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ARTICLE

Quantifying the Spatial Structure of Invasive Lake Trout in Yellowstone Lake to Improve Suppression Efficacy

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Abstract
Invasive Lake Trout *Salvelinus namaycush* have altered the once-pristine Yellowstone Lake ecosystem through top-down effects by consuming Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*. To conserve Yellowstone Cutthroat Trout and restore the ecosystem, a Lake Trout gillnetting program was implemented to suppress the invasive population. We evaluated the spatial structure of Lake Trout in Yellowstone Lake with the intent of increasing suppression efficiency. Specifically, we addressed questions related to adult Lake Trout aggregation and movement during summer and autumn (spawning) periods and how Lake Trout used locations in the context of suppression efforts. We tracked 373 Lake Trout (>500 mm TL) during the summer and autumn of 2016 and 2017. Based on kernel density estimates, Lake Trout were highly aggregated at 9 locations during summer and 22 locations during the spawning period. Using a novel metric, individual days (product of mean individuals per survey and mean length of stay), five summer locations and five spawning locations had at least 30 individual days. These locations are suggested as priority areas for targeting Lake Trout suppression. Lake Trout were less aggregated and moved less during the summer, making them less vulnerable to a passive gear in the summer than during the autumn spawning period. Lake Trout exhibited low spawning site fidelity compared to populations elsewhere, possibly due to decades of intensive gill netting at spawning locations. Given the aggregation and movement patterns observed in Yellowstone Lake, continuing to target adult Lake Trout during the spawning period is the most cost-effective approach to Lake Trout suppression.

Invasive fish are common in aquatic ecosystems, and their establishment causes adverse ecological effects (Beck et al. 2008; Britton et al. 2011) and threatens biological diversity (CBD 2008). Invasive fishes are a contributing factor in 68% of fish extinctions and 70% of fishes listed as endangered or threatened in the United States (Miller

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et al. 1989; Jelks et al. 2008). Mitigating the negative effects of invasive fishes is a high priority for natural resource managers because the number of invasive fish species in North America has doubled since 1970 (Matlock 2014) and invasive species introductions continue to increase worldwide (Gozlan et al. 2010). Eradication of invasive fishes is generally not feasible (Britton et al. 2011; Rytwinski et al. 2018); however, actions to suppress invasive fish populations may mitigate the negative effects of predation or competition on sympatric native species or on desired populations of introduced sport fish (Fredenberg et al. 2017; Dux et al. 2019). Long-term commitments are required to maintain suppression actions and to ensure that the invasive populations do not recover (Hansen et al. 2019b).

Lake Trout *Salvelinus namaycush* are an important commercial and recreational fish that have been widely introduced outside of their native range in North America (Crossman 1995) and have caused the decline of desired native and sport fish populations throughout the intermountain western United States (Martinez et al. 2009). In Yellowstone Lake, Lake Trout have altered the food web by consuming Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, which are an important food for terrestrial species, such as grizzly bears *Ursus arctos* and osprey *Pandion haliaetus* (Koel et al. 2019). Given that Lake Trout have been overexploited by commercial harvest within their native range (Hansen et al. 1995; Muir et al. 2012), natural resource managers in the intermountain western United States have implemented suppression programs to increase harvest in order to mitigate the negative effects of Lake Trout on native fishes (Martinez et al. 2009; Hansen et al. 2016; Koel et al. 2020a).

Invasive species suppression programs are often monetarily burdensome to natural resource agencies worldwide (Simberloff et al. 2005; Simberloff 2014). For example, the current Lake Trout suppression effort in Yellowstone Lake is costly—more than US$2,000,000 are spent annually to meet management objectives (Koel et al. 2020a). Improving the efficacy of suppression programs is a top priority for the National Park Service and other natural resource agencies (Buhle et al. 2005). When suppression effort is limited, using the most efficient gear during periods 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 nontarget species (Christie and Goddard 2003; Brown and Gilligan 2014). In Yellowstone Lake, research and development of novel suppression methods have resulted in up to 100% mortality of Lake Trout embryos on spawning sites (Thomas et al. 2019; Koel et al. 2020c). Identification of Lake Trout spawning aggregations will assist in prioritizing the use of novel methods on spawning sites (Koel et al. 2020c). In addition, tracking tagged “Judas” fish can identify spatial patterns of Lake Trout that can be used to target areas where suppression will be most effective (Travis and Park 2004; Dauphinais et al. 2018). In Lake Pend Oreille, Idaho, for example, identifying the distribution and spawning locations of Lake Trout increased the efficacy of suppression (Dux et al. 2019; Hansen et al. 2019a). Similarly, the targeting of telemetered aggregations of Lake Trout with gill nets in Yellowstone Lake increased the catch rates of adult fish (Williams et al. 2020).

