QUANTIFYING THE SPATIAL STRUCTURE OF INVASIVE LAKE TROUT IN YELLOWSTONE LAKE TO IMPROVE SUPPRESSION EFFICACY

by

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ABSTRACT

Conserving Yellowstone Cutthroat Trout by suppressing invasive Lake Trout in Yellowstone Lake is a high priority for Yellowstone National Park natural-resource managers. Insight into the spatial structure of Lake Trout throughout the lake will help increase the efficacy of the Lake Trout suppression program. Lake Trout (N = 578) were surgically implanted with dual acoustic and radio transmitters from 2015 through 2017. Mobile acoustic (boat) and radio (fixed-wing aircraft) telemetry surveys were performed to identify aggregations of Lake Trout. Telemetry surveys occurred during the spawning period (autumn) in 2016 and during the summer and spawning period in 2017. Lake Trout exhibited distinct aggregations during the summer and spawning period. Lake Trout aggregated at nine locations during the summer 2017 and were most frequently located in the West Thumb. Lake Trout aggregated at 22 locations during the spawning period including 12 previously undocumented putative spawning locations. Two aggregations in the West Thumb, Carrington Island and Anglers Bluff, had the highest relative densities of Lake Trout. Aggregations during the summer were generally farther from shore, greater in depth, and more dispersed than aggregations during the spawning period. Targeting locations of Lake Trout, as identified through telemetry, with gill nets was an effective strategy for increasing catch-per-unit-effort. The Lake Trout suppression program is probably altering the behavior of Lake Trout in Yellowstone Lake, which explains the high number of spawning locations and low spawning site fidelity relative to other research studies on Lake Trout spawning behavior. This study provided valuable insight into the spatial structure of Lake Trout in Yellowstone Lake. The areas Lake Trout aggregated will continue to be targeted by gillnetting and novel embryo suppression methods.

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Introduction

Non-native species introductions are common in aquatic ecosystems, with fishes being one of the most introduced and threatened aquatic taxa (1,201 threatened species; Gozlan et al. 2010). The number of non-native introductions is increasing world-wide (Gozlan et al. 2010), and the number of non-native fish species in North America has doubled since 1970 (Matlock 2014). A non-native species becomes invasive when it causes adverse ecological effects including the decline or extirpation of native species (Beck et al. 2006; Britton et al. 2011). The Convention on Biological Diversity defines an invasive species as "an alien species whose introduction and/or spread threaten biological diversity" (CBD 2008). Invasive fishes are a contributing factor in 68% of extinctions and 70% of fishes listed as endangered or threatened by the US government (Miller et al. 1989; Jelks et al. 2008).

Lake Trout *Salvelinus namaycush* are an important commercial and sport fish that have been widely introduced in North America (Crossman 1995). Through predation, competition, or both, invasive Lake Trout have been a factor in the decline of salmonid populations throughout the Intermountain West (Martinez et al. 2009; Guy et al. 2011; Cox et al. 2013; Syslo et al. 2013; Fredenberg et al. 2017). For example, the introduction of invasive Lake Trout into Lake Tahoe led to the extirpation of native Lahontan Cutthroat Trout *Oncorhynchus clarkii henshawi* (Crossman 1995). By the end of the

20th century, invasive Lake Trout had replaced Bull Trout *S. confluentus* as the most abundant salmonid in several lakes in Glacier National Park (Fredenberg 2002).

Lake Trout within their native range have been overexploited because they are long lived, slow growing, late maturing, and have a low adult replacement rate (Shuter et al. 1998). Commercial harvest contributed to the collapse of the Lake Trout fishery in all the Laurentian Great Lakes (Hartman 1972; Wells and McLain 1972; Coble et al. 1990; Hansen et al. 1995; Muir et al. 2012). Given the vulnerability of Lake Trout to overexploitation in their native range, natural-resource managers in the Intermountain West have implemented suppression programs to mitigate the negative effects of Lake Trout on native fishes (Koel et al. 2005; Hansen et al. 2008; Martinez et al. 2009; Hansen et al. 2016).

Lake Trout were first discovered in Yellowstone Lake in 1994 and were believed to have been introduced in the mid-1980s (Kaeding et al. 1996; Munro et al. 2005). The introduction and establishment of invasive Lake Trout are a threat to the largest population of genetically unaltered Yellowstone Cutthroat Trout *O. clarkii bouvieri* (Endicott et al. 2016). An adult Lake Trout can consume 20 – 32 Cutthroat Trout per year (Syslo et al. 2016), which has resulted in a decline of Cutthroat Trout abundance over the last three decades (Koel et al. 2015). Cutthroat Trout are an important ecological resource within the Yellowstone Lake ecosystem because they are a food source for terrestrial species such as grizzly bears *Ursus arctos horribilis* and osprey *Pandion haliaeetus* (Koel et al. 2005; Koel et al. in press). Cutthroat Trout are also targeted by anglers and nonconsumptive users making them a valuable socio-economic

resource (Gresswell and Liss 1995; Koel et al. 2005). The Cutthroat Trout population in Yellowstone Lake ranks as one of the highest in conservation value for the persistence of the species (Al-Chokhachy et al. 2018). The National Park Service implemented gillnetting in 1995 to suppress Lake Trout abundance, which would reduce the negative effects of Lake Trout on the Cutthroat Trout population (Koel et al. 2007). About 3.2 million Lake Trout have been removed since suppression began (Todd Koel, National Park Service, personal communication) and population modeling indicates the present suppression effort is resulting in a decrease in adult Lake Trout abundance (Travis Brenden, Michigan State University, personal communication).

The current Lake Trout suppression effort in Yellowstone Lake is costly—about two million US dollars per year to meet the management objectives (Koel et al. 2010). Suppression programs are often expensive and monetarily burdensome to natural-resource agencies worldwide (Veitch and Clout 2002; Simberloff et al. 2005; Simberloff 2014). Improving the efficacy and cost-effectiveness of a suppression program are top priorities for natural-resources agencies (Buhle et al. 2005); nevertheless many suppression programs fail to meet management objectives (Gozlan et al. 2010; Britton et al. 2011). When suppression effort is limited, using the most efficient gear at the time when the target species is most vulnerable can increase the efficacy of suppression (Britton et al. 2011). Some suppression programs have invested in research to develop novel suppression methods that will increase suppression efficacy and minimize suppression effects on non-target species (Christie and Goddard 2003; Britton et al. 2011; Brown and Gilligan 2014). Suppression of Lake Trout is a high priority in Yellowstone

National Park, and the National Park Service has invested in research and development of novel suppression methods (Doepke et al. 2017). Lake Trout embryo suppression methods show promise in Yellowstone Lake; for example, mortality of Lake Trout embryos was nearly 100% in Lake Trout carcass-deposition experiments (Thomas et al. in press), and lab trials with Lake Trout carcass analog pellets produced similar results (Alex Poole, Montana State University, unpublished data). For these novel methods to be successful, all Lake Trout spawning areas need to be identified.

Understanding the spatial structure of invasive species can improve suppression efficacy (Travis and Park 2004). Telemetry is used in the suppression of invasive fishes by identifying aggregations that can be targeted (Penne and Pierce 2008; Lechelt et al. 2016; Lennox et al. 2016; Crossin et al. 2017, Rust et al. 2018). For targeting locations to be effective, the target species must be social or form aggregations at some point during its life history. Many fish species form aggregations at some point during their life history (Pitcher 1986); therefore, targeting these locations can be an effective strategy for suppressing invasive fishes. For example, targeting aggregations of invasive Common Carp *Cyprinus carpio* was successful at suppressing the adult population in experimental lakes (Bajer et al. 2011). Mature Lake Trout exhibit shoaling behavior during spawning and also aggregate in preferred environmental conditions during the summer (Martin and Olver 1980; Binder et al. 2014). Thus, targeting aggregations of Lake Trout should increase the efficacy of the Lake Trout suppression program in Yellowstone Lake.

The goal of this study was to quantify the spatial structure of the Lake Trout population in Yellowstone Lake to increase the efficacy of the Lake Trout suppression

program. The objectives of this study were to: 1) identify spawning aggregations of Lake Trout throughout Yellowstone Lake, 2) identify dispersal and aggregations of Lake Trout during the summer and compare these to dispersal and aggregations of Lake Trout during the spawning period, 3) evaluate the efficacy of targeting telemetered aggregations of Lake Trout with gill nets during the summer, and 4) compare Lake Trout locations derived by radio telemetry (fixed-wing aircraft) and acoustic telemetry (boat). Given the understanding of Lake Trout movements from previous studies, I predicted that Lake Trout will exhibit clear aggregations during the spawning period that will differ from those during summer when Lake Trout will be more dispersed and less aggregated. Identifying Lake Trout locations in the summer will increase the efficacy of the suppression program by increasing catch per unit effort. Finally, I predicted that acoustic telemetry would be a more effective method for identifying aggregations than radio telemetry given the depth of Yellowstone Lake, but that radio telemetry could be useful during the spawning season when Lake Trout use shallower habitat.

Study Area

Yellowstone Lake is located in Yellowstone National Park, Wyoming, USA (Figure 1). With a surface area of 34,020 ha, Yellowstone Lake is the largest lake above 2,000 m in North America (Gresswell et al. 1997). Yellowstone Lake has a mean depth of 48 m and maximum depth of 133 m (Kaplinski 1991). In 2017, surface water temperature varied from 1.8˚C in May to 18.6˚C in August with a thermocline developing between 9.5 m and 17.6 m. Yellowstone Lake destratified on 19 September 2017 and

surface water temperatures were below 10˚C for the remainder of the study (Jeff Arnold, National Park Service, unpublished data). The Yellowstone Cutthroat Trout and Longnose Dace *Rhinichthys cataractae* are the only two native fish species in the lake. Four non-native fish species are established; Lake Trout, Longnose Sucker *Catastomous catastomus*, Red Side Shiner *Richardsonius balteatus*, and Lake Chub *Couesius plumbeus* (Gresswell et al. 1994).

Methods

Transmitter Implantation and Allocation

Yellowstone Lake was divided into four regions (North, Southeast Arm, South Arm, and West Thumb) to ensure equal allocation of telemetered Lake Trout throughout the lake (Figure 1). Lake Trout were collected using gill nets in each region. Lake Trout of total length (TL) > 500 mm were implanted with Lotek CART series transmitters (Lotek Wireless, Inc., Newmarket, ON, Canada), which emit both acoustic and radio signals. Two different sized transmitters were used throughout the study: MM-MC-11-45 (78-mm long, 12-mm diameter, and weighed 16 g) and MM-MC-16-25 (63-mm long, 16-mm diameter, and weighed 28 g). Lake Trout selected for transmitter implantation were anesthetized using AQUI-S 20E (AQUI-S New Zealand LTD, Lower Hutt, New Zealand) at 20 mg/L and transmitters were surgically implanted using standard surgical procedures (Wagner et al. 2011). Determination of sex and stage of maturity was conducted by observing the gonads through the incision made for transmitter implantation. A grove director was used to gently move the stomach aside to reveal gonads, if needed. Lake

Trout were implanted with transmitters and assigned sexes when ovaries or testes were easily identified as mature; transmitters were not implanted in immature fish. In some instances, sex and stage of maturity were not identified and Lake Trout implanted with transmitters were assigned sex as unknown. Sex and stage of maturity of unknown-sex Lake Trout were determined when recaptured by Lake Trout suppression crews.

Five hundred seventy-nine Lake Trout > 500 mm (mean TL = 588.2 mm; SE = 2.58) were implanted with transmitters from June 2015 through July 2017. Transmitters were allocated among the four tracking regions with 74 in the North, 187 in the South Arm, 143 in the Southeast Arm, and 175 in the West Thumb. Only four of 114 Lake Trout recaptured with gill nets throughout the study were immature (mean TL = 547.8 mm; SE = 14.04); they were removed from analyses. One hundred thirty-eight females (mean TL = 614.9 mm; SE = 4.71) and 197 males (mean TL = 565.3 mm; SE = 4.23) were tagged throughout the Lake. The sexes of 240 Lake Trout were unknown (mean TL = 592.4 mm; SE = 3.98).

Mortality motion sensors in transmitters emitted a mortality code if Lake Trout were motionless for 24 consecutive hours. Transmitters emitting the mortality code were often deleted from subsequent relocation to increase efficiency of tracking. Post-hoc mortality analysis was performed on all Lake Trout because some Lake Trout were stationary during the entire study and the mortality sensor was not activated. Lake Trout were considered mortalities if the mean distance traveled between sequential locations throughout the study period was < 500 m. Lake Trout identified as mortalities in the

post-hoc analysis or with mortality codes activated were excluded from analyses (N = 204).

