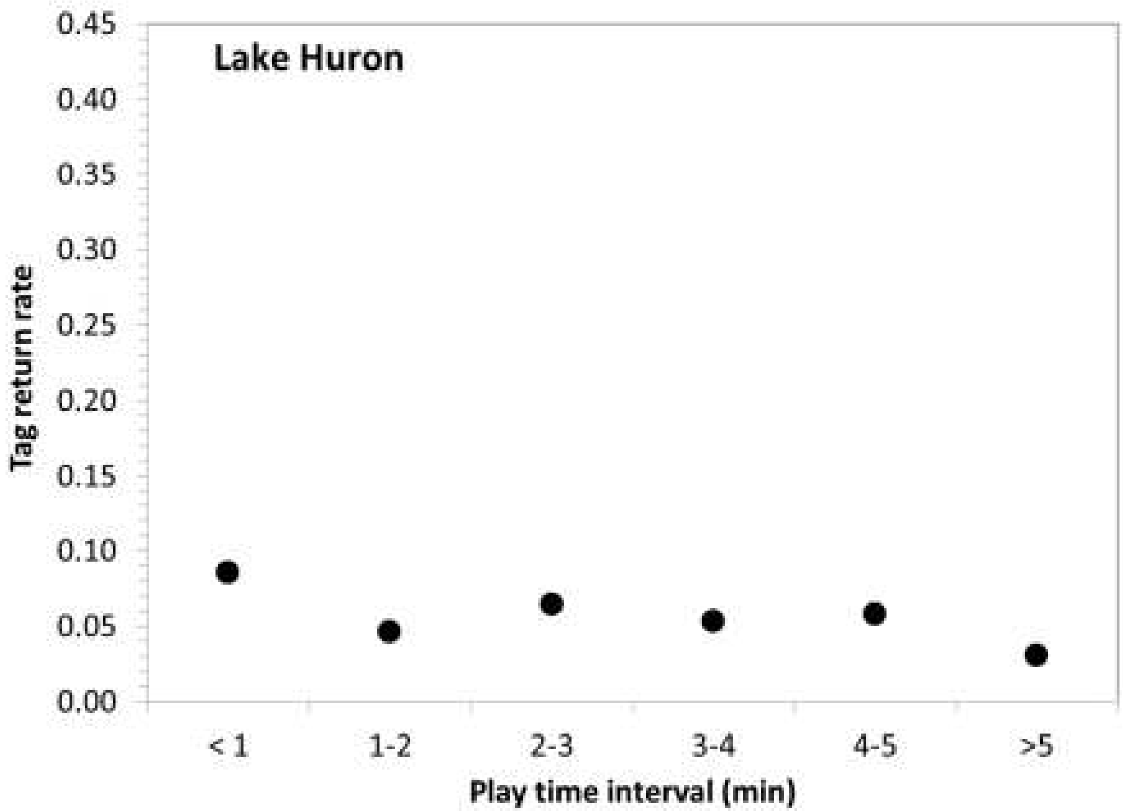
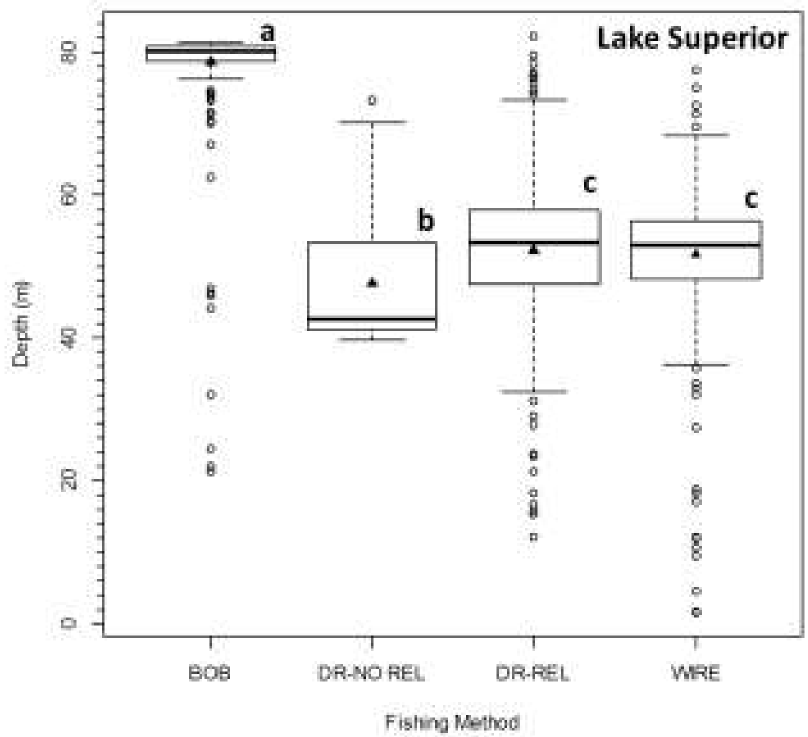

Lake Huron
Tag return rate
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
< 1
1-2
2-3
3-4
4-5
>5
Play time interval (min)

Figure 3. Tag return rate by play time for Lake Trout caught and tagged by volunteer anglers in Lake Superior and Lake Huron.