Yellowstone Lake has the largest population of genetically unaltered Yellowstone Cutthroat Trout in existence (Gresswell 2011), and this population ranks as one of the highest in conservation value for the persistence of the subspecies (Al-Chokhachy et al. 2018). Invasive Lake Trout were first discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996) and were believed to have been introduced during the mid-1980s (Munro et al. 2005) or earlier (Koel et al. 2020b). The establishment of predatory Lake Trout resulted in a decline of native Yellowstone Cutthroat Trout abundance (Koel et al. 2005). Because Yellowstone Cutthroat Trout are an important food source for terrestrial species, such as grizzly bears and osprey, the Lake Trout-induced loss of Yellowstone Cutthroat Trout resulted in displacement of these charismatic wildlife taxa (Koel et al. 2005, 2019). Management objectives are to suppress Lake Trout abundance, reduce the negative effects of Lake Trout on the Yellowstone Cutthroat Trout population, and restore the natural food web of Yellowstone Lake (Koel et al. 2010; Syslo et al. 2011). During 1995–2019, more than 3.2 million Lake Trout were harvested, primarily by gillnetting, to force the Lake Trout population into decline (Syslo et al. 2020) and allow for a positive response by Yellowstone Cutthroat Trout (Koel et al. 2020a).

Our goal was to improve suppression efficacy by answering the following questions: (1) Where do Lake Trout aggregate during the summer and autumn (spawning) periods?; (2) Does length of stay at a spawning site vary by spawning site and sex?; and (3) Does the movement rate of Lake Trout differ temporally and by sex? In addition to answering these questions, we further confirmed known spawning sites and identified potential new (putative) spawning sites to guide suppression actions on Yellowstone Lake. Furthermore, we built on the body of knowledge regarding Lake Trout ecology and addressed the question of whether Lake Trout outside the native range have a movement ecology similar to that of populations within the native range (Hansen et al. 2019b, 2021).

METHODS

Study Area

Yellowstone Lake is located in southeastern Yellowstone National Park, Wyoming, USA (Figure 1). Yellowstone Lake is the largest lake above 2,000 m in North America, with a mean depth of 48 m, a maximum depth of 133 m, and a surface area of 34,020 ha (Kaplinski 1991). The lake is dimictic, with summer stratification occurring from mid-July to mid-September. During the ice-free season, surface water temperatures range from 3°C after ice-off to 18°C in mid-summer, the dissolved oxygen concentration ranges from 7 to 11 mg/L, the water is slightly basic (pH 7.2–8.3), and conductivity is low (69–96 μS/cm; Koel et al. 2019).

Transmitter Implantation and Allocation

Yellowstone Lake was divided into four regions (North, Southeast Arm, South Arm, and West Thumb), and Lake Trout were collected using gill nets in each region (Syslo et al. 2020) to ensure equal allocation of telemetered fish throughout the lake (Figure 1). During 2015–2017, Lake Trout larger than 500 mm TL were implanted with Lotek CART series transmitters (Lotek Wireless, Inc., Newmarket, Ontario), 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 16 g in weight; MM-MC-16-25: 63 mm long, 16-mm diameter, and 28 g in weight), and both transmitters had a battery life of 3 years. Lake Trout selected for transmitter implantation were anesthetized using AQUI-S 20E (AQUI-S New