Acoustic Tracking

Lake Trout were located using portable Lotek MAP 600 acoustic receivers equipped with two Lotek LHP_1 directional hydrophones (Lotek Wireless, Inc, Newmarket, ON, Canada). Transects were delineated into the four regions of Yellowstone Lake (i.e., North, Southeast Arm, South Arm, and West Thumb) to maximize tracking efficiency. Within each region, tracking transects were stratified by depth. Tracking effort focused on lake depths < 60 m to further increase tracking efficiency, with minor exceptions in 2017 (see below). Depth categories were based on prior knowledge of substrate type throughout Yellowstone Lake (Bigelow 2009), spawning substrate used by Lake Trout (Marsden et al. 1995), and the depths where adult Lake Trout are commonly sampled during annual monitoring in Yellowstone Lake (Syslo et al. 2016).

Tracking transects were constructed in ArcMap 10.3.1 (ESRI 2016) for each tracking region (Melnychuck and Christensen 2009) where the first transect was parallel to shore and spaced 500 m from shore and subsequent transects were parallel and spaced 1,000 m from the previous transect. Adjacent transects continued until all depths < 60 m were sampled. Transect starting locations were distributed at 10-km increments along each transect. The starting location and direction of tracking were randomly selected for each tracking survey.

Lake Trout spawning occurs primarily during the evening immediately after sunset (Martin and Olver 1980). However, during previous studies no evidence of diel patterns in spawning behavior of Lake Trout in Yellowstone Lake exists (Jason Romine, USFWS, personal communication). Therefore, tracking surveys were conducted from 0600 h through 1600 h. Boats traveled at a maximum speed of 9.7 km/h during tracking surveys. Lotek MapHost software (Lotek Wireless, Inc., Newmarket, ON, Canada) was used to determine Lake Trout locations. After a Lake Trout was detected, the boat was slowed to 4.8 km/h and oriented in the direction of the target Lake Trout. Boat operators continued toward the Lake Trout (i.e., signal), marking the Universal Transverse Mercator (UTM) position each time the signal strength increased, until the hydrophones passed over top of the target Lake Trout (indicated by a sudden change from high-signal strength to low-signal strength or no detection). The UTM position where the signal was lost was the estimated Lake Trout location. When tracking multiple Lake Trout in the same aggregation, the point when the signal was lost was sometimes missed; in such cases, the UTM position of the strongest signal strength was considered the estimated Lake Trout location.

Tracking procedures were similar during the summer in 2017 (June – August) and the spawning period (September – October) in 2016 and 2017. Tracking in 2016 occurred each day only during the spawning period in the South Arm and Southeast Arm tracking regions. Two boats performed tracking surveys from 12 September 2016 through 13 October 2016. In 2017, two boats tracked all four tracking regions during the spawning period, each region was surveyed every other day, from 4 September 2017

through 12 October 2017. Each tracking region was surveyed twice per month in the summer of 2017.

Efforts were focused on depths where Lake Trout were most likely to spawn. However, Lake Trout have been documented spawning in deep water (Beauchamp et al. 1992; Fitzsimons et al. 2005). When a third boat was available during the 2017 spawning period, depths > 60 m were sampled (designated as deep transect) to ensure sampling covered all potential Lake Trout spawning habitat. Deep transects started 1,000 m from the deepest adjacent transect (see above) and maintained a parallel path; additional deep transects were conducted until all depths were sampled. Each deep transect was surveyed once in August 2017 and five times during the spawning period in 2017.

Radio Tracking

Radio tracking was conducted by a fixed-wing aircraft service contracted by the National Park Service. Flights started at sunrise and each flight surveyed the entire shoreline of Yellowstone Lake twice. Locations (UTM) were recorded to the receiver when a radio signal was detected. The UTM position of the highest signal strength was used to estimate a Lake Trout location. The following criteria were used after the data were collected to eliminate false detections: 1) individual Lake Trout must have been detected at least five times on a given day, 2) mean time between detections was < 60 s, and 3) signal strength for the estimated location was > 50. Five flights occurred in 2016 from 25 September through 30 September and only one flight occurred in 2017; because of the low sample size in 2017, these data were excluded from analyses.

Detection Range, Location Accuracy, and Detection Probability

Detection range of acoustic transmitters can be highly variable and dependent on water conditions in the study area (Pincock and Johnston 2012). In situ detection range tests were conducted 10 times prior to tracking and under varying environmental conditions. Four transmitters were attached to a buoy line at depths of 5, 10, 20, and 40 m. A boat would start 1 km from the buoy line and move directly toward the buoy at 9.7 km/h. The location of the first detection of each transmitter was recorded as the detection range.

Location accuracy and detection probability were determined using blind trials for acoustic and radio tracking. Two transmitters were concealed in the lake and within the detection range of tracking transects at depths of 5 m and 14 m in 2016, and 6 m and 18 m in 2017. The tracking crew used the same procedures as if the concealed transmitter was a Lake Trout to determine the estimated position. The estimated UTM location was compared with the true UTM location to measure location accuracy. Trials were repeated during each tracking survey. Detection probability was calculated as the total number of detections of the concealed transmitters divided by the number of tracking surveys in the areas the concealed transmitters were located.

Data Analysis

Movement Rate and Nearest Neighbor Distance Total movement was calculated between sequential locations of individual Lake Trout. Euclidian distances between sequential locations were calculated in R (R Core Team 2013). Estimated daily movement rate was calculated by dividing the total distance by the number of days

between sequential locations. A Wilcoxon rank-sum nonparametric test was used to test for differences in daily movement rates between the summer and spawning period in 2017.

Nearest-neighbor distance (i.e., distance from a given point to the next closest point) was calculated for each Lake Trout location. Mean nearest-neighbor distance was compared between the summer and spawning period in 2017. A Wilcoxon rank-sum nonparametric test was used to test for differences in nearest-neighbor distance between the summer and spawning period in 2017.

<u>Dispersal</u> The G-function ($\hat{G}(r)$; Bivand et al. 2013) was used to quantify and identify patterns of Lake Trout point locations. The G-function is the cumulative distribution of the distances from randomly selected points to the nearest neighboring point. Given a distance *r*, $\hat{G}(r)$ is the probability that the nearest neighbor distance is less than or equal to *r* (Brunsdon and Comber 2015). Similar point-pattern analyses, such as Ripley's K-function, have been used to quantify spatial patterns of other lacustrine fish species (Hennen and Brown 2014; Weller et al. 2016). However, the G-function uses nearest neighbor distance, which is a good indicator of social behavior such as spawning (Clark and Evans 1954; Heupel and Simpfendorfer 2005; Miranda et al. 2008). The G-function is also more informative than other point-pattern analysis techniques in ecological sciences (Wiegand et al. 2013). Yellowstone Lake was the spatial window and the border correction for $\hat{G}(r)$ was used to account for edge effects and bias around the border of the spatial window (i.e., Yellowstone Lake) (Stoyan 2006). $\hat{G}(r)$ was visually compared to the G-function ($G(r)$) of complete spatial randomness (CSR) to test

if Lake Trout point locations from each period were randomly dispersed. A maximum absolute deviation (MAD) test was used to determine if a statistical difference existed between $\hat{G}(r)$ and $G(r)$ (Baddeley et al. 2014). The MAD test uses Monte Carlo simulation and is the maximum vertical separation of $G(r)$ over the range of r. The null (i.e., observed points are randomly distributed) is rejected if the difference between $\hat{G}(r)$ and $G(r)$ is greater than the maximum difference from the Monte Carlo simulations (Baddeley et al. 2014).

Aggregations Kernel density estimation (KDE) was used to quantify locations and concentrations of Lake Trout aggregations. A KDE map was created in ArcMap 10.3.1 (ESRI 2016) to identify areas where adult Lake Trout aggregated. Bandwidth of the kernel was set at the detection range of the transmitters (500 m). The maximum relative density was scaled to one to identify the most concentrated Lake Trout aggregations. Kernel density estimation was used to identify Lake Trout aggregations using acoustic tracking data collected during the summer of 2017 and the spawning period in 2016 and 2017.

Kernel density estimate maps from the 2016 and 2017 spawning periods were used to identify putative spawning locations. As of 2016, Lake Trout spawning was confirmed (i.e., presence of Lake Trout embryos or larvae) at 12 locations in Yellowstone Lake (Doepke and Puchany 2017). Aggregations, as determined by KDE maps, with similar or higher relative densities than confirmed spawning locations were considered putative spawning locations. The raster to polygon function in ArcMap 10.3.1 (ESRI

2016) was used to map the approximate size of Lake Trout aggregation areas. Minimum, maximum, and mean depth of each summer aggregation area were calculated.

Lake Trout use of each putative spawning location was summarized to prioritize Lake Trout suppression program effort. Total number of individuals that visited a site, mean individuals per tracking survey, mean length of stay, minimum length of stay, maximum length of stay, and mean individual days of putative and confirmed spawning locations were calculated. Length of stay was the number of days between the first and last consecutive tracking surveys during which an individual Lake Trout was detected at a location. Mean individual days was calculated for each site and was the product of mean individuals per survey and the mean length of stay.

<u>Differences in Seasonal Dispersal Patterns</u> The difference in the degree of aggregation ($D(r)$) between the summer and spawning periods in 2017 was calculated as the difference between seasonal $\hat{G}(r)$ values

(1) $$D(r) = \hat{G}_1(r) - \hat{G}_0(r),$$

where $\hat{G}_1(r)$ is the G-function (see definition above) during the spawning period and $\hat{G}_0(r)$ is the summer G-function. The test statistic, D_G, was calculated as

(2) $$D_G = \sum \frac{D(r)}{var[D(r)]^{\frac{1}{2}}},$$

where $D(r)$ is from equation 1 and $var\ [D(r)]$ is the variance of $D(r)$ calculated by the random labeling hypothesis. The random-labeling hypothesis pools all points and each point is randomly assigned to a type, in this case a sampling period (i.e., spawning or summer), where each point is equally likely to be assigned to each type (Schabenberger

and Gotway 2017). One hundred Monte Carlo simulations of equations 1 and 2 were conducted to test for significance, and the p-value was calculated as $k/100$, where k is the rank (1-101) of the observed D_G compared to 100 simulations of D_G (Besag and Diggle 1977). Originally developed for comparing Ripley's K-function ($K(r)$) in case-control studies in epidemiology (Diggle and Chetwynd 1991; Diggle et al. 2007), in this study $K(r)$ was substituted with $\hat{G}(r)$ to test for a difference in $\hat{G}(r)$ between two seasonal data sets. For additional details on the original equations see Diggle and Chetwynd (1991).

Targeting Telemetered Lake Trout with Gill Nets Hickey Brothers Research, LLC (HBR) Lake Trout suppression crews targeted groups of telemetered Lake Trout to increase catch rates of adult Lake Trout. The locations of Lake Trout groups were relayed to HBR crews during summer tracking surveys. Groups were defined as two or more tagged Lake Trout in close proximity (e.g., 500 m) of each other. Locations (UTM) and depths of groups were relayed in real time by radio, cell phone, or text message to HBR crews. After each tracking survey, a map of all Lake Trout locations and depths was printed and provided to the HBR project leader to use for setting nets the following morning. After locations, maps, or both were provided to HBR, the boat captain decided where to set nets at the identified locations.

Monofilament gill-net sets were 3-m high and 3,000 m to 3,600 m long. Gill-net sets were constructed with a single mesh size (stretch) of either 89 mm, 102 mm, 114 mm, or 127 mm. Catch-per-unit-effort (CPUE) from gill-net sets targeting telemetry groups (target nets) were compared to the CPUE of gill-net sets not targeting telemetry groups (non-target nets). Catch-per-unit-effort was calculated as the number of Lake

Trout captured per 100 m of net per night set. Non-target nets were all HBR gill nets with the same mesh sizes set during the same time frame as target nets (June through August). A Wilcoxon rank-sum nonparametric test was used to test whether CPUE from target and non-target nets differed.

Results

Three hundred seventy-three Lake Trout (mean TL = 589 mm; SE = 3.06) survived and were used in the analyses (Table 1); 99 were females (mean TL = 611 mm; SE = 5.40), 135 were males (mean TL = 569 mm; SE = 5.04), and 139 were of unknown sex (mean TL = 593 mm; SE = 4.96). Detection range of transmitters varied during surveys with a maximum distance of 5 km and a mean of 897.0 m (SE = 188.5) for acoustic tracking. Mean location accuracy of concealed transmitters was 70.8 m (SE = 13.5) during acoustic tracking surveys. The detection probability of concealed transmitters was 0.95.