Lake Superior
a
b
c
c
Depth (m)
0
20
40
60
80
BOB
DR-NO REL
DR-REL
WIRE
Fishing Method

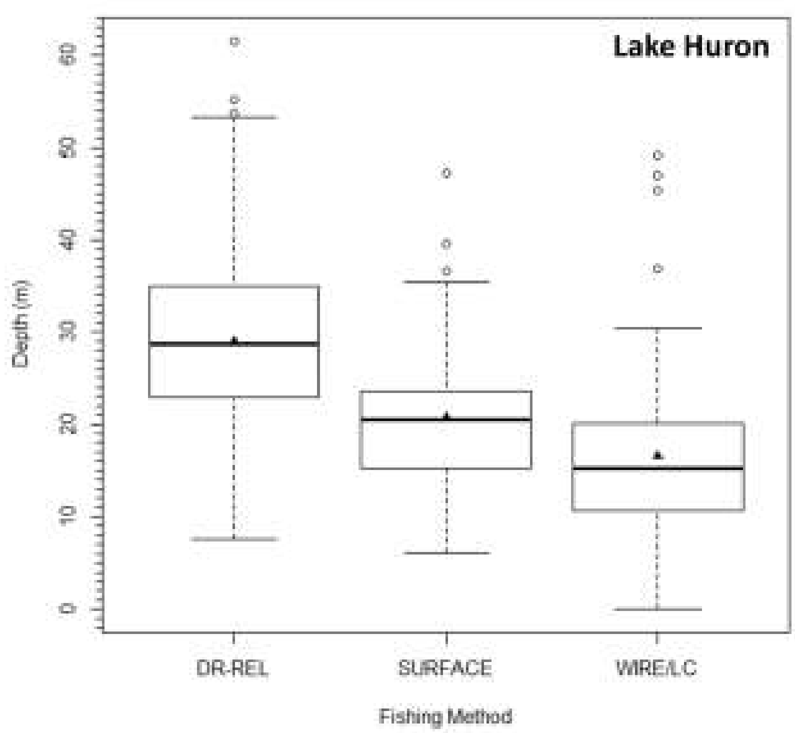
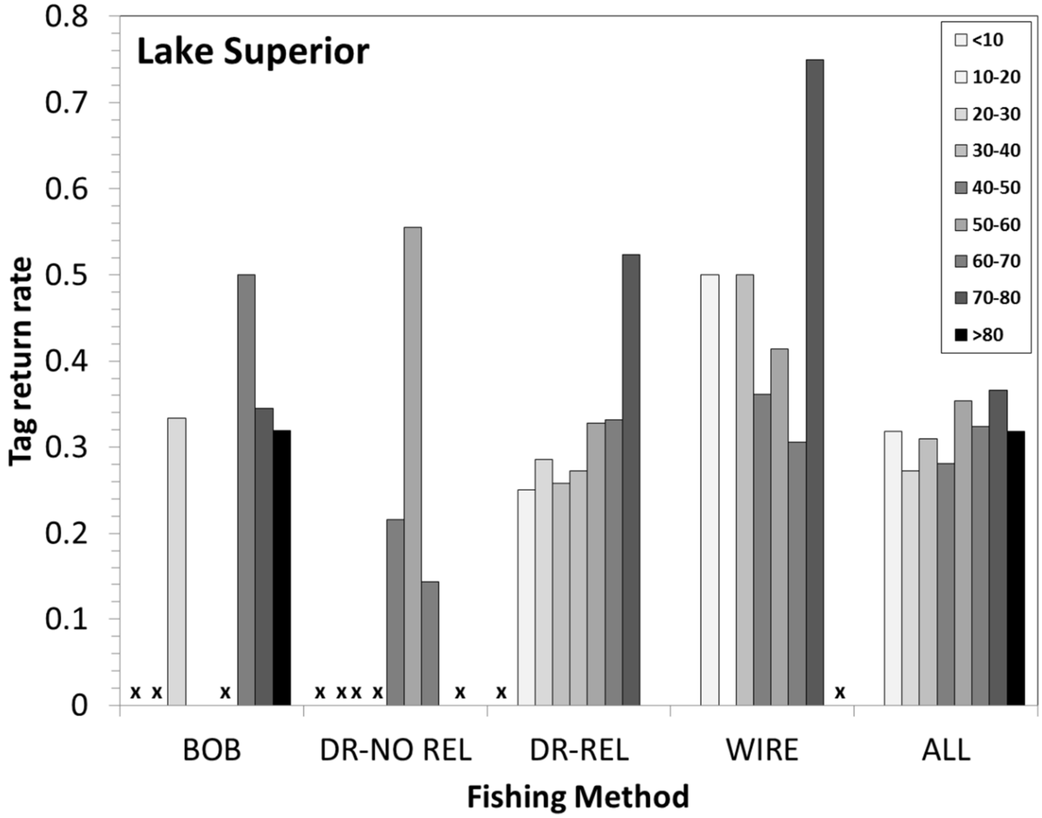

Lake Huron
Depth (m)
0
10
20
30
40
50
60
DR-REL
SURFACE
WIRE/LC
Fishing Method

Figure 4. Box plots of capture depth of Lake Trout tagged by volunteer anglers in Lake Superior (top panel) and Lake Huron (bottom panel) compared among different fishing methods (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* interquartile range of the 25th and 75th percentiles, and the dots are outliers. Mean Depth is indicated by solid triangles. Different letters indicate statistical difference ($P < 0.05$) between fishing methods based on Kruskal-Wallis Test followed with multiple comparisons using Nemenyi post-hoc test.