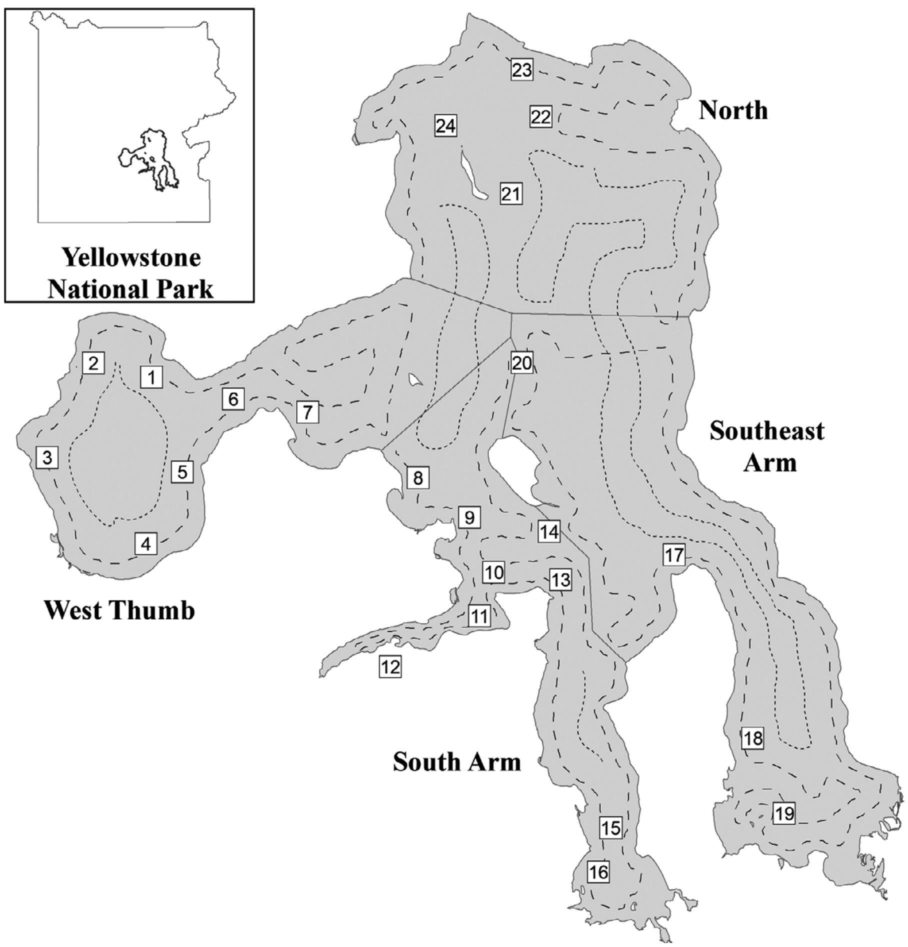

FIGURE 1. Yellowstone Lake in southeast Yellowstone National Park, with four mobile telemetry tracking regions (North, West Thumb, South Arm, and Southeast Arm) delineated by gray lines. Tracking transects are delineated by dashed (shallow transects, depths <60 m) and dotted (deep transects, depths >60 m) lines. Numbers in boxes reference the 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.

Zealand Ltd., Lower Hutt, New Zealand) at 20 mg/L, and transmitters were implanted using standard surgical procedures (Wagner et al. 2011). Determination of sex and maturity was conducted by observing the gonads through the incision made for transmitter implantation. A groove director was used to gently move the stomach aside to reveal gonads if needed. Lake Trout were implanted with transmitters and assigned sex when ovaries or testes were easily identified as mature. In some instances, sex and stage of maturity were not identified and Lake Trout implanted with transmitters were classified as "unknown sex." Sex and stage of maturity of unknown-sex Lake Trout were later determined if those individuals were recaptured during suppression gill netting.

Mortality motion sensors in the 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 the efficiency of tracking. Post hoc mortality analysis was performed on all Lake Trout because some were stationary during the entire study, but their mortality sensors were not activated. Lake Trout were considered mortalities if the mean distance traveled between sequential locations throughout the study period was less than 500 m. Lake Trout identified as mortalities in the post hoc analysis or with mortality codes activated were excluded from analyses ($N = 206$). The apparent mortality of 35.6% was expected; postrelease mortality of Lake Trout captured in gill nets elsewhere has been estimated to be 41% (Ng et al. 2015). The surviving ($N = 373$) Lake Trout (mean TL = 589 mm; SE = 3.06) were used in analyses, including 99 females (mean TL = 611 mm; SE = 5.40), 135 males (mean TL = 569 mm; SE = 5.04), and 139 fish of unknown sex (mean TL = 593 mm; SE = 4.96).