Summer Locations

One hundred ninety-five Lake Trout were tracked during the summer in 2017 resulting in 516 detections. The West Thumb had the greatest number of locations of individual Lake Trout (N = 85) and total locations (N = 198), and the North had the least number of individuals (N = 49) and locations (N = 104) (Table 2). The West Thumb had the shortest nearest neighbor distance (mean = 180 m; SE = 22.5) and the South Arm had the longest (mean = 370 m; SE = 32.0) (Table 2). Mean movement rate of Lake Trout during the summer was 362 m/day (SE = 60.2).

Locations of Lake Trout during summer 2017 were spatially aggregated, as indicated by the larger observed $\hat{G}(r)$ than expected $G(r)$ given complete spatial randomness (Figure 2). Evidence of spatial aggregation was strong (MAD = 0.469; P < 0.01). Aggregations of Lake Trout occurred in several areas throughout the summer; however, nine areas had relative density values at or near one: South Solution, Breeze Channel, Breeze Bay, South Frank, South Arm Shelf, Southeast Arm West, Molly Islands, Pelican Creek, and North Stevenson (Figure 3).

Lake Trout were most common in Breeze Bay (N = 26) and least common at Southeast Arm West (N = 7) (Table 3). Breeze Bay had the greatest individual Lake Trout per survey and the Molly Islands had the lowest (Table 3). Pelican Creek had the greatest individual days and the Molly Islands had the lowest. Aggregation sites varied in size from 44.2 ha at the Molly Islands to 210.9 ha at South Solution; the Molly Islands site was the shallowest (15.6 m) and Breeze Channel was the deepest (30.3 m; Table 4).

Spawning Locations

In 2016, 168 individual Lake Trout were tracked resulting in 1,166 locations, and in 2017, 181 individuals were tracked resulting in 1,167 locations. In 2016, the Southeast Arm had more locations of individual Lake Trout and mean locations per survey than the South Arm. In 2017, the West Thumb had the greatest number of locations for individual Lake Trout and the greatest mean locations per survey, whereas the North had the lowest number of individuals and mean locations per survey (Table 5). Movement rate of Lake Trout was greater in 2016 (mean = 1,096 m/day; SE = 55.9) than 2017 (mean = 801

m/day; SE = 58.4). Mean nearest neighbor distance was shortest in the West Thumb and longest in the Southeast Arm (Table 5).

Locations of Lake Trout during the 2016 and 2017 spawning periods exhibited an aggregated spatial pattern; the observed $\hat{G}(r)$ was larger than the expected $G(r)$ under complete spatial randomness (Figure 4). Evidence of spatial aggregation was strong in 2016 (MAD = 0.512; P < 0.01) and 2017 (MAD = 0.497; P < 0.01). Lake Trout aggregated at nine locations in 2016; the aggregations with the highest relative densities were at the Molly Islands in the Southeast Arm and the northeast area of Flat Mountain Arm (Figure 5). Lake Trout aggregated at 19 locations in 2017, including two distinct locations in the West Thumb — Carrington Island and Anglers Bluff (Figure 6).

Lake Trout aggregated in 22 areas during the spawning period in 2016, 2017, or both (Figure 7). Ten aggregations were at confirmed spawning locations and twelve aggregations were considered putative spawning locations (Figure 7). Lake Trout were most commonly located at Carrington Island (a confirmed spawning location); this site had the greatest mean number of individuals detected per survey (N = 4.9) and the greatest number of individual days (64; Table 6). However, more individual Lake Trout visited the confirmed spawning locations in Flat Mountain Arm and Olson Reef, but these areas were surveyed in 2016 and 2017. Solution had the longest mean length of stay (19 days) among confirmed spawning locations and Wolf Point was the confirmed spawning location with the lowest number of individual Lake Trout, Lake Trout per survey, and individual days. Anglers Bluff was the putative spawning location where Lake Trout were most commonly detected and had the greatest individuals per survey,

greatest individual days, and longest length of stay (84; Table 6). Anglers Bluff also had the greatest relative density among all confirmed and putative spawning locations (Figure 6). Plover Point had the greatest number of individual Lake Trout at a putative spawning location, East Stevenson had the lowest number of individuals per survey, and South Arm Shelf had the shortest length of stay and was identical with South Arm Hump for lowest individual days (13; Table 6).

Two hundred sixteen Lake Trout visited putative spawning locations, confirmed spawning locations, or both in 2016 and 2017. Forty-seven percent visited multiple spawning locations (mean = 2; maximum = 5). Sixty-eight Lake Trout were tracked during the spawning period in both 2016 and 2017, and 41% returned to the same spawning location in 2017 as in 2016 — 19 to confirmed spawning locations and nine to putative. The confirmed spawning location in Flat Mountain Arm had the most Lake Trout return each year (N = 11) and Southeast Arm West was the putative spawning location with the most fish returning each year (N = 3).

Differences in Seasonal Locations

Daily movement rate was lower during the summer (mean = 362 m/day; SE = 60.2) than the spawning period (mean = 801 m/day; SE = 57.4), and strong evidence supported a difference in daily movement rates between periods ($W = 1.1 \times 10^5$; $P < 0.001$). Nearest neighbor distance was greater among Lake Trout locations during the summer (mean = 260 m; SE = 15.4) than the spawning period (mean = 159 m; SE = 7.9). Furthermore, strong evidence supported a difference in mean nearest neighbor distance between the summer and spawning period in 2017 ($W = 1.5 \times 10^5$; $P < 0.001$), suggesting

Lake Trout are more aggregated during the spawning period. However, Lake Trout were spatially aggregated during both periods.

Visually assessing the difference in the G-function plots for each period (Figures 2 and 4b) illustrates a difference in the degree of aggregation (i.e., the G-function plot for the summer and the spawning period reach a proportion of 0.75 at different nearest neighbor distances). During summer, 75% of the Lake Trout had a nearest neighbor distance of about 400 m whereas during the spawning period, the nearest neighbor distance for 75% of the Lake Trout was 150 m, indicating a higher degree of aggregation during the spawning period. The mean $D(r)$ between seasons was 0.151, which is a positive value indicating a higher degree of aggregation during the spawning period and corroborates the G-function plots. In addition, strong statistical evidence supports a difference in the degree of aggregation between the summer and spawning periods (D_G = 1,005; P = 0.01), the observed $D(r)$ was above the expected $D(r)$ with complete spatial randomness and outside the Monte Carlo significance bands (Figure 8).

Targeting Telemetered Lake Trout with Gill Nets

During the summer of 2017, suppression crews set 30 gill net sets for a total of 2,319 net nights targeting Lake Trout groups identified through telemetry (target nets). Suppression crews also set 124 gill net sets for a total of 13,575 net nights that did not target Lake Trout groups (non-target nets). Target net sets removed 3,033 Lake Trout and non-target net sets removed 12,025 Lake Trout (Figure 9). Target net sets had a greater mean CPUE (1.77; SE = 0.21) than that of non-target net sets (0.95; SE = 0.08).

Strong statistical evidence supports a difference in CPUE of Lake Trout between target net sets and non-target net sets ($W = 908$; $P < 0.001$).

Radio Tracking

No concealed test transmitters were detected by radio tracking from fixed-wing aircraft indicating that transmitters at depths greater than 5 m were undetectable to radio tracking. Fourteen individual Lake Trout were located during flights for a total of 36 locations. Only four of the 14 Lake Trout were detected with acoustic tracking; two were live Lake Trout that were detected in similar locations by both radio and acoustic tracking, and two were known mortalities. No further analyses were performed on the radio-tracking data because of the low sample size.

Discussion

Lake Trout Locations and Spatial Structure

Lake Trout aggregated during the summer and spawning period (autumn) in Yellowstone Lake. I identified nine areas where Lake Trout aggregated in the summer and twelve putative spawning locations, verified high concentrations of Lake Trout at confirmed spawning locations, and validated that targeting known locations of telemetered Lake Trout increases catch rates.

Lake Trout aggregations differed in size and location by season. Lake Trout aggregations were generally farther from shore and in deeper water during the summer than the spawning period. Aggregation areas with the highest use by Lake Trout during the spawning period (e.g., Flat Mountain Arm, Carrington Island, and Anglers Bluff)

were rarely used by Lake Trout during the summer. Aggregation patterns of Lake Trout in Yellowstone Lake were consistent with those of other Lake Trout populations within (e.g., Blanchfield et al. 2009; Pinheiro et al. 2017) and outside (e.g., Dux et al. 2011; Fredenberg et al. 2017) their native range. Invasive Lake Trout were deeper, farther from shore, and more dispersed in the summer than during the spawning period in Lake McDonald, Glacier National Park (Dux et al. 2011). Interestingly, some Lake Trout in Yellowstone Lake used the same locations during the summer and spawning period. For example, South Solution, Breeze Channel, and Breeze Bay were commonly used by Lake Trout during both periods, suggesting that Lake Trout used these areas throughout the year for feeding and spawning. These results were corroborated by high catch rates in the same region as the aggregations (e.g., West Thumb) during annual summer assessment netting (Arnold et al. 2017) and suppression netting during the spawning period (Bigelow 2018). The locations used during both the summer and spawning periods were deeper than other spawning locations, providing both preferred environmental conditions (e.g., water temperature) in the summer as well as suitable substrate for spawning in the autumn.

As expected, Lake Trout were more dispersed during the summer than the spawning period but were more aggregated during summer than in other invasive Lake Trout populations (Dux et al. 2011), probably in response to preferred environmental conditions (Martin and Olver 1980; Olson et al. 1988; Blanchfield et al. 2009; Plumb and Blanchfield 2009) and forage distributions. Lake Trout require cold water temperatures (5-15 ˚C; Snucins and Gunn 1995; Sellers et al. 1998) with high dissolved oxygen

concentrations (> 6-7 mg/L; Evans 2007). Warm surface water temperatures and lake stratification in the summer force Lake Trout to the hypolimnion (Dux et al. 2011; Guzzo et al. 2017). Aggregations and movements of Lake Trout are also influenced by the distribution of prey species (Ahrenstorff et al. 2011; Guzzo et al. 2017). In Lake Huron, Lake Trout moved to the hypolimnion as the abundance of pelagic prey fish declined, ultimately shifting their diet to demersal prey fishes (Bergstedt et al. 2012). Post-spawn migration of Lake Trout in Lake Superior was related to the distribution of their preferred prey (Binder et al. 2017). Lake Trout in Yellowstone Lake feed primarily on amphipods during the summer (Syslo et al. 2016), which may cause Lake Trout to aggregate—if amphipods are spatially aggregated in Yellowstone Lake. Amphipods in Lake Superior aggregate (Auer et al. 2013) and their distribution influences the spatial patterns of fishes (Hondrop et al. 2005).

The identification of nine key areas where Lake Trout aggregate in the summer will help guide gillnetting efforts to improve catch rates. Understanding patterns in seasonal distributions is essential for effective suppression of an established invasive species (Hennen and Brown 2014). For example, understanding the movement patterns of Sea Lamprey *Petromyzon marinus* identified areas where traps would be most effective (Holbrook et al. 2016), and exploiting predictable seasonal dispersal patterns caused the eradication of Common Carp from a large lacustrine system in Australia (Donkers et al. 2012; Taylor et al. 2012).

Lake Trout were distinctly aggregated at 22 locations during the spawning period; 12 locations were previously undocumented and considered putative spawning locations.

Lake Trout also aggregated at all confirmed spawning locations. Number of individuals, relative densities, mean length of stay, and individual days were similar at confirmed and putative spawning areas—providing evidence that Lake Trout probably spawn at the putative spawning locations. However, visual confirmation of embryos is needed to verify these locations as Lake Trout spawning locations. Furthermore, mean length of stay and number of sites visited by an individual Lake Trout were similar to other Lake Trout populations. For example, Lake Trout remained on spawning sites between 15 and 30 days and visited 2 to 3 sites per year in Lake Champlain (Pinheiro et al. 2017).

Abiotic characteristics at putative spawning locations (e.g., depth and substrate type) were similar to those at confirmed spawning locations in Yellowstone Lake. Minimum depths at confirmed and putative spawning locations varied from less than 1 m to 26 m in Yellowstone Lake, which are similar to spawning depths of Lake Trout elsewhere (Martin and Olver 1980; Esteve et al. 2007; Riley et al. 2010; Dux et al. 2011; Fredenberg et al. 2017). In general, substrate type was similar between putative and confirmed Lake Trout spawning locations (Wright et al. 2017) and comparable to substrate type at spawning locations within and outside their native range. Lake Trout generally spawn on clean, angular substrate with deep interstitial spaces (Marsden et al. 1995; Binder et al. 2014) but have been observed spawning on small gravel (Binder et al. 2018). Similar variation in substrate type was observed at spawning locations in Yellowstone Lake, from spawning on thermal volcanic substrate with small interstitial spaces at Geyser Basin (confirmed spawning location) to silt substrate interspersed with cobble and large boulders at Plover Point (putative spawning location) (Wright et al.