Lake Superior
Tag return rate
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
<10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
>80
BOB
DR-NO REL
DR-REL
WIRE
ALL
Fishing Method

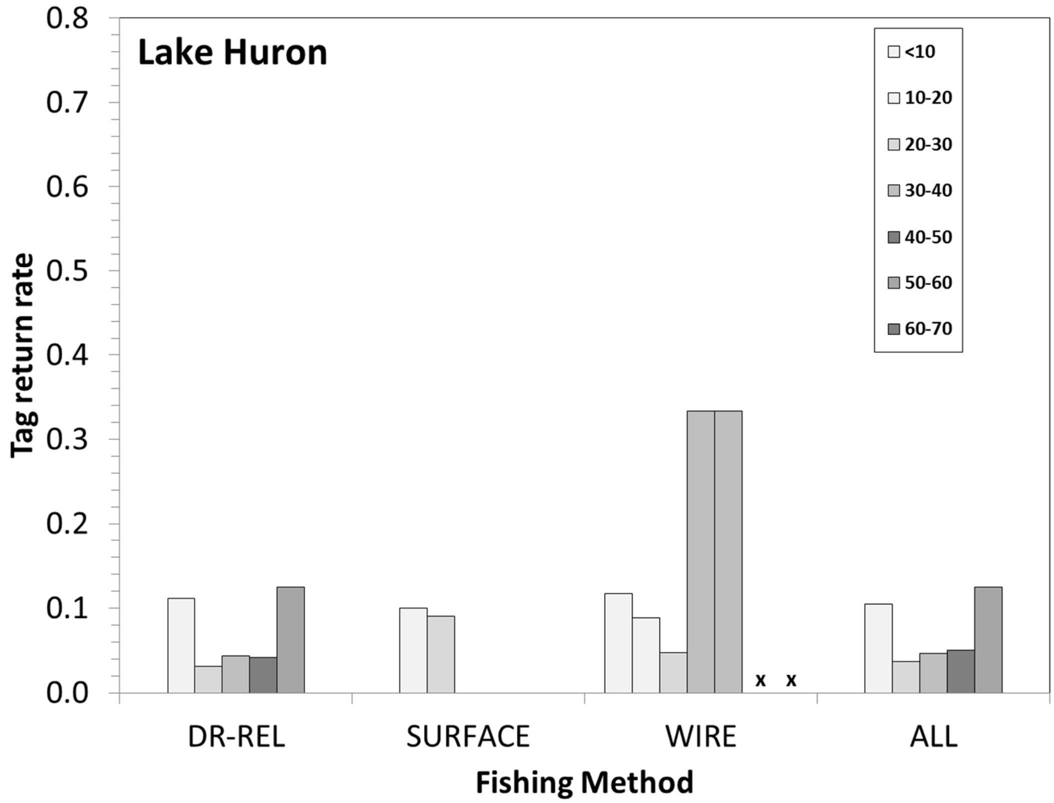
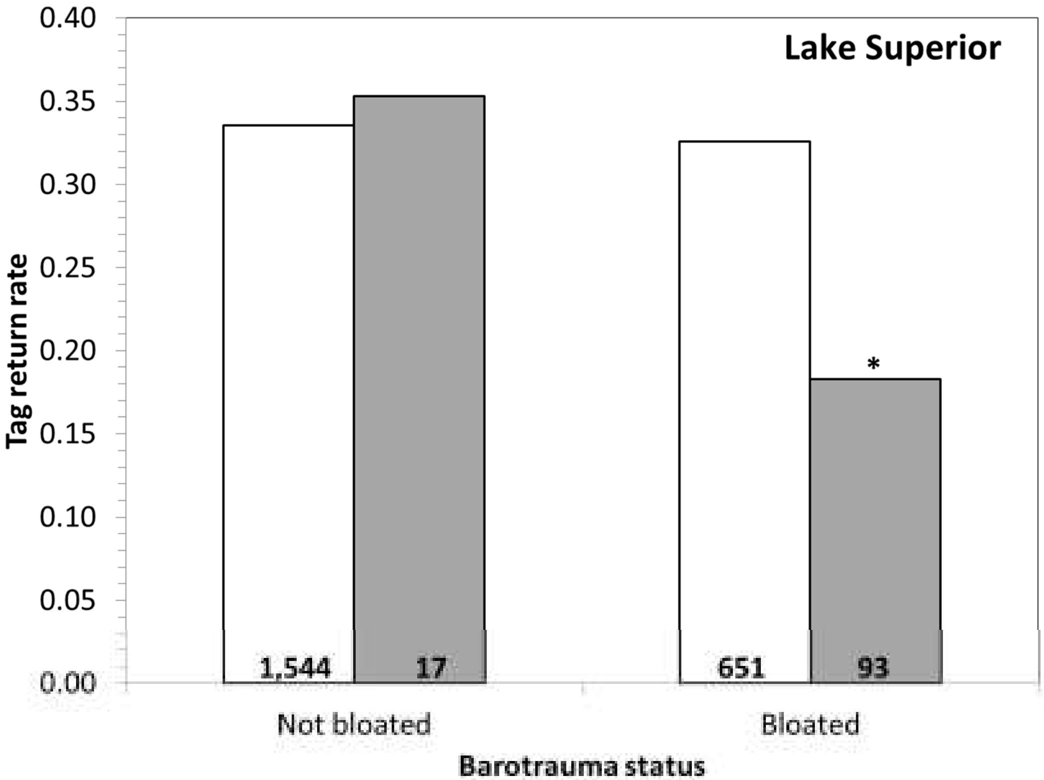

Lake Huron
Tag return rate
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
<10
10-20
20-30
30-40
40-50
50-60
60-70
DR-REL
SURFACE
WIRE
ALL
Fishing Method

Figure 5. Tag return rate by capture depth (m) and fishing method (Table 1) for Lake Trout caught and tagged in Lake Superior and Lake Huron. X= no data for depth interval.