Acoustic Tracking

Lake Trout were located using portable Lotek MAP 600 acoustic receivers equipped with two Lotek LHP_1 directional hydrophones. Tracking transects, stratified by depth, were delineated in the four regions of Yellowstone Lake (i.e., North, Southeast Arm, South Arm, and West Thumb; Figure 1) to maximize tracking efficiency. Tracking effort focused on lake depths less than 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 previously used by Lake Trout in Yellowstone Lake (Koel et al. 2020c) and elsewhere (Marsden et al. 1995), and the depths at which adult Lake Trout are commonly sampled during annual monitoring in Yellowstone Lake (Syslo et al. 2016). Tracking transects were created in ArcMap version 10.3.1 (ESRI 2016) for each tracking region, 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 (Melnychuk and Christensen 2009). Adjacent transects continued until all depths less than 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 activity across the species' range in North America typically increases during the evening, immediately after sunset (Martin and Olver 1980). However, during previous studies of broad-scale movement patterns of Lake Trout in Yellowstone Lake, there was no evidence of diel patterns in spawning behavior (Gutowsky et al. 2020). Therefore, tracking surveys were conducted from 0600 to 1600 hours with boats traveling at a maximum speed of 9.7 km/h. Lotek MapHost software 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 targeted fish. The boat continued toward the Lake Trout signal, marking the Universal Transverse Mercator (UTM) position each time the signal strength increased, until hydrophones passed over top of the targeted Lake Trout as indicated by a sudden change from high signal strength to low signal strength or no detection. The UTM position where the signal suddenly changed was the estimated Lake Trout location. When tracking multiple Lake Trout in the same aggregation, the point at which the signal was lost was sometimes missed; in such cases, the UTM position of the greatest signal strength was considered the estimated Lake Trout location.

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

Although tracking effort was focused on depths less than 60 m (see above), when a third boat was available during the 2017 spawning period, we also sampled depths greater than 60 m (designated as "deep transects") to ensure that sampling covered all potential Lake Trout spawning habitat (Beauchamp et al. 1992; Fitzsimons et al. 2005). 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. Depths greater than 60 m were surveyed once in August 2017 and five times during the spawning period in 2017.

Data Analysis

Movement rate.— Total distance was calculated between sequential locations of individual Lake Trout. Euclidian distances between sequential locations were calculated in R (R Core Team 2019). 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 the spawning period in 2017.

Aggregations.— Kernel density estimation (KDE) was used to quantify locations and concentrations of Lake Trout aggregations. A KDE map was created in ArcMap version 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; Williams 2019), and the maximum relative density was scaled to 1.0 to identify the most concentrated Lake Trout aggregations. Kernel density estimation was used to identify Lake Trout aggregations from acoustic tracking data collected during the summer of 2017 and the spawning period in 2016 and 2017. The "raster to polygon" function in ArcMap version 10.3.1 (ESRI 2016) was used to map the approximate size of Lake Trout summer aggregation areas. The area (ha) and minimum, maximum, and mean depth of each summer aggregation area were calculated. The KDE maps from the 2016 and 2017 spawning periods were then used to identify putative spawning locations. Lake Trout spawning was previously confirmed (i.e., presence of Lake Trout embryos or larvae) at 14 locations in Yellowstone Lake (Koel et al. 2020c). Aggregations (as determined by KDE maps) with relative densities that were similar to or higher than those of confirmed spawning locations were considered putative spawning locations.

Lake Trout use of each summer aggregation area, confirmed spawning location, and putative spawning location was summarized to prioritize the Lake Trout suppression gillnetting effort. Total number of individuals that visited a site, mean individuals per tracking survey, mean length of stay, maximum length of stay, and mean individual days 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 mean length of stay.