2017). Given the variability in substrate selection by spawning Lake Trout, continued acoustic telemetry will be important to identify spawning aggregations because identifying spawning areas only based on predefined spawning substrate type could reduce suppression efficiency.

The identification of 12 putative spawning locations provides additional areas to be targeted with gill nets that were not historically targeted. Targeting putative spawning locations will undoubtedly lead to an increase in the CPUE of adult Lake Trout and improve the overall efficacy of the suppression program. Spawning Lake Trout were targeted in Lake Pend Oreille, which resulted in doubling the CPUE of adults (Wahl et al. 2015a, 2015b). As of 2015, targeting Lake Trout on confirmed spawning locations in Yellowstone Lake has resulted in the highest numbers of mature fish captured in gill nets (Koel et al. 2015). Population growth rates of Lake Trout in Yellowstone Lake are most sensitive to changes in age-0 survival; therefore, increasing removal of adult female Lake Trout, thereby resulting in no reproductive output for that individual, will increase the efficacy of the suppression program (Syslo et al. 2011).

Identifying spawning locations is also needed for implementing novel embryo suppression methods. Novel methods for suppressing Lake Trout embryos are currently being investigated by Yellowstone National Park and results indicate they are effective at causing high mortality rates (Thomas et al. in press). The confirmation of high Lake Trout densities at the 10 confirmed spawning locations in this study will help fisheries managers identify areas to be targeted with the carcass deposition embryo suppression methods as described by Thomas (2017). Furthermore, the identification of 12 putative

spawning locations provide additional areas that can be targeted in the future after Lake Trout spawning is confirmed. Applying varying suppression methods that target multiple life stages are more effective than a single suppression method (Weber et al. 2011; Simberloff 2014; Lechelt and Bajer 2016). Therefore, targeting putative and confirmed spawning locations with mechanical removal, embryo suppression, or both will probably increase the efficacy of the Lake Trout suppression program.

Lake Trout in Yellowstone Lake spawned at more locations than other invasive and native Lake Trout populations. For example, invasive Lake Trout used three spawning locations in Lake Pend Oreille (Rust et al. 2018) and two locations in Lake McDonald (Dux et al. 2011), and native Lake Trout used eight locations in Lake Champlain (Ellrott and Marsden 2004). Furthermore, Lake Trout in Yellowstone Lake exhibited low spawning location fidelity compared to other Lake Trout populations. Lake Trout within their native range have a high degree of spawning location fidelity (Binder et al. 2016); for example, nearly 90% of tagged Lake Trout in Lake Huron and 74% of tagged Lake Trout in Lake Champlain returned to the same spawning location in subsequent years (Binder et al. 2016; Pinheiro et al. 2017). Although spawning location fidelity differed between Yellowstone Lake and other systems, mean length of stay at spawning locations was similar (Pinheiro et al. 2017).

The high amount of suppression effort on Lake Trout spawning locations during the spawning period could be resulting in fishing-induced selection that is altering behavioral traits of Lake Trout in Yellowstone Lake (Uusi-Heikkilä et al. 2008; Diaz and Sih et al. 2017) — selecting for fish that move more among spawning locations and use a

broader range of spawning substrate types. Fishing gear (e.g., gill nets) can have behavioral effects on target species (Arlinghaus et al. 2016; Diaz and Sih 2017). For example, spawning aggregations of Atlantic Cod *Gadus morhua* were disrupted by commercial fishing with fish leaving spawning locations within 18 h after the onset of netting (Dean et al. 2012), Flannelmouth Suckers *Catostomus latipinnis* abandoned spawning after being captured and released from fyke nets (Fraser et al. 2017), and Atlantic Salmon *Salmo salar* captured in gill nets moved downstream rapidly after release (Mäkinen et al. 2000).

The tendency of salmonids to stray from natal spawning locations could explain the high number of spawning locations and lower spawning location fidelity of Lake Trout in Yellowstone Lake. Straying is an adaptive strategy that supports rapid colonization and establishment of new spawning locations (Keefer and Caudill 2014). Lake Trout were documented straying from established spawning locations to spawn at recently constructed spawning reefs in Lake Huron (Marsden et al. 2016) and Lake Trout will stray to previously unused spawning locations when historical sites are degraded (McAughey and Gunn 1995). Two decades of gill net suppression, with an emphasis on targeting spawning adults, has likely caused avoidance, straying, and pioneering of novel spawning locations throughout Yellowstone Lake.

Targeting all areas where Lake Trout aggregate in Yellowstone Lake will increase the efficiency of achieving the management objectives for Lake Trout and Yellowstone Cutthroat Trout. Failing to identify and target all aggregations may enable Lake Trout to persist at abundance levels above management goals because of refuge areas. Aquatic-

protected areas (refuge areas) have been used to protect fisheries from collapse (Hedges et al. 2010). These areas are often the ‘source’ in source-sink population dynamics (Travis and Parker 2004). For example, the Drummond Island Refuge in Lake Huron is a source population of Lake Trout (Binder et al. 2017) and the Gulf Island Shoal Refuge in Lake Superior enhanced population growth of wild Lake Trout in the Apostle Islands Region (Johnson et al. 2015). Population-growth models indicated that the Gulf Island Shoal Refuge will protect Lake Trout from extirpation under all harvest scenarios evaluated; however, without the refuge, Lake Trout were harvested to extirpation with relatively low fishing effort (Akins et al. 2015). The Gulf Island Shoal Refuge in Lake Superior and the Drummond Island Refuge in Lake Huron are both relatively small (< 1% of the surface area) in comparison to their respective lakes (Stanley et al. 1987), illustrating the influence of small aquatic protected areas on conserving fisheries. Applying the opposite of the aquatic-protected area concept by targeting all areas that are a potential source will increase suppression efficacy (Travis and Park 2004). For example, describing the source-sink population dynamics of invasive Common Carp in the upper Mississippi River Basin allowed natural-resource managers to target areas where suppression would be most effective (Dauphinais et al. 2018). This study clearly identified areas with high concentrations of adult Lake Trout; targeting these areas will increase the overall efficacy of the suppression program.

Targeting Lake Trout in the Summer with Gill Nets

Lake Trout movement rates were lower in the summer than during the spawning period. These results are corroborated by passive telemetry studies of Lake Trout in

Yellowstone Lake (Gutowsky et al. 2017). The low movement rate of Lake Trout in the summer contributed to the reduced CPUE of Lake Trout in gill nets. Gill nets are a passive gear and catch is a function of fish activity (Hubert et al. 2012) such that catch rates are higher for fishes with high movement rates compared to fishes with lower movement rates (Kellner et al. 2007). Nevertheless, mobile telemetry identified that Lake Trout form distinct groups during the summer and suppression crews were able to exploit this behavior to increase the efficiency of the suppression program.

Targeting known locations of tagged Lake Trout during the summer increased CPUE in large-mesh gill nets compared to standard gillnetting protocol in Yellowstone Lake. The strategy of targeting known locations has been successful on a variety of terrestrial invasive species (McCann and Garcelon 2008; Cruz et al. 2009) and was essential for the eradication of invasive goats from small islands in the Pacific Ocean (Taylor and Katahira 1988; Campbell and Donlan 2005). Targeting groups of radio-tagged Common Carp with seining removed about 94% of the adult population, demonstrating the potential effectiveness of targeting telemetry locations as a removal strategy for invasive fish (Bajer et al. 2011). This study is the first that I am aware of that experimentally tested the use of telemetered invasive fish to increase suppression efficacy.

Despite the observed increase in CPUE in target nets, there was little reduction in the cost-benefit ratio of using telemetry to target Lake Trout groups. The Lake Trout suppression contract for HBR is valued at approximately US$1,660,000 annually (Todd Koel, National Park Service, personal communication). To meet contract requirements,

HBR must set 79,000 units of effort, which values each unit of effort at US$21.01. The cost of target nets was approximately US$48,722 and non-target nets approximately US$285,210. Cost per fish removed with target nets was US$16.07, which was lower than a cost of US$23.72 per fish in non-target nets but did not include the cost of telemetry equipment and personnel. Accounting for the additional telemetry costs increases the cost per fish caught in target nets to US$22.25, primarily because the CART tags used in this study were expensive (US$455 – US$600). That cost could be reduced by using standard acoustic tags (US$300), which would reduce the cost-benefit ratio in favor of using telemetry to target Lake Trout aggregations. In addition, the scale of this experiment was relatively small in comparison to the overall effort of the Lake Trout suppression program. If this strategy was implemented on a larger scale, the telemetry costs would be distributed over more Lake Trout removed (assuming CPUE would remain similar) reducing the cost-benefit ratio.

Radio-Acoustic Telemetry Comparison

The poor performance of radio telemetry in this study was unexpected. Yellowstone Lake has a relatively low conductivity (mean = 100 µS/cm; Koel et al. 2007), which should have been appropriate for radio tracking (Adams et al. 2012). Only four of 14 Lake Trout detected by radio telemetry were also detected with acoustic telemetry. Therefore, the CART series transmitters used in this study may not have produced enough power output to be detected at depths greater than 5 m in Yellowstone Lake. Radio tags with a higher power output have a farther detection range than tags with lower power output (Shroyer and Logsdon 2009). Limitations in power output of

the CART transmitters was evident with ten transmitters that were detected by radio telemetry but never detected by acoustic telemetry—indicating a potential failure in the acoustic capabilities. Alternatively, transmitters detected only by radio telemetry may have been from Lake Trout that died and were deposited on shore by wave action, an angler, or by a predator. Two transmitters that were not detected by acoustic tracking were detected on four radio-tracking surveys on or near the Molly Islands. The Molly Islands are a known American White Pelican *Pelecanus erythrorhynchos* nesting colony; these fish were probably consumed by pelicans and the transmitters were deposited on the islands, making them undetectable to acoustic telemetry.

Radio telemetry using CART series dual radio and acoustic transmitters is not an effective strategy for locating spawning Lake Trout in Yellowstone Lake. Using tags that only emit a radio frequency may yield different results and should be studied further. For example, Yellowstone Cutthroat Trout implanted with radio transmitters were detected throughout Yellowstone Lake (Ertel et al. 2017). Nevertheless, radio tags will still provide limited information when Lake Trout use deep-water habitat. For the immediate future, I recommend using simplistic acoustic tags (i.e., without a mortality signal or depth sensor) to reduce the cost-benefit ratio to the suppression program.

Conclusions

This study described the spatial structure of Lake Trout in Yellowstone Lake during the summer and spawning period, which should improve suppression efficacy. Identifying the seasonal distributions of Lake Trout aggregations throughout Yellowstone Lake will ensure that refuge areas are eliminated as a potential source contributing to the

Lake Trout population. The high gill-net effort in Yellowstone Lake may be altering Lake Trout behavior, which would require continued acoustic telemetry efforts to monitor changes in the spatial structure. Investigation into more cost-effective ways to track Lake Trout, such as low-cost tags and autonomous watercraft (i.e., drones) that could continuously track fish and provide real-time locations to gillnetters is needed. Autonomous underwater vehicles have potential for tracking marine species (Lin et al. 2017). Recent technical advancements in autonomous surface vehicles (Liu et al. 2016) has pushed the conversation forward about automated tracking in aquatic systems (Lennox et al. 2017). As adult Lake Trout densities decrease in Yellowstone Lake, which is predicted from statistical catch-at-age models, continued monitoring of the spatial structure of Lake Trout will be necessary to maintain suppression efficacy.

Tables

Table 1. Descriptive statistics for tagged Lake Trout that survived in the four regions (North, West Thumb, Southeast Arm, and South Arm) of Yellowstone Lake from 2015 through 2017 (years pooled). Recaptures are Lake Trout that were caught and removed with gill nets.