Lake Superior
Tag return rate
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
*
1,544
17
651
93
Not bloated
Bloated
Barotrauma status

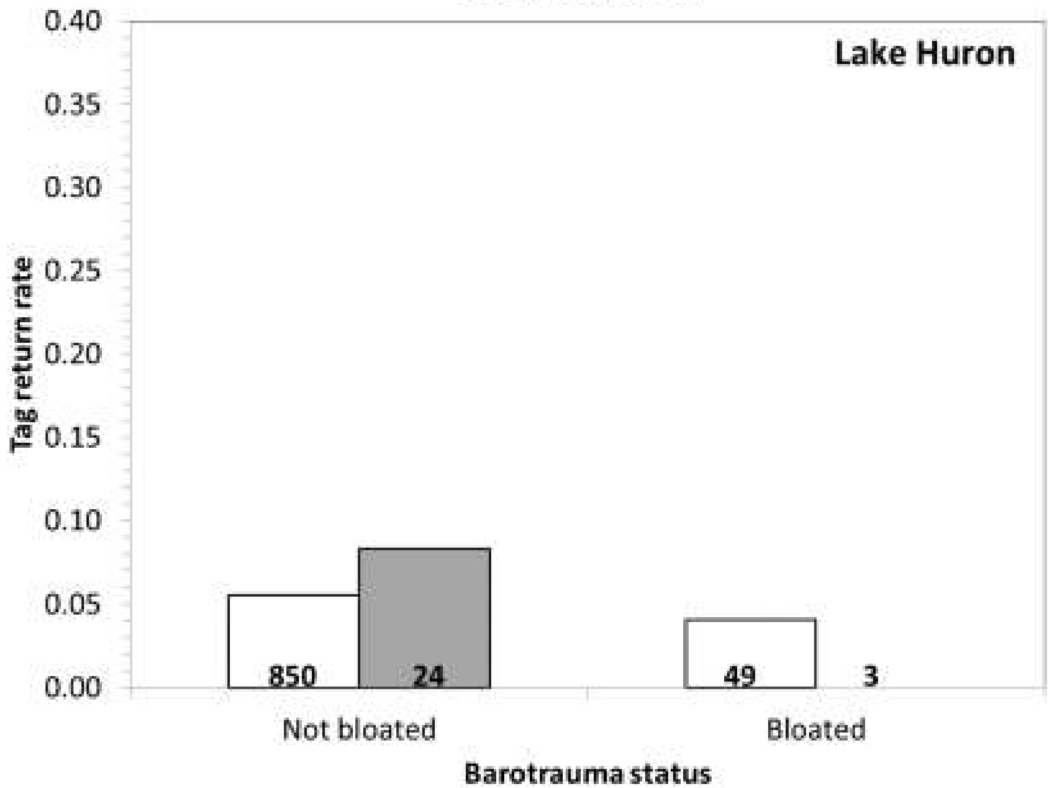
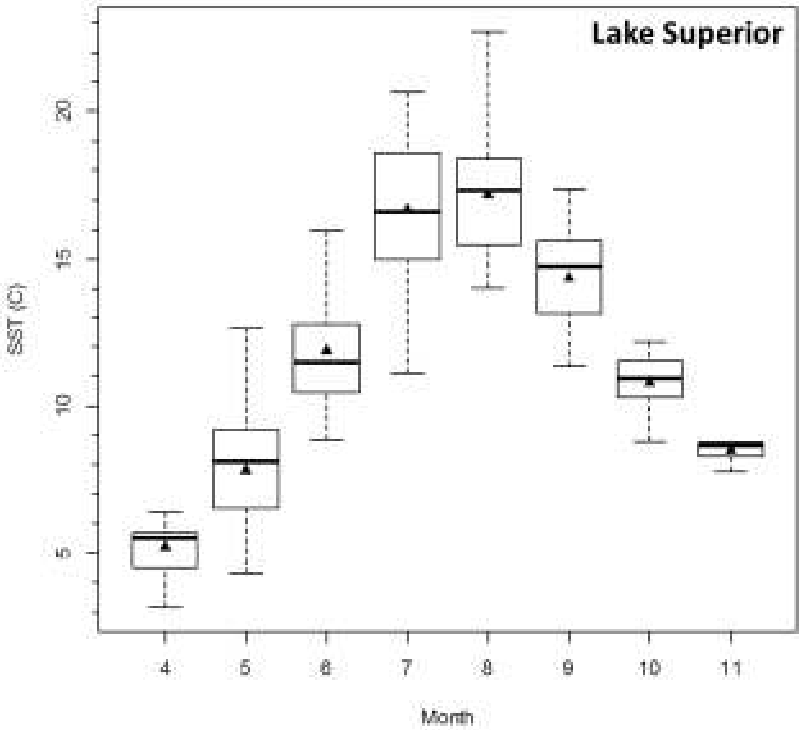

Lake Huron
Tag return rate
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
850
24
49
3
Not bloated
Bloated
Barotrauma status

Figure 6. Influence of barotrauma and incidence of gulls on tag return rate for Lake Trout tagged by volunteer anglers in Lake Superior and Lake Huron. At bottom center of each column is number of fish tagged. White columns represent return rates when gulls were not present upon release, gray columns are return rates for fish released in the presence of gulls. *=statistically different tag return rate for gull presence (2x2 Contingency table analysis: $P < 0.05$).