Differences in seasonal dispersal patterns.— The G-function $\widehat{G}(r)$, which is the cumulative distribution of the distances from randomly selected points to the nearest neighboring point (Bivand et al. 2013), was used to quantify and identify patterns of Lake Trout point locations. Given a distance r, $\widehat{G}(r)$ is the probability that the nearest neighbor distance is less than or equal to r (Brunsdon and Comber 2015). Yellowstone Lake was the "spatial window," and the border correction for $\widehat{G}(r)$ was used to account for edge effects and bias around its border (Stoyan 2006). Refer to the Supplemental Materials (available in the online version of this article) for a more detailed description of methods for and results from the G-function analysis.

The difference in the degree of aggregation ($D[r]$) between the summer and spawning periods in 2017 was calculated as the difference between seasonal $\widehat{G}(r)$ values,

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

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

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

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 epidemiological case–control studies (Diggle and Chetwynd 1991; Diggle et al. 2007), in this study $K(r)$ was substituted with $\widehat{G}(r)$ to test for a difference in $\widehat{G}(r)$ between two seasonal data sets.

RESULTS

Aggregations of Lake Trout in the summer occurred at several locations throughout Yellowstone Lake, and nine locations had relative density values at or near 1.0: South Solution, Breeze Channel, Breeze Bay, South Frank, South Arm Shelf, Southeast Arm West, Molly Islands, Pelican Creek, and North Stevenson (Figure 2). Of the nine aggregation sites, Lake Trout spent the most time at Breeze Bay, Pelican Creek, Breeze Channel, South Solution, and South Arm Shelf (individual days $\geq$ 30; Table 1). Breeze Bay had the longest mean and maximum lengths of stay and the most individual days when all tracked Lake Trout were considered (Table 1). The Molly Islands had the shortest length of stay (Table 1). The mean of mean length of stay at a summer location was 9.5 d (80% CI = 7.2–11.7), and the mean number of individuals