		Total length (mm)		
Sex	N	Mean (SE)	Minimum - Maximum	Recaptures
		North		
Female	18	634 (15.8)	545 - 788	8
Male	12	600 (23.9)	510 - 737	5
Unknown	20	618 (13.6)	526 - 808	0
		West Thumb		
Female	33	603 (9.2)	525 - 700	15
Male	38	565 (11.2)	502 - 830	14
Unknown	40	572 (9.9)	500 - 715	0
		Southeast Arm		
Female	20	607 (10.3)	542 - 709	12
Male	30	573 (10.5)	501 - 706	12
Unknown	31	611 (11.6)	513 - 773	0
		South Arm		
Female	28	610 (9.3)	510 - 705	20
Male	55	563 (5.6)	472 - 685	24
Unknown	48	589 (6.0)	517 - 696	0

Table 2. Number of individuals tracked, number of locations, mean number of locations per tracking survey, and mean nearest neighbor distance (m) by lake region (i.e., North, West Thumb, Southeast Arm, South Arm) for Lake Trout tracked in Yellowstone Lake, Yellowstone National Park during the summer in 2017.

Sex	Individuals	Locations	Mean locations per survey	Mean nearest neighbor (SE)[a]
		North		
Female	12	26	3.2	
Male	13	33	3.7	
Unknown	24	45	4.8	
Total	49	104	11.6	271.2 (41.5)
		West Thumb		
Female	25	48	5.3	
Male	23	51	5.1	
Unknown	37	99	9.9	
Total	85	198	19.8	180.2 (22.5)
		Southeast Arm		
Female	9	15	3.0	
Male	23	45	7.5	
Unknown	25	36	6.2	
Total	57	96	16.2	355.3 (53.0)
		South Arm		
Female	17	25	6.2	
Male	18	36	6.0	
Unknown	35	57	9.5	
Total	70	118	19.7	370.14 (32.0)

[a] Lake Trout locations were pooled by region for nearest neighbor calculations.

Table 3. Number of individual Lake Trout, mean individuals per tracking survey, length of stay, and individual days at each Lake Trout aggregation site in Yellowstone Lake, Yellowstone National Park during the summer in 2017. Individual day values are the product of mean individuals per survey and mean length of stay.

	Individuals		Length of stay (days)			Individual
Aggregation site[a]	Total	Per survey	Mean	Minimum	Maximum	days
Pelican Creek	20	5.2	31	9	71	161
Breeze Bay	26	6.3	22	6	77	139
South Arm Shelf	9	3.8	28	15	45	106
South Solution	22	6.3	16	6	42	101
Breeze Channel	22	5.5	18	1	49	99
Southeast Arm West	7	2.4	29	4	69	70
South Frank	14	2.4	26	6	57	62
North Stevenson	9	2.8	12	7	21	34
Molly Islands	9	1.5	12	1	21	18

[a] See Figure 3 for locations.

Table 4. Size and depth of locations where Lake Trout aggregated in Yellowstone Lake, Yellowstone National Park during the summer in 2017.

		Depth (m)		
Aggregation site[a]	Size (ha)	Mean	Minimum	Maximum
Breeze Bay	208.5	21.5	5.8	39.3
South Solution	210.9	26.3	9.1	67.7
Breeze Channel	177.6	30.3	1.0	48.2
Pelican Creek	199.4	19.5	5.8	51.8
South Arm Shelf	67.6	19.4	2.4	46.9
North Stevenson	74.7	26.4	14.6	41.4
South Frank	94.4	24.3	14.6	34.4
Southeast Arm West	58.3	23.6	1.0	50.6
Molly Islands	44.2	15.6	1.0	35.6

[a] See Figure 3 for locations.

Table 5. Number of individuals tracked, number of locations, mean number of locations per tracking survey, and mean nearest neighbor distance (m) by lake region (i.e., North, West Thumb, Southeast Arm, South Arm) for Lake Trout tracked in Yellowstone Lake, Yellowstone National Park during the spawning period (September and October) in 2016 and 2017.

Sex	Individuals	Locations	Mean locations per survey	Mean nearest neighbor (SE)[a]
		South Arm 2016		
Female	14	107	5.6	
Male	31	200	10.5	
Unknown	30	211	11.0	
Total	75	518	26.5	123.6 (6.1)
		Southeast Arm 2016		
Female	14	79	3.9	
Male	47	324	15.4	
Unknown	40	245	11.6	
Total	101	648	30.4	120.8 (7.3)
		South Arm 2017		
Female	18	71	7.1	
Male	21	93	9.3	
Unknown	37	184	18.4	
Total	76	348	34.8	128.7 (8.5)
		Southeast Arm 2017		
Female	10	38	3.7	
Male	19	83	7.5	
Unknown	30	83	7.7	
Total	59	204	18.8	251.9 (24.8)
		North 2017		
Female	9	46	4.1	
Male	15	46	4.3	
Unknown	33	114	11.1	
Total	57	206	18.7	220.3 (32.3)
		West Thumb 2017		
Female	20	88	8.7	
Male	23	135	12.8	
Unknown	37	186	16.6	
Total	80	409	35.0	107.6 (10.2)

[a] Lake Trout locations were pooled by region for nearest neighbor calculations.

Table 6. Number of individual Lake Trout, mean individuals per tracking survey, length of stay, and individual days at each putative and confirmed Lake Trout spawning location in Yellowstone Lake, Yellowstone National Park for 2016 and 2017. Individual day values are the product of mean individuals per survey and mean length of stay.

	Individuals		Length of stay (days)			Individual
Spawning site[a]	Total	Per survey	Mean	Minimum	Maximum	days
			Putative			
Anglers Bluff	17	4.4	19	6	34	84
South Solution	14	4.4	15	2	30	66
Molly Islands[b]	21	3.5	16	2	24	56
Promontory Point[b]	11	2.8	14	2	27	39
Plover Point[b]	22	2.7	11	1	22	29
Northeast Stevenson	8	2.3	12	5	24	28
Southeast Arm West[b]	18	2.8	9	1	19	25
Breeze Bay	7	2.2	11	2	22	24
East Stevenson	2	1.3	33	33	33	22
Frank Finger[b]	4	1.4	15	13	18	21
South Arm Shelf[b]	14	1.4	9	3	16	13
South Arm Hump[b]	7	1.4	9	6	14	13
			Confirmed			
Carrington Island	22	4.9	13	4	34	64
Flat Mountain Arm[b]	43	4.8	12	1	31	58
Solution	7	2.7	19	18	20	51
Thomas Bank[b]	20	2.8	14	6	31	39
Geyser Basin	12	2.4	14	2	28	34
Breeze Channel	21	4.0	8	2	18	32
Snipe Point[b]	15	2.0	13	1	23	26
Olson Reef[b]	26	2.5	9	4	17	22
South Frank[b]	8	1.4	12	10	13	17
Wolf Point[b]	6	1.1	9	4	14	10

[a] See Figure 7 for locations.
[b] Sites surveyed during the spawning period in 2016 and 2017.

Figures

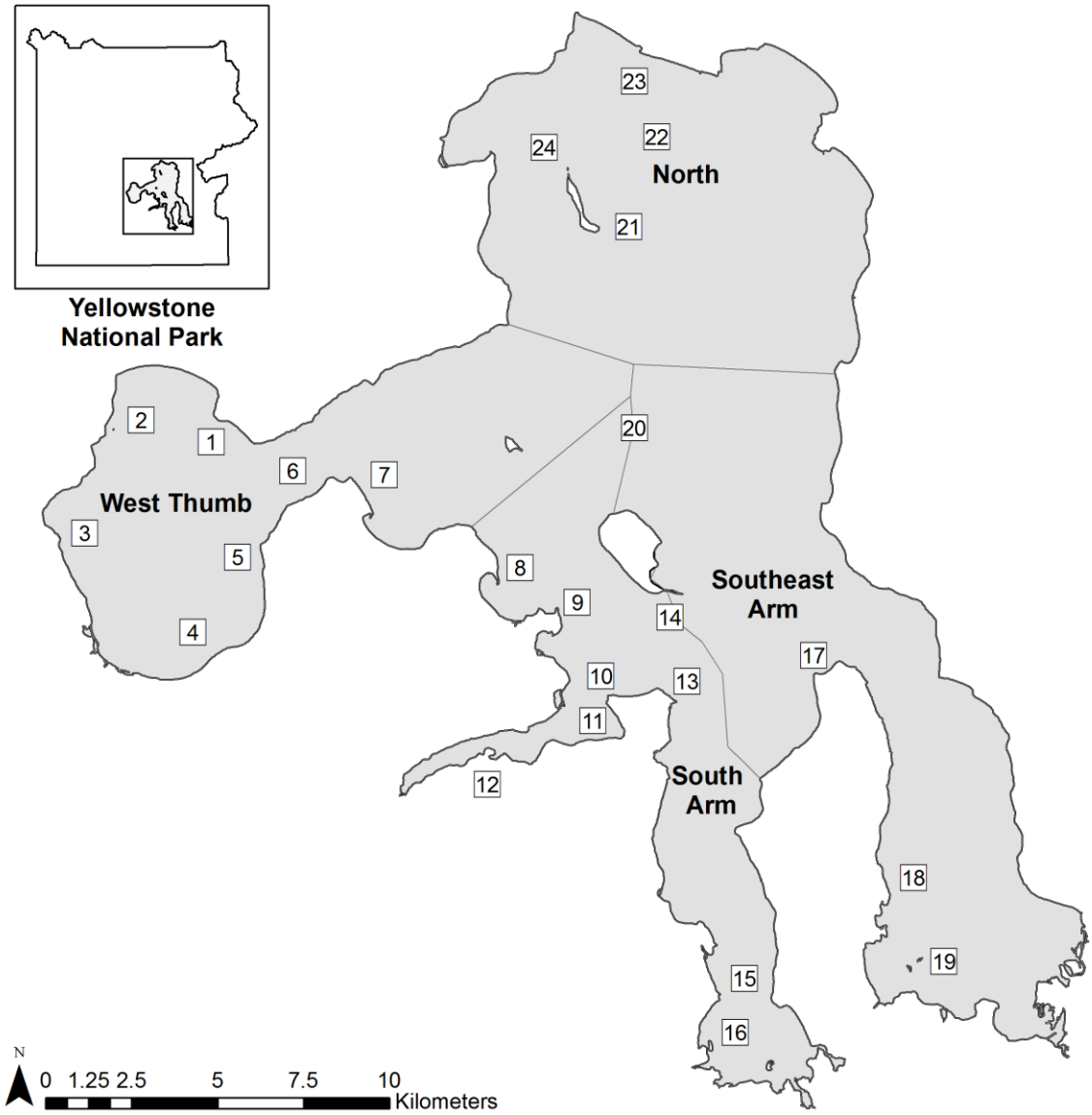

Figure 1. Map of Yellowstone Lake, Yellowstone National Park. Grey lines delineate the four tracking regions (North, West Thumb, South Arm, and Southeast Arm). Numbers reference locations mentioned throughout the methods and results: 1) Anglers Bluff, 2) Carrington Island, 3) Geyser Basin, 4) South Solution, 5) Solution, 6) Breeze Channel, 7) Breeze Bay, 8) Wolf Point, 9) Snipe Point, 10) Olsen Reef, 11) Flat Mountain Arm, 12) Thomas Bank, 13) Plover Point, 14) South Frank, 15) South Arm Hump, 16) South Arm Shelf, 17) Promontory Point, 18) Southeast Arm West, 19) Molly Islands, 20) Frank Finger, 21) East Stevenson, 22) Northeast Stevenson, 23) Pelican Creek, and 24) North Stevenson.