Lake Superior
SST (C)
5
10
15
20
Month
4
5
6
7
8
9
10
11

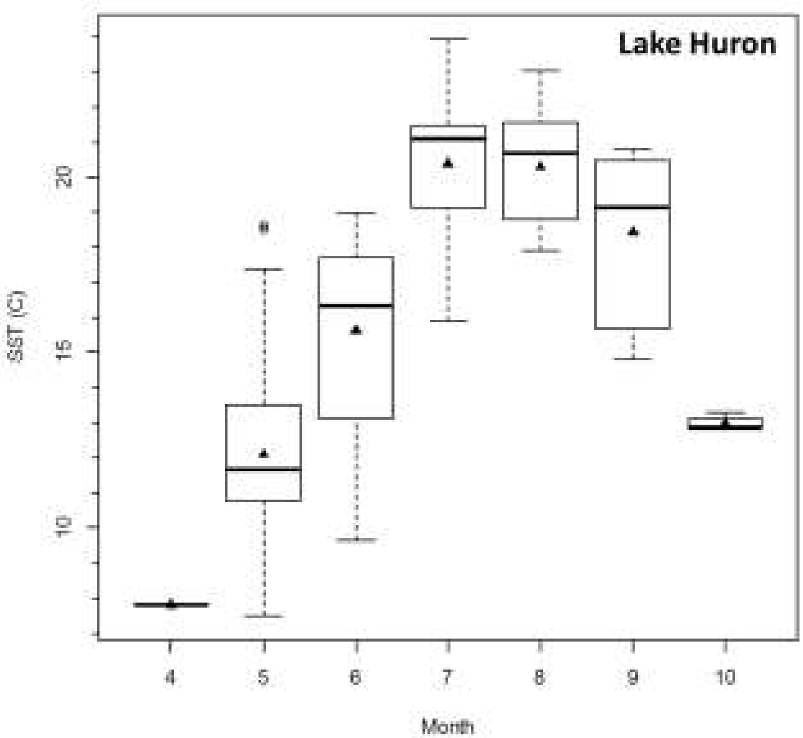
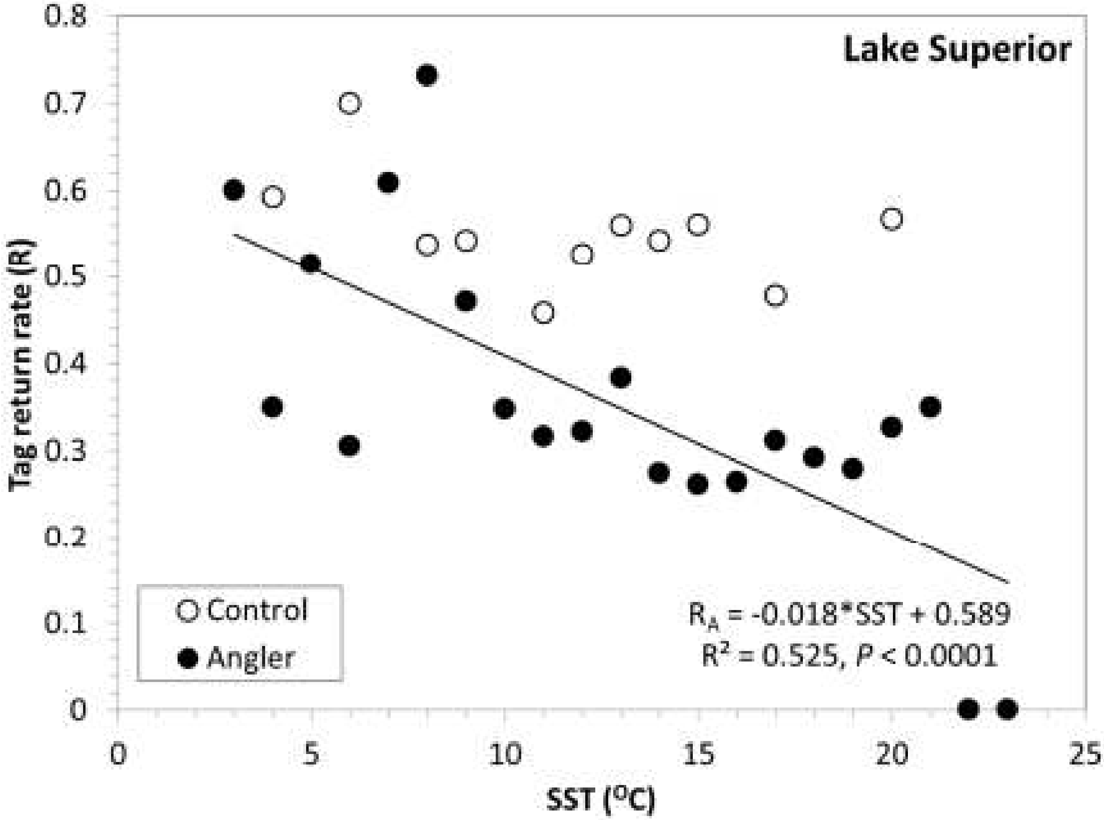

Lake Huron
SST (C)
10
15
20
Month
4
5
6
7
8
9
10

Figure 7. Box plot of surface temperature (ST) at time of release for Lake Trout tagged by volunteer boat-anglers in Lake Superior (top) and Lake Huron (bottom) 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* interquartile range of the 25th and 75th percentiles, and the dots are outliers. Mean monthly ST is shown by solid triangles.


Lake Superior
Tag return rate (R)
SST (°C)
Control
Angler
R_A = -0.018*SST + 0.589
R^2 = 0.525, *P* < 0.0001
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25