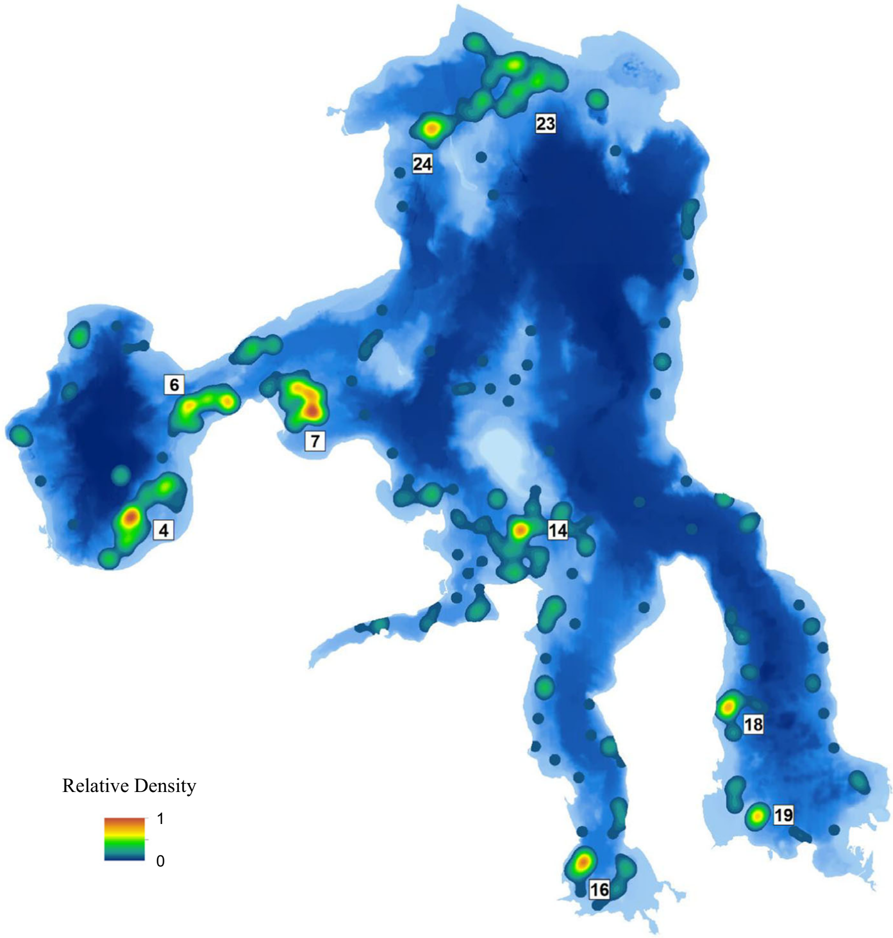

FIGURE 2. Kernel density map of Lake Trout locations in Yellowstone Lake during summer 2017. Relative densities indicate the degree of Lake Trout aggregation. Numbers in boxes indicate locations defined in Figure 1.

using a summer location was 15.2 (80% CI = 11.9–18.5). The longest length of stay at a summer location was 75 d and occurred at Breeze Bay (Table 1). Length of stay and individual days varied by sex, with mean length of stay for females at summer locations varying from 1.0 to 13.8 d (Table S1 available in the Supplemental Material in the online version of this article). Female Lake Trout had the highest number of individual days at Pelican Creek and South Solution. Mean length of stay at summer locations for males varied from 1.0 to 24.5 d, and the highest number of days for a male to stay at a summer location was 48 d (Table S1). Males had the most individual days at Southeast Arm West and South Solution during the summer (Table S1).

For the truncated tracking area examined during the spawning period in 2016, Lake Trout aggregated at nine locations and 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 3A). Lake Trout aggregated at 19 sites in 2017, including two distinct sites in the West Thumb: Carrington Island and Anglers Bluff (Figure 3B). During 2016 and 2017 combined, 10 Lake Trout aggregations occurred at previously confirmed spawning locations and 12 aggregations were considered new (putative) spawning sites. Thus, 22 spawning sites have been identified in Yellowstone Lake (Figure 3B; Table 1).

During the Lake Trout spawning period, most individual days were spent at Anglers Bluff, Carrington Island, Flat Mountain Arm, South Solution, and the Molly Islands (individual days $\geq$ 30; Table 1). The highest number of individual days was observed at Anglers Bluff and was 1.7 times greater than that at Carrington Island, the location with the second-highest number of individual days (Table 1). The mean of mean length of stay at a spawning location was 6.8 d (80% CI = 5.8–7.9), and the mean number of individuals using a spawning site was 14.8 (80% CI = 12.2–17.3). The longest length of stay at a spawning location was 34 d and occurred at Anglers Bluff and Carrington Island (Table 1). Mean length of stay at a

TABLE 1. Number of individual Lake Trout, mean individuals per tracking survey, length of stay, and individual days at each site during the summer aggregation and spawning periods in Yellowstone Lake, Yellowstone National Park for 2016 and 2017.

	Individuals		Length of stay (d)		
Site[a]	Total	Per survey	Mean	Maximum	Individual days
Summer					
Breeze Bay	26	7.3	15.2	75	111.0
Pelican Creek	19	4.8	13.5	71	64.8
Breeze Channel	22	5.5	9.6	49	52.8
South Solution	22	6.3	8.2	28	51.7
South Arm Shelf	9	2.5	13.0	45	32.5
Southeast Arm West	7	2.0	13.8	21	27.6
North Stevenson	9	2.3	6.6	5	15.2
South Frank	14	2.8	4.2	27	11.8
Molly Islands	9	1.5	1.0	1	1.5
Spawning					
Anglers Bluff[b]	17	5.1	12.3	34	62.7
Carrington Island	22	5.3	7.0	34	37.1
Flat Mountain Arm	43	4.5	7.7	31	34.7
South Solution[b]	14	3.5	9.3	30	32.6
Molly Islands[b]	21	2.8	10.7	24	30.0
Thomas Bank	19	2.1	9.0	31	18.9
East Stevenson[b]	2	1.0	17.0	33	17.0
Breeze Channel	21	3.9	4.0	18	15.6
Northeast Stevenson[b]	8	2.0	7.6	15	15.2
Breeze Bay[b]	8	1.8	7.4	22	13.3
Southeast Arm West[b]	18	1.9	6.0	19	11.4
Snipe Point	15	1.5	7.5	23	11.3
Geyser Basin	12	2.0	5.5	28	11.0
Promontory Point[b]	11	1.2	8.2	27	9.8
Plover Point[b]	22	1.6	5.4	22	8.6
Olson Reef	26	1.3	3.4	17	4.4
South Arm Shelf[b]	14	1.0	3.0	16	3.0
Solution	7	0.6	3.7	20	2.2
South Arm Hump[b]	7	0.5	3.6	14	1.8
Frank Finger[b]	4	0.2	8.3	18	1.7
South Frank	8	0.4	2.3	13	0.9
Wolf Point	6	0.2	1.5	4	0.3