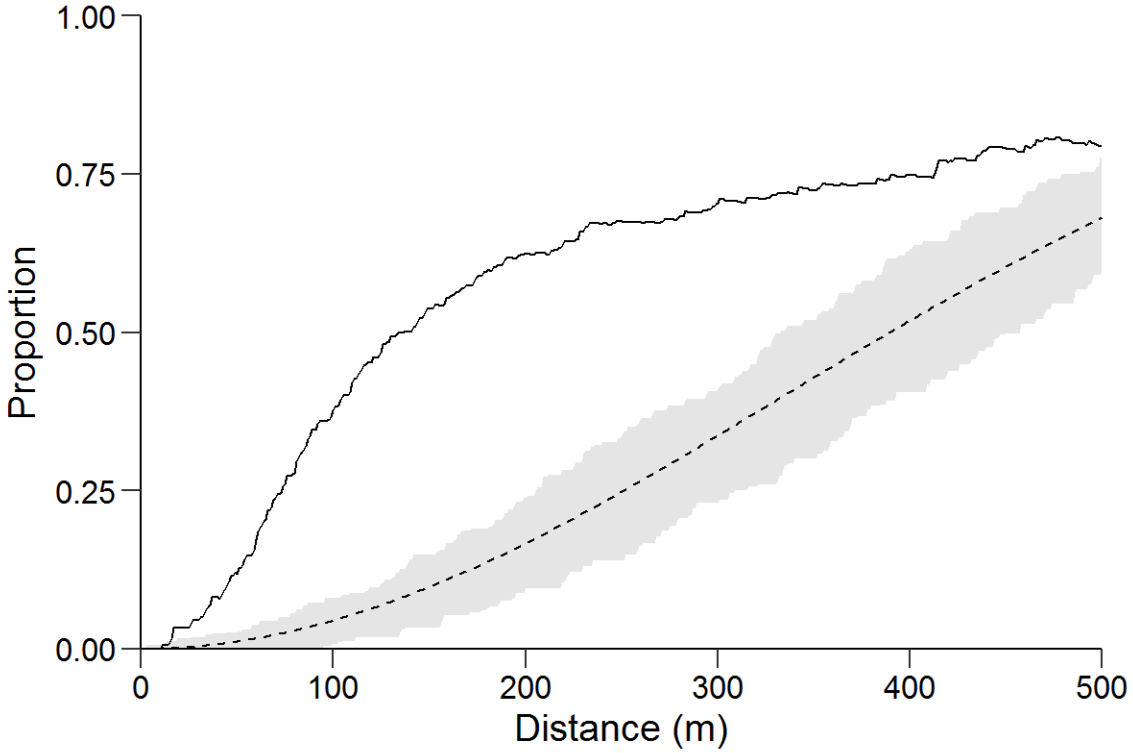

Figure 2. G-function plot of the proportion of Lake Trout locations in Yellowstone Lake, Yellowstone National Park from summer 2017 that have a nearest neighbor within a given distance (Distance [m]). Dashed line is the expected proportion under complete spatial randomness, gray shaded area is the confidence band generated from Monte Carlo simulations, and the solid line is the observed proportion from tagged Lake Trout in Yellowstone Lake. A solid line above the grey confidence band indicates an aggregated spatial pattern.

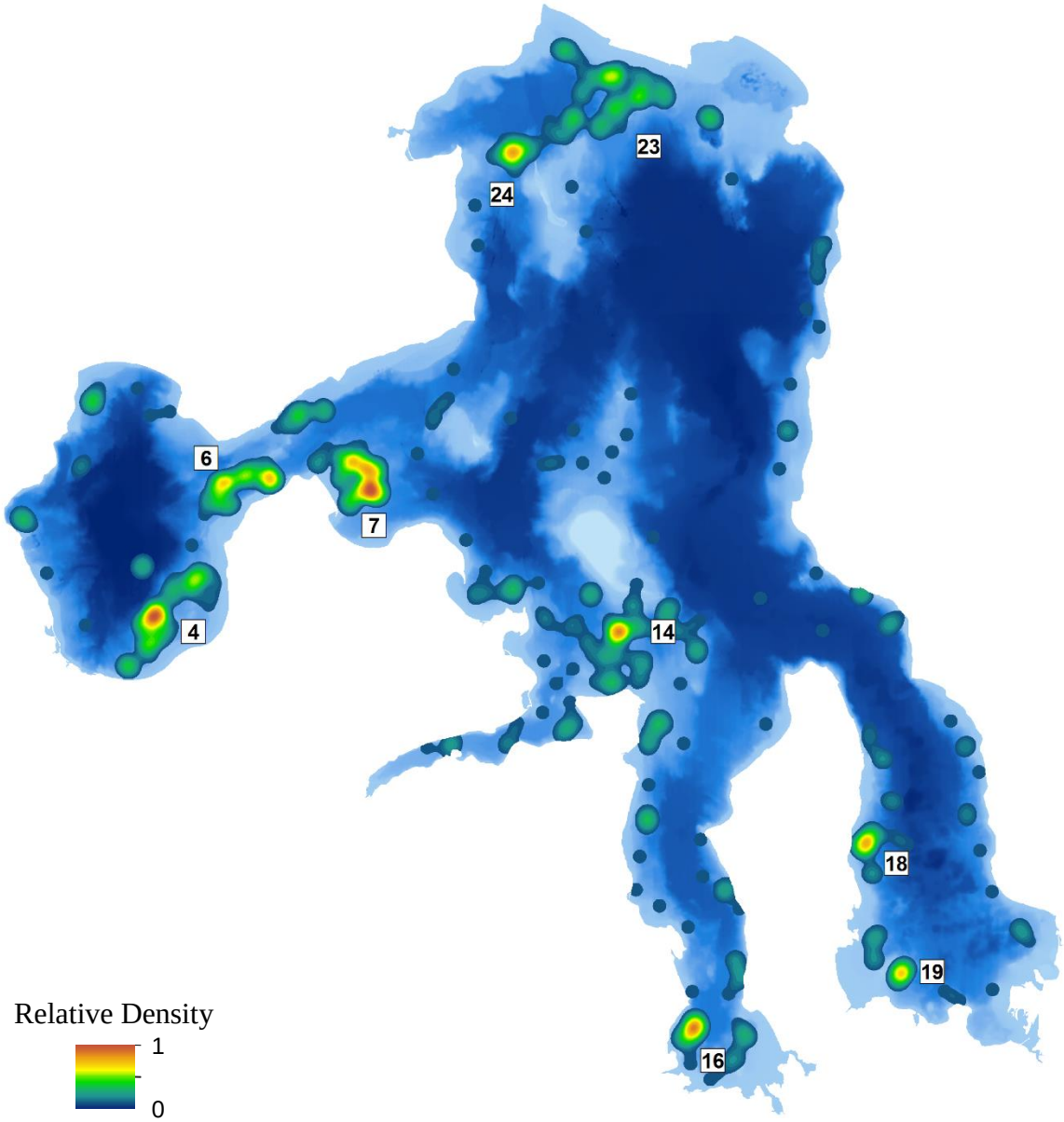

Figure 3. Kernel-density map of Lake Trout locations from the summer 2017 in Yellowstone Lake, Yellowstone National Park. Relative densities indicate the degree of Lake Trout aggregation. Numbers delineate locations: 4) South Solution, 6) Breeze Channel, 7) Breeze Bay, 14) South Frank, 16) South Arm Shelf, 18) Southeast Arm West, 19) Molly Islands, 23) Pelican Creek, and 24) North Stevenson.

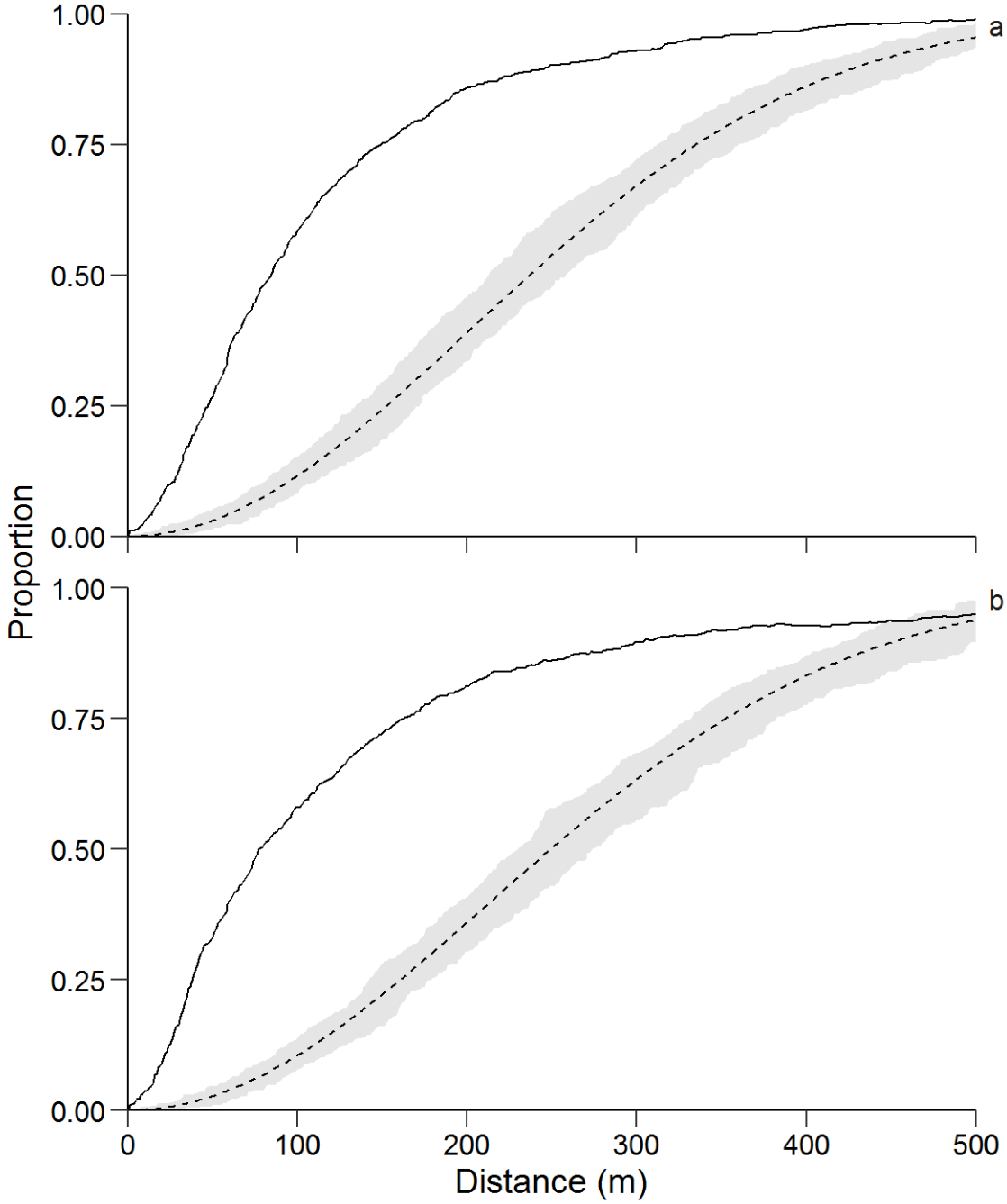

Figure 4. G-function plot of the proportion of Lake Trout locations in Yellowstone Lake, Yellowstone National Park from the spawning period in 2016 (a) and 2017 (b) that have a nearest neighbor within a given distance (Distance [m]). Dashed line is the expected proportion under complete spatial randomness, gray shaded area is the confidence band generated from Monte Carlo simulations, and the solid line is the observed proportion from tagged Lake Trout in Yellowstone Lake. A solid line above the grey confidence band indicates an aggregated spatial pattern.

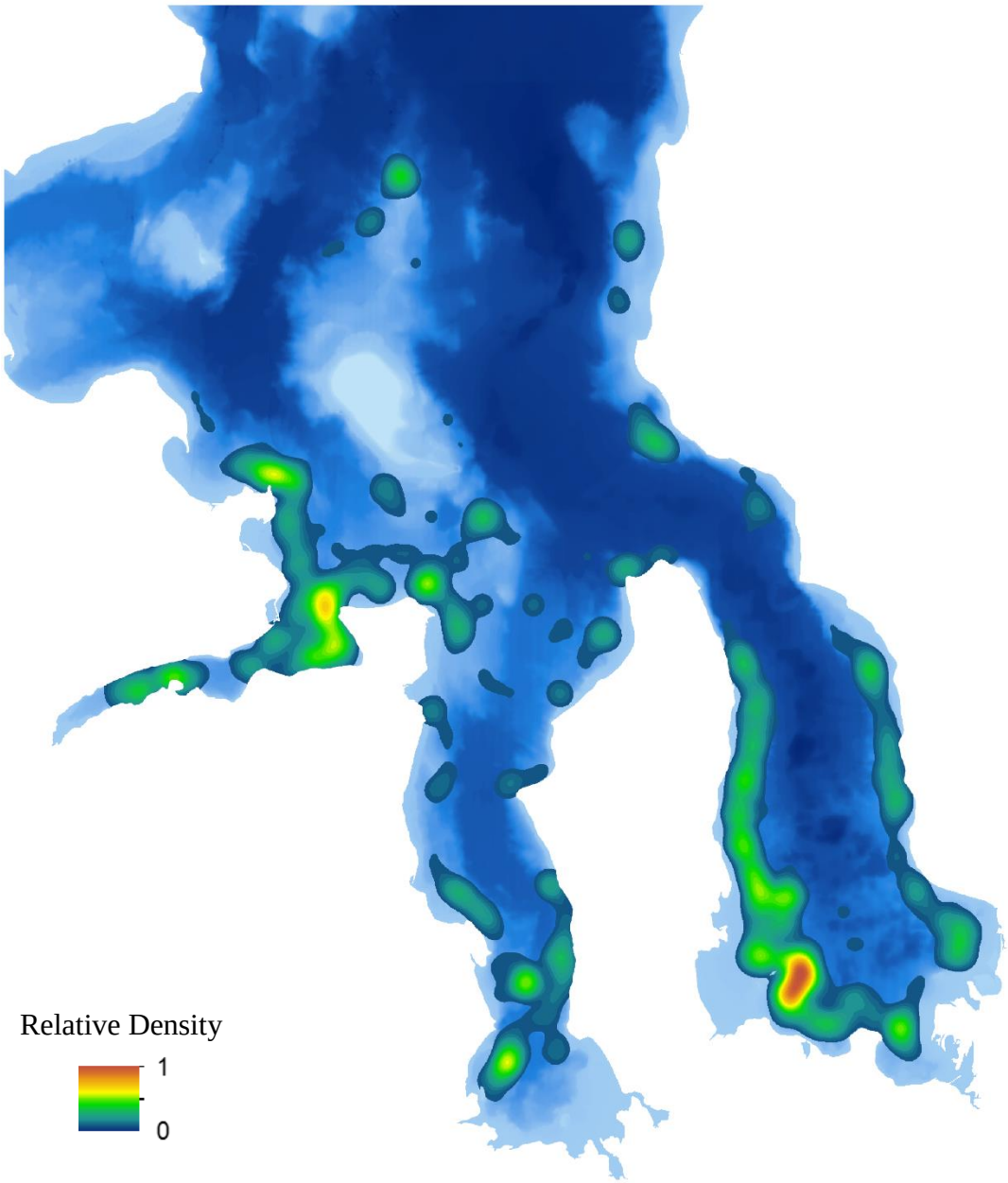

Figure 5. Kernel-density map for Lake Trout locations during the 2016 spawning period (autumn) in Yellowstone Lake, Yellowstone National Park. Relative densities indicate the degree of Lake Trout aggregation.