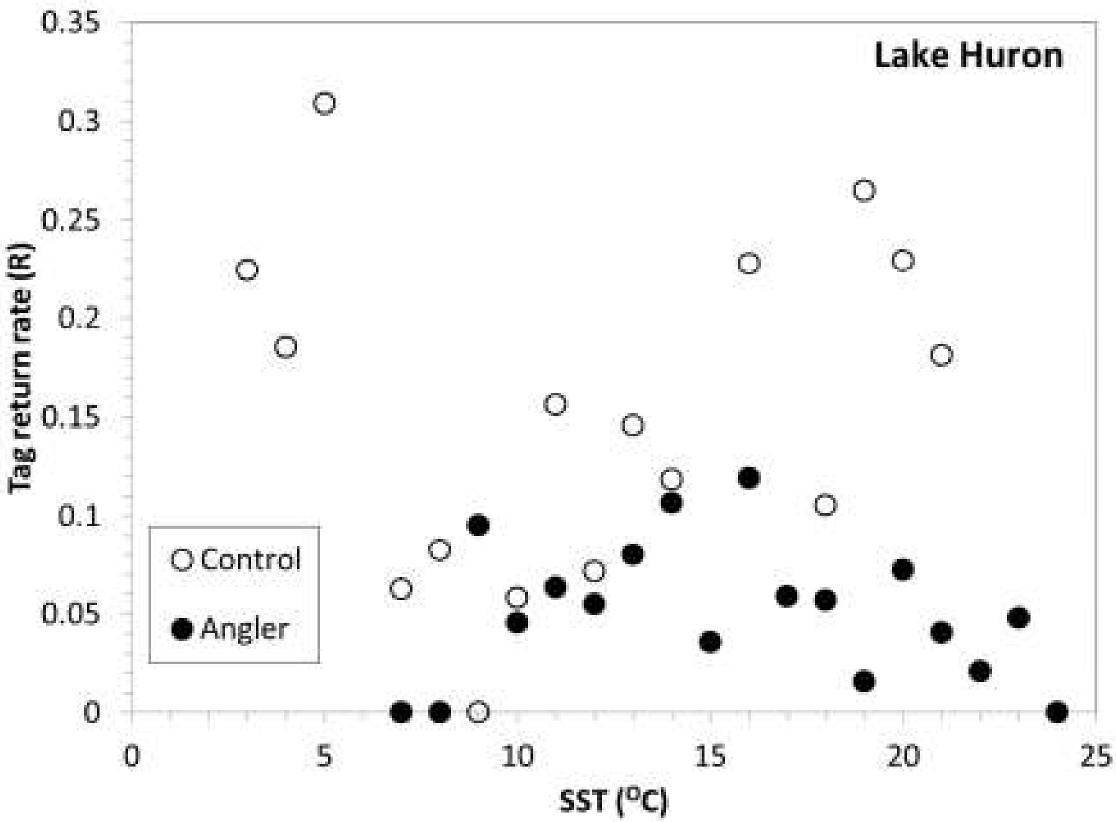

Lake Huron
Tag return rate (R)
SST (°C)
Control
Angler
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0
5
10
15
20
25

Figure 8. Relationship between Tag return rate (*R*) and surface temperature (ST) for Lake Superior (top) and Lake Huron (bottom) for angler and control group tagged Lake Trout during 2010-2013.

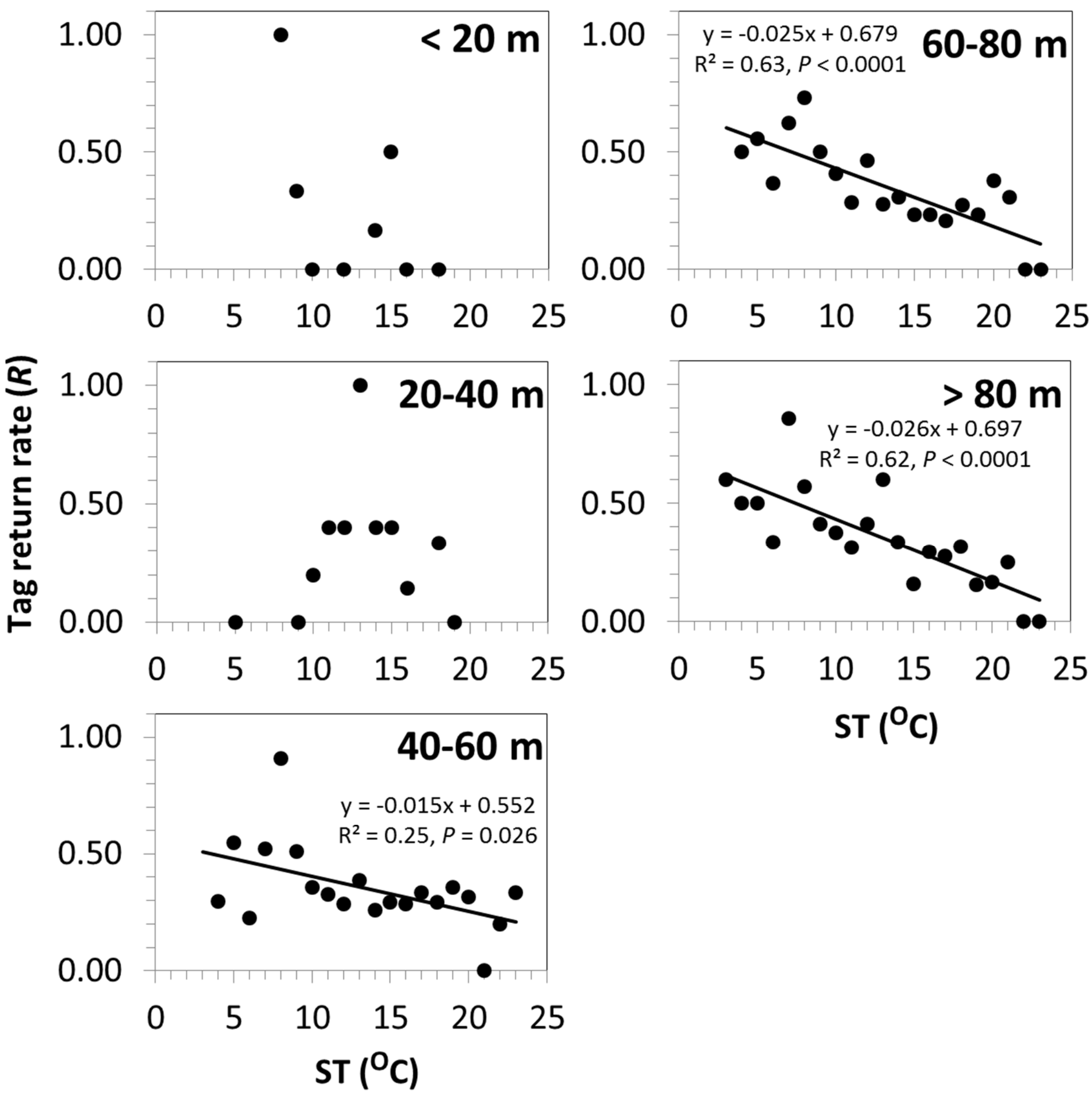


Figure 9. Relationship between tag return rate (R) and surface temperature (ST) by depth of capture for Lake Trout caught and released by volunteer anglers in Lake Superior.