Note "Individual days" are the product of mean individuals per survey and mean length of stay.
[a]See Figure 1 for locations.
[b]Putative spawning locations.

spawning location was similar between sexes (Table S2). Maximum length of stay varied by sex, with males staying at a spawning site for an average of 15.7 d (80% CI = 12.4–18.9) and females staying for an average of 10.9 d (80% CI = 7.8–13.9; Table S2). The longest length of stay at a spawning site was 34 d for male Lake Trout and 24 d for female Lake Trout (Table S2).

A total of 216 Lake Trout visited confirmed spawning locations, putative spawning locations, or both in 2016 and 2017. Of these, 47% visited multiple spawning locations (mean = 2; maximum = 5) in the same year. Sixty-eight Lake Trout were tracked during the spawning period in both 2016 and 2017, and 41% ($N = 28$; 3 females, 5 males, and 20 unknown-sex individuals) returned to the same spawning location in 2017 as in 2016. Flat Mountain Arm had the most Lake Trout return each year.

Lake Trout were clearly aggregated in the summer relative to complete spatial randomness (i.e., observed $\widehat{G}[r]$ was larger than the $G[r]$ that would be expected given

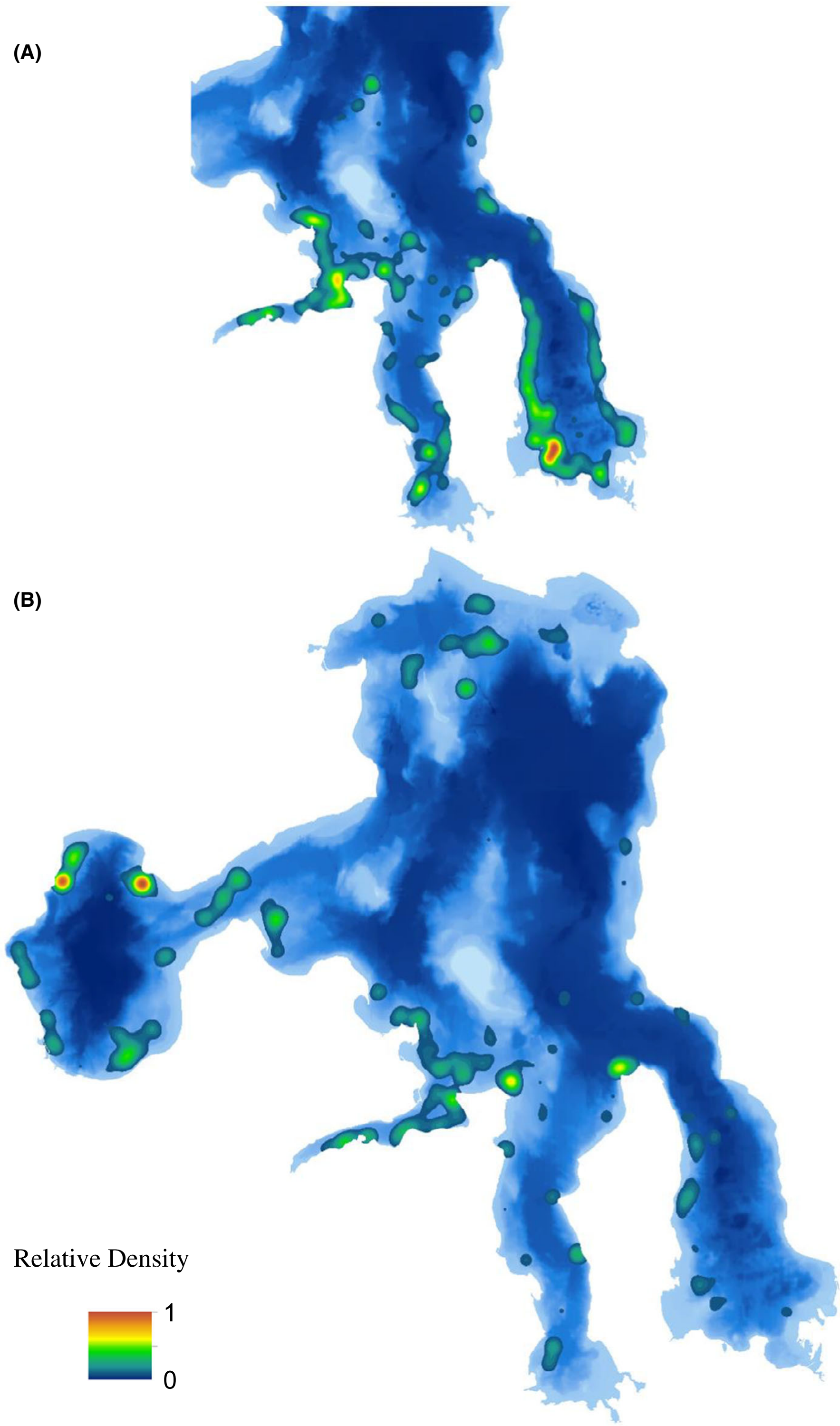

FIGURE 3. Kernel density map for Lake Trout locations in Yellowstone Lake during the spawning period (autumn) in **(A)** 2016 (only the two regions surveyed are shown) and **(B)** 2017. Relative densities indicate the degree of Lake Trout aggregation.

complete spatial randomness; Figure S1 available in the Supplemental Material in the online version of this article). The fish were aggregated during the 2016 and 2017 spawning periods (Figure S2). In 2017, Lake Trout were more tightly aggregated during the spawning period than during the summer. Strong statistical evidence supported a

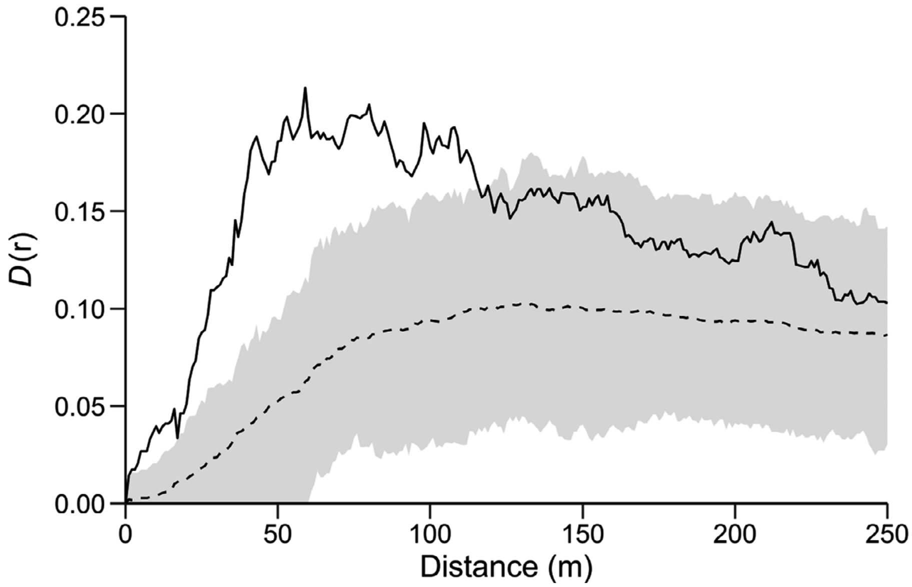

FIGURE 4. Difference ($D[r]$) in the G-function at a given distance (m) between the spawning period and summer in 2017 for Lake Trout locations in Yellowstone