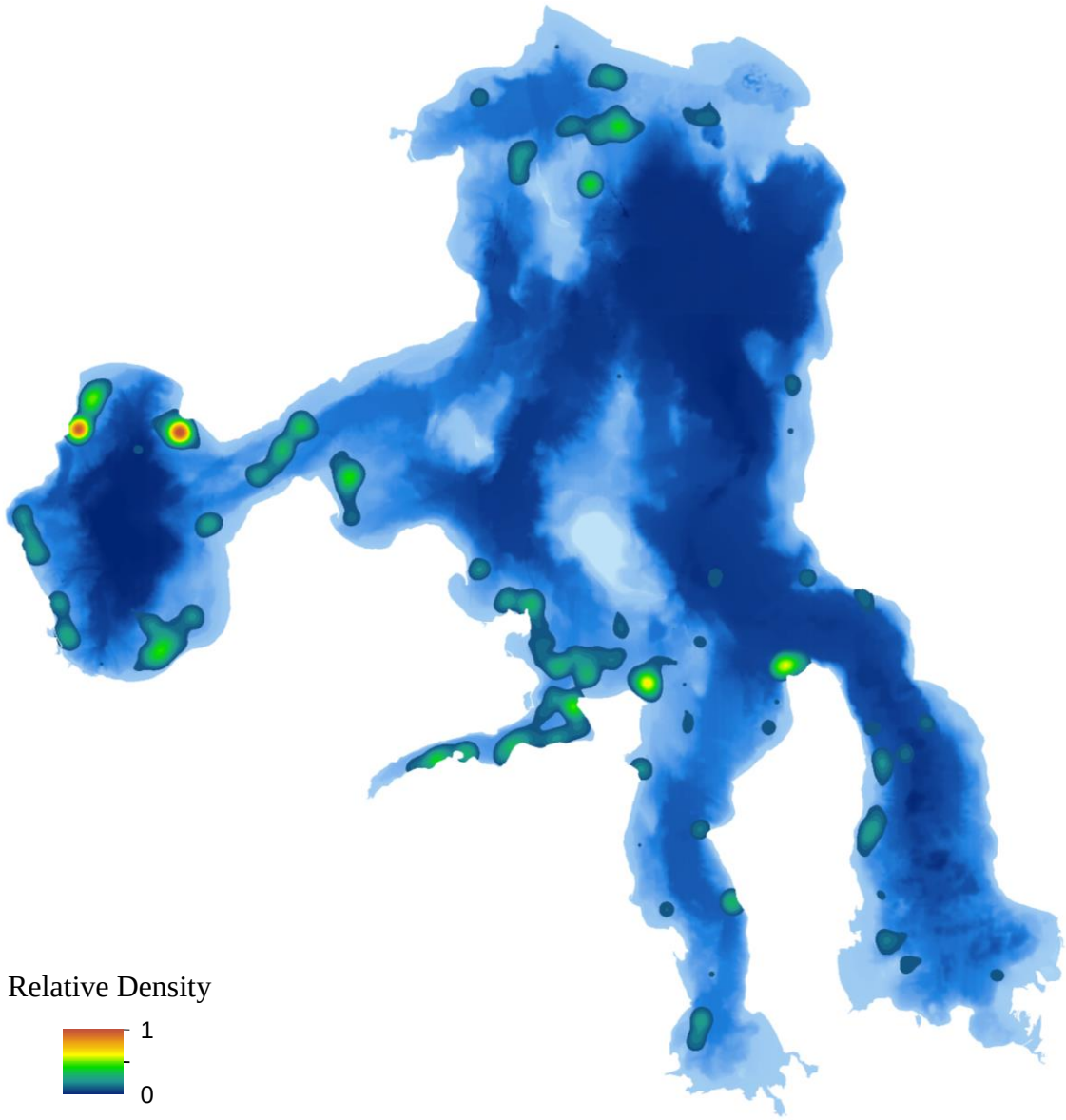

Figure 6. Kernel-density map for Lake Trout locations during the 2017 spawning period (autumn) in Yellowstone Lake, Yellowstone National Park. Relative densities indicate the degree of Lake Trout aggregation.

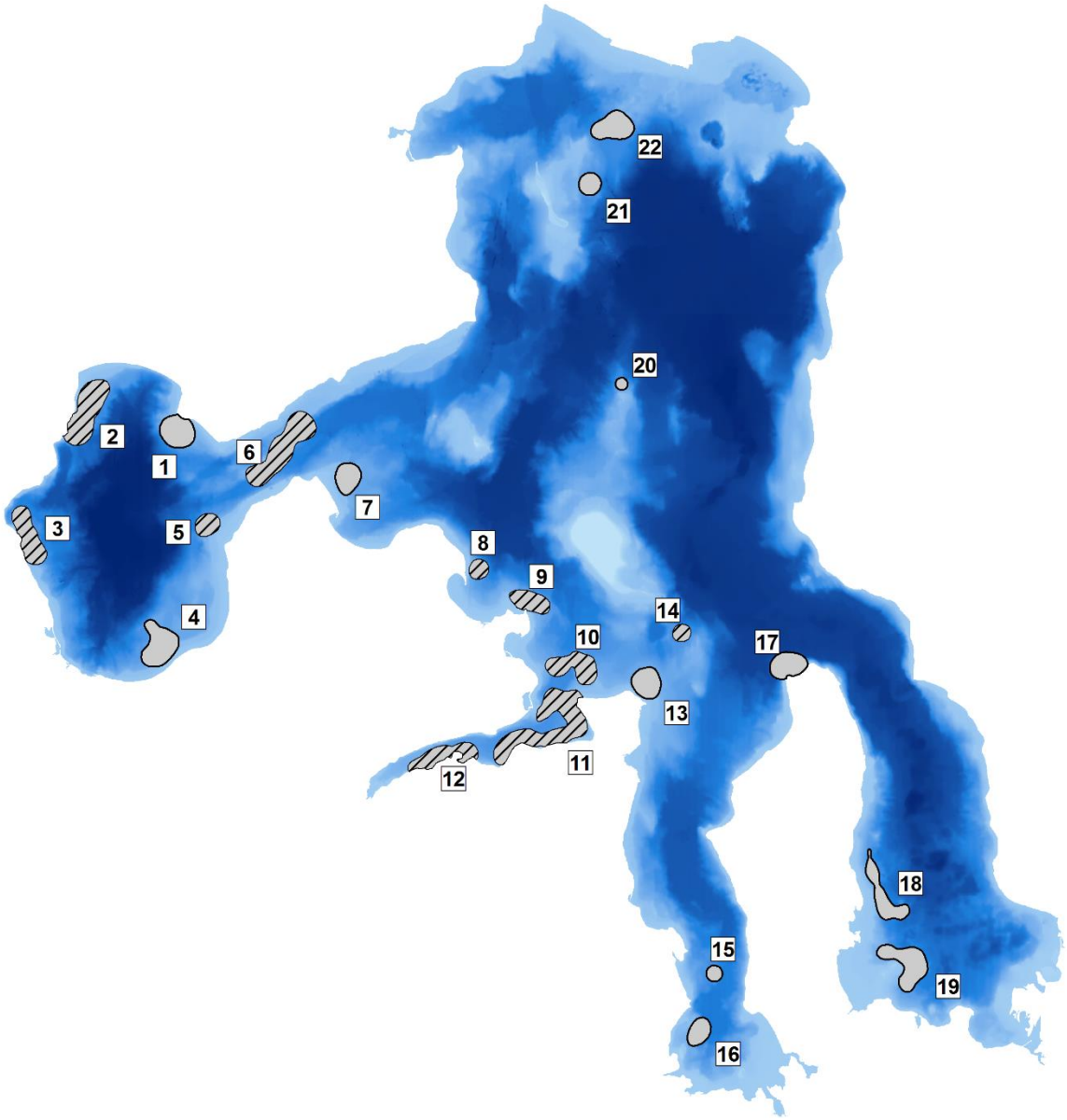

Figure 7. Map of twelve putative (solid grey) and ten confirmed (grey with crosshatch) spawning locations for Lake Trout in Yellowstone Lake, Yellowstone National Park from 2016 through 2017. Numbers delineate locations: 1) Anglers Bluff, 2) Carrington Island, 3) Geyser Basin, 4) South Solution, 5) Solution, 6) Breeze Channel, 7) Breeze Bay, 8) Wolf Point, 9) Snipe Point, 10) Olsen Reef, 11) Flat Mountain Arm, 12) Thomas Bank, 13) Plover Point, 14) South Frank, 15) South Arm Hump, 16) South Arm Shelf, 17) Promontory Point, 18) Southeast Arm West, 19) Molly Islands, 20) Frank Finger, 21) East Stevenson, and 22) Northeast Stevenson.

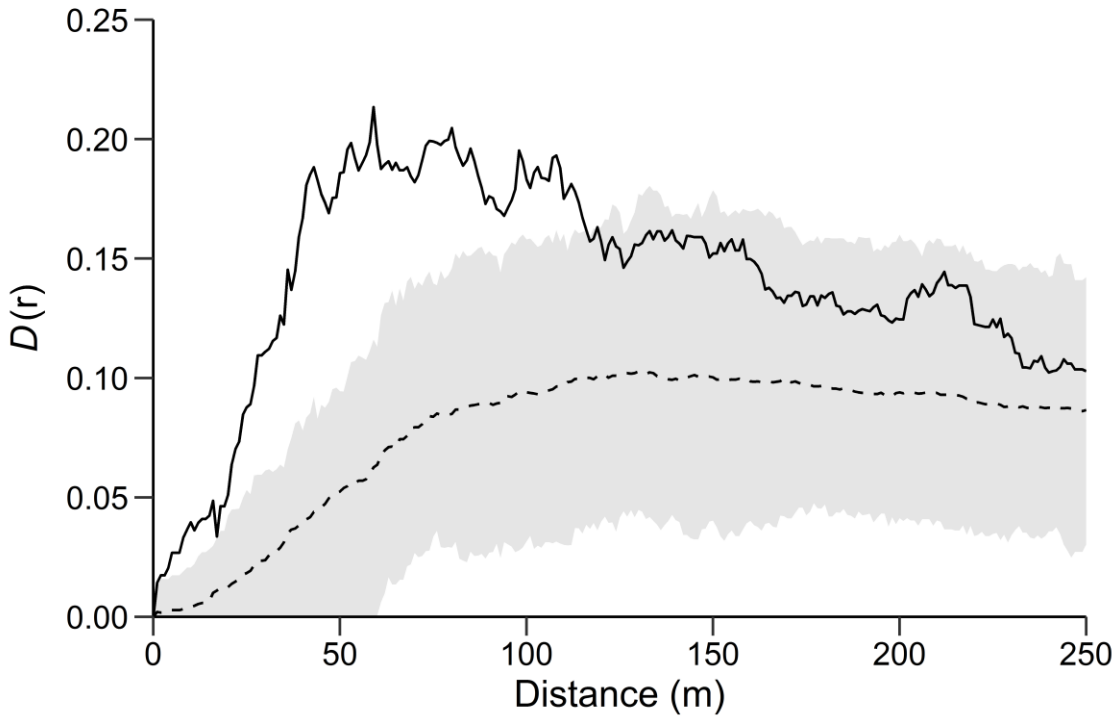

Figure 8. Difference (*D*(r)) in the G-function at a given distance (Distance [m]) between the spawning period and summer in 2017 from Lake Trout locations in Yellowstone Lake, Yellowstone National Park. Solid line is the observed *D*(*r*), dashed line is the expected *D*(*r*) under complete spatial randomness, and the gray shaded areas are significance bands from Monte Carlo simulations. A solid line outside of the confidence bands indicate a significant difference in G-function. A positive *D*(*r*) indicates a higher degree of aggregation during the spawning period.