Appendix: Detailed Data

Table A.1. Marascuilo procedure for all pairwise comparisons of tag return rates according to angler handling times for Lake Trout tagged in Lake Superior. Handling time intervals were < 1, 1-1.5, 1.5-2, 2-2.5, >2.5 min. Marascuilo test statistics: a= absolute difference in proportions, r= critical value, Sig= Statistical significance at α=0.05 indicated by yes or no.

Comparison pair	a	r	a-r	Sig
< 1 versus 1-1.5 min	0.011	0.102	-0.091	no
< 1 versus 1.5-2 min	0.013	0.117	-0.104	no
< 1 versus 2-2.5 min	0.045	0.166	-0.121	no
< 1 versus > 2.5 min	0.035	0.210	-0.175	no
1-1.5 versus 1.5-2 min	0.002	0.098	-0.096	no
1-1.5 versus 2-2.5 min	0.034	0.153	-0.119	no
1-1.5 versus > 2.5 min	0.046	0.098	-0.052	no
1.5-2 versus 2-2.5 min	0.032	0.163	-0.130	no
2-2.5 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 for Lake Trout tagged in Lake Huron. Handling time intervals were < 1, 1-1.5, 1.5-2, 2-2.5, >2.5 min. Marascuilo test statistics: *a*= absolute difference in proportions, *r*= critical value, Sig= Statistical significance at $\alpha=0.05$ indicated by yes or no.

Comparison pair	a	r	a-r	Sig
< 1 versus 1-1.5 min	0.003	0.063	-0.060	no
< 1 versus 1.5-2 min	0.016	0.097	-0.081	no
< 1 versus 2-2.5 min	0.054	0.161	-0.107	no
< 1 versus > 2.5 min	0.038	0.152	-0.113	no
1-1.5 versus 1.5-2 min	0.019	0.098	-0.079	no
1-1.5 versus 2-2.5 min	0.057	0.162	-0.105	no
1-1.5 versus > 2.5 min	0.041	0.098	-0.056	no
1.5-2 versus 2-2.5 min	0.038	0.177	-0.140	no
2-2.5 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 described in Table 1. Marascuilo test statistics: *a*= absolute difference in proportions, *r*= critical value, Sig= Statistical significance at α=0.05 indicated by yes or no.

Comparison pair	a	r	a-r	Sig
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 described in Table 1. Marascuilo test statistics: *a*= absolute difference in proportions, *r*= critical value, Sig= Statistical significance at α=0.05 indicated by y(yes) or n(no).

Comparison pair	*a*	*r*	*a-r*	Sig
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 (min) for each fishing method for Lake Trout tagged in Lake Superior. Play time intervals are: p1= < 1 min, p2= 1-2 min, p3= 2-3 min, p4= 3-4 min, p5= 4-5 min, p6= > 5 min. Fishing methods described in Table 1. Marascuilo test statistics: *a*= absolute difference in proportions, *r*= critical value, Sig= Statistical significance at $\alpha=0.05$ indicated by y(yes) or n(no). There were no fish caught by Bob method with play times > 4 min, by DR-NR and WIRE with play times < 1 min.

	Bob				DR-NR				DR-REL				WIRE			
Pair	*a*	*r*	*a-r*	Sig	*a*	*r*	*a-r*	Sig	*a*	*r*	*a-r*	Sig	*a*	*r*	*a-r*	Sig
p1 v p2	0.19	0.41	-0.22	n				n	0.30	0.16	0.14	y				
p1 v p3	0.18	0.37	-0.19	n				n	0.34	0.08	0.25	y				
p1 v p4	0.31	0.56	-0.25	n				n	0.32	0.08	0.24	y				
p1 v p5								n	0.30	0.12	0.18	y				
p1 v p6								n	0.30	0.11	0.19	y				
p2 v p3	0.01	0.19	-0.18	n	0.05	0.37	-0.33	n	0.04	0.18	-0.13	n	0.03	0.73	-0.70	n
p2 v p4	0.12	0.46	-0.34	n	0.09	0.43	-0.34	n	0.02	0.17	-0.15	n	0.03	0.70	-0.67	n
p2 v p5					0.20	0.64	-0.44	n	0.01	0.20	-0.19	n	0.03	0.69	-0.66	n
p2 v p6					0.52	0.72	-0.20	n	0.00	0.19	-0.19	n	0.00	0.68	-0.68	n
p3 v p4	0.13	0.42	-0.30	n	0.13	0.42	-0.28	n	0.02	0.11	-0.09	n	0.07	0.34	-0.27	n
p3 v p5					0.25	0.63	-0.38		0.04	0.15	-0.11	n	0.06	0.32	-0.26	n
p3 v p6					0.57	0.71	-0.15		0.04	0.14	-0.10	n	0.04	0.30	-0.26	n
p4 v p5					0.11	0.66	-0.55		0.01	0.14	-0.13	n	0.00	0.25	-0.24	n
p4 v p6					0.43	0.74	-0.31		0.02	0.13	-0.11	n	0.03	0.22	-0.19	n
p5 v p6					0.32	0.88	-0.56		0.01	0.16	-0.16	n	0.03	0.19	-0.17	n