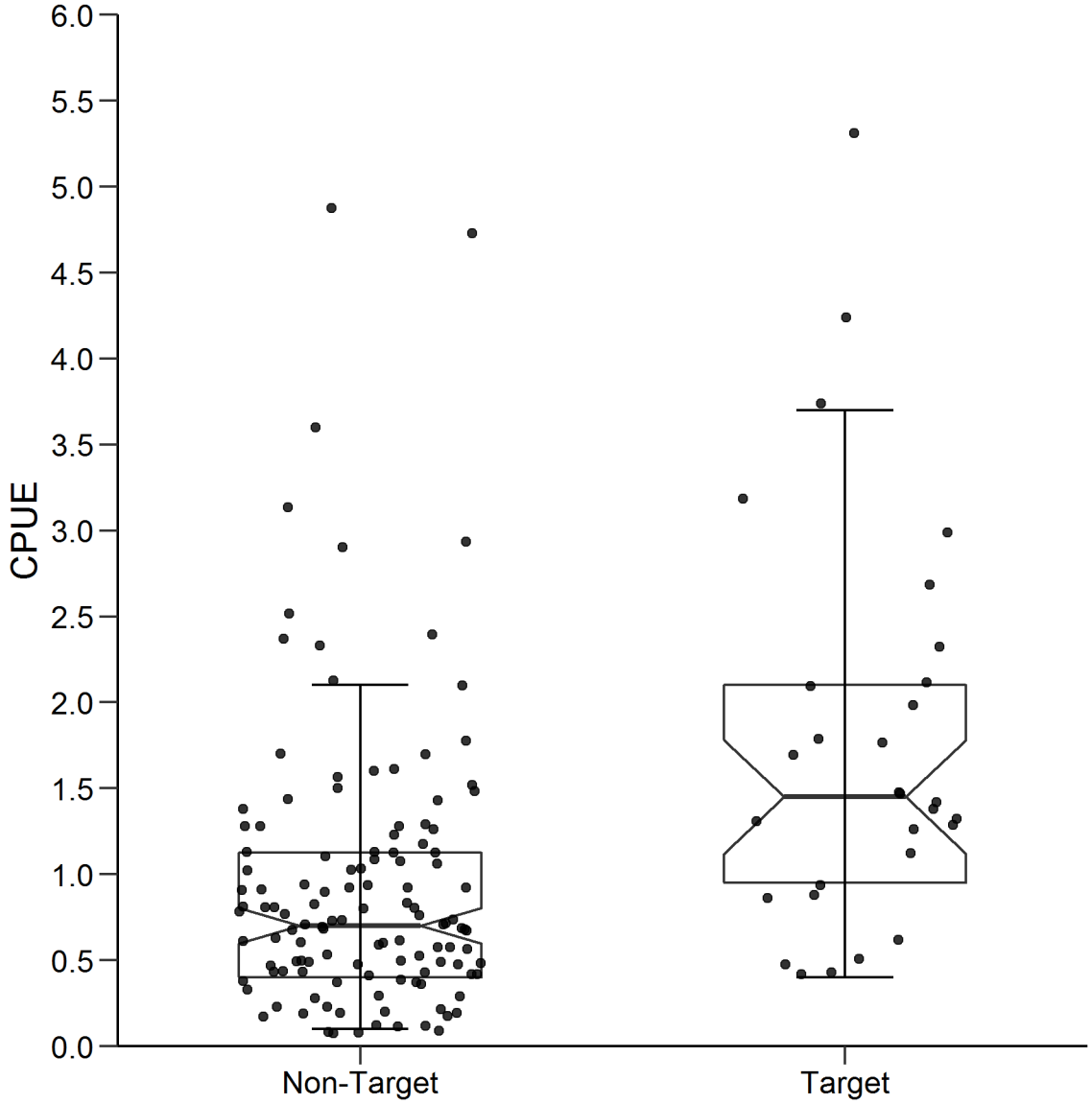

Figure 9. Box plot of catch-per-unit-effort (CPUE) for gill nets targeting (Target; N = 30) Lake Trout groups identified by telemetry and gill nets not targeting (Non-target; N = 124) Lake Trout groups in Yellowstone Lake, Yellowstone National Park during the summer in 2017. Data points have been offset on the horizontal axis within each group to reduce overlapping. Horizontal bar within the box delineates the median, box boundaries delineate first and third quartiles, whiskers delineate largest and smallest values within 1.5 times the interquartile range.

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APPENDIX

2015 LAKE TROUT TRACKING

Methods

A pilot study was initiated by the National Park Service in 2015 to determine the feasibility and logistics of conducting lake wide-mobile telemetry surveys in 2016 and 2017. Lake Trout were located using portable Lotek MAP 600 acoustic receivers equipped with two Lotek LHP_1 directional hydrophones (Lotek Wireless, Inc, Newmarket, ON, Canada). Each morning the area to be tracked was subjectively selected by Yellowstone National Park fisheries managers. Areas selected for tracking surveys were based on previous research in Yellowstone Lake. For example, Carrington Island, a confirmed spawning location, had been studied extensively by fisheries managers, therefore this area was selected less for acoustic tracking surveys than other areas.

Tracking surveys were conducted from 0600 h through 1600 h, boats would travel at a maximum speed of 9.7 km/h. Lotek MapHost software (Lotek Wireless, Inc, Newmarket, ON, Canada) was used to determine Lake Trout locations. After a Lake Trout was detected, the boat was slowed to 4.8 km/h and oriented in the direction of the target Lake Trout. Boat operators continued in this direction until the hydrophones passed over top of the target Lake Trout (indicated by a sudden change from high-signal strength to low-signal strength or no detection). The UTM position of the strongest signal strength upon approach was used to estimate fish location.

Kernel density estimate (KDE) was used to quantify where Lake Trout aggregations were located and identify areas with the highest concentrations of Lake Trout locations. A KDE map was created in ArcMap 10.3.1 (ESRI 2016) to identify

areas where adult Lake Trout aggregated. Bandwidth of the kernel was set at the detection range of the transmitters (i.e., 500 m). Maximum relative density was scaled to one to identify the most concentrated Lake Trout aggregations.

Results

Acoustic Tracking

One hundred six individual Lake Trout were tracked during the spawning period in 2015 resulting in 305 detections. Lake Trout were most commonly detected in the South Arm region (N = 69), and least commonly in the North (N = 19) (Table 1). However, effort was not even among regions, the South Arm had the most surveys (N = 17) and the North had the least (N = 5). Aggregations of Lake Trout occurred in several areas during the spawning period in 2015. Aggregations with the highest relative densities occurred at Carrington Island, Flat Mountain Arm, Promontory Point, and three areas in the South Arm Shelf.

Although there were distinct aggregations, effort was not equal for each region, likely resulting in higher relative densities in areas with more effort. For example, the South Arm had the most effort and four of the six aggregations. Nevertheless, valuable information was gained during tracking. Tracking was able to identify aggregations at confirmed spawning locations in Flat Mountain Arm and Carrington Island. Tracking also identified unexpected Lake Trout refuges in the South Arm Shelf, areas that would ultimately be targeted with gill nets.

Caution should be taken when comparing these results to data collected in 2016 and 2017 because of the difference in data collection procedures. However, Lake Trout were located in similar areas in 2015, 2016, and 2017. For example, the areas with the highest relative densities in 2015 (see above) all had high relative densities in 2016, 2017, or both.

Tables

Table 1. Number of individuals tracked, number of locations, and mean number of locations per tracking survey by lake region for Lake Trout tracked in Yellowstone Lake, Yellowstone National Park during the spawning period 2015.

Region	Individuals	Locations	Locations per survey
North	19	21	4.2
South Arm	69	197	10.8
Southeast Arm	22	38	3.7
West Thumb	29	49	3.4

Figures

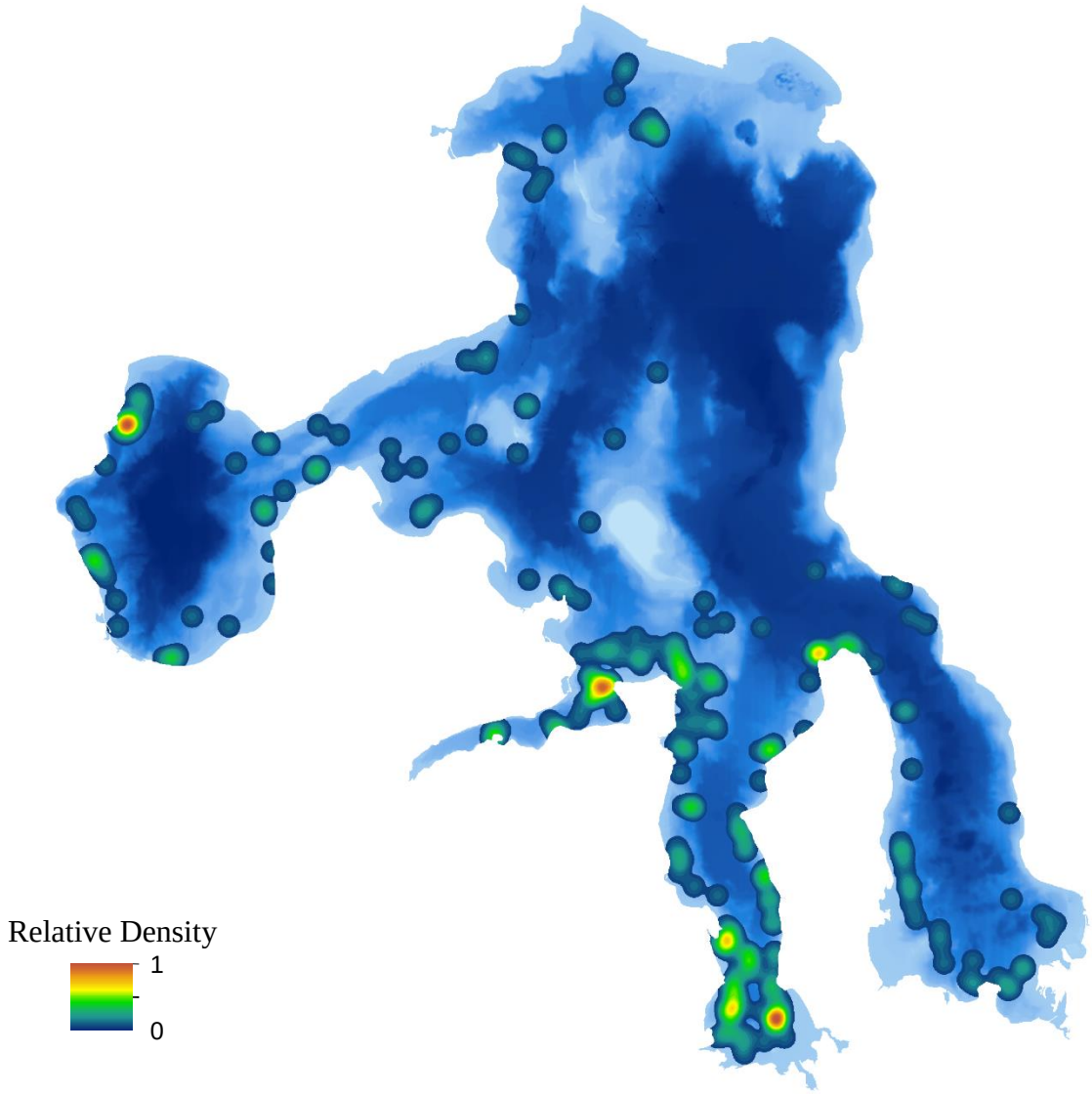

Figure 1. Kernel density map for Lake Trout locations during the 2015 spawning period in Yellowstone Lake, Yellowstone National Park. Relative densities indicate the degree of Lake Trout aggregation.