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

	SURF				DR-REL				WIRE/LC			
Pair	*a*	*r*	*a-r*	Sig	*a*	*r*	*a-r*	Sig	*a*	*r*	*a-r*	Sig
p1 v p2	0.05	0.17	-0.12	n	0.04	0.11	-0.07	n	0.07	0.23	-0.16	n
p1 v p3	0.17	0.36	-0.19	n	0.03	0.12	-0.09	n	0.06	0.19	-0.13	n
p1 v p4	0.05	0.16	-0.11	n	0.06	0.12	-0.06	n	0.27	0.38	-0.11	n
p1 v p5	0.11	0.35	-0.24	n	0.04	0.15	-0.11	n	0.06	0.20	-0.14	n
p1 v p6	0.00	0.00	0.00	n	0.07	0.13	-0.06	n	0.06	0.20	-0.14	n
p2 v p3	0.11	0.40	-0.28	n	0.01	0.07	-0.06	n	0.01	0.30	-0.29	n
p2 v p4	0.01	0.23	-0.23	n	0.02	0.06	-0.04	n	0.20	0.44	-0.25	n
p2 v p5	0.06	0.39	-0.33	n	0.00	0.11	-0.11	n	0.01	0.31	-0.30	n
p2 v p6	0.05	0.17	-0.12	n	0.02	0.08	-0.06	n	0.01	0.31	-0.30	n
p3 v p4	0.12	0.39	-0.27	n	0.03	0.08	-0.04	n	0.21	0.43	-0.22	n
p3 v p5	0.06	0.50	-0.44	n	0.01	0.12	-0.11	n	0.00	0.28	-0.27	n
p3 v p6	0.17	0.36	-0.19	n	0.04	0.09	-0.05	n	0.00	0.28	-0.27	n
p4 v p5	0.06	0.38	-0.32	n	0.02	0.12	-0.10	n	0.20	0.43	-0.23	n
p4 v p6	0.05	0.16	-0.11	n	0.01	0.09	-0.08	n	0.20	0.43	-0.23	n
p5 v p6	0.11	0.35	-0.24	n	0.02	0.13	-0.10	n	0.00	0.29	-0.29	n

Table A.7. Marascuilo procedure for all pairwise comparisons of tag return rates by depth of capture interval (m) for all fishing methods combined for Lake Trout tagged in Lake Superior. Fishing methods described in Table 1. Marascuilo test statistics: a= absolute difference in proportions, r= critical value, Sig= Statistical significance at $\alpha=0.05$ indicated by y(yes) or n(no).

Comparison pair	*a*	*r*	*a-r*	Sig
< 20 versus 20-30 m	0.003	0.6	-0.597	n
< 20 versus 30-40 m	0.04	0.422	-0.382	n
< 20 versus 40-50 m	0.011	0.335	-0.323	n
< 20 versus 50-60 m	0.084	0.332	-0.248	n
< 20 versus 60-70 m	0.055	0.344	-0.288	n
< 20 versus 70-80 m	0.097	0.348	-0.251	n
< 20 versus > 80 m	0.049	0.339	-0.29	n
20-30 versus 30-40 m	0.037	0.57	-0.533	n
20-30 versus 40-50 m	0.008	0.509	-0.501	n
20-30 versus 50-60 m	0.081	0.507	-0.427	n
20-30 versus 60-70 m	0.052	0.515	-0.463	n
20-30 versus 70-80 m	0.093	0.518	-0.425	n
20-30 versus > 80 m	0.045	0.512	-0.467	n
30-40 versus 40-50 m	0.029	0.278	-0.249	n
30-40 versus 50-60 m	0.044	0.274	-0.231	n
30-40 versus 60-70 m	0.015	0.288	-0.273	n
30-40 versus 70-80 m	0.057	0.294	-0.237	n
30-40 versus > 80 m	0.008	0.283	-0.274	n
40-50 versus 50-60 m	0.073	0.096	-0.024	n
40-50 versus 60-70 m	0.044	0.131	-0.087	n
40-50 versus 70-80 m	0.085	0.142	-0.056	n
40-50 versus > 80 m	0.037	0.118	-0.08	n
50-60 versus 60-70 m	0.029	0.124	-0.095	n
50-60 versus 70-80 m	0.013	0.135	-0.123	n
50-60 versus > 80 m	0.035	0.11	-0.074	n
60-70 versus 70-80 m	0.042	0.162	-0.12	n
60-70 versus > 80 m	0.007	0.141	-0.135	n
70-80 versus > 80 m	0.048	0.151	-0.103	n

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

Comparison pair	*a*	*r*	*a-r*	Sig
< 10 versus 10-20 m	0.031	0.186	-0.155	n
< 10 versus 20-30 m	0.037	0.171	-0.134	n
< 10 versus 30-40 m	0.028	0.173	-0.145	n
< 10 versus 40-50 m	0.024	0.183	-0.159	n
< 10 versus > 50 m	0.037	0.387	-0.35	n
10-20 versus 20-30 m	0.068	0.086	-0.019	n
10-20 versus 30-40 m	0.059	0.091	-0.032	n
10-20 versus 40-50 m	0.055	0.108	-0.053	n
10-20 versus > 50 m	0.006	0.358	-0.351	n
20-30 versus 30-40 m	0.009	0.054	-0.045	n
20-30 versus 40-50 m	0.013	0.079	-0.067	n
20-30 versus > 50 m	0.074	0.35	-0.276	n
30-40 versus 40-50 m	0.004	0.084	-0.081	n
30-40 versus > 50 m	0.065	0.351	-0.286	n
40-50 versus > 50 m	0.061	0.356	-0.295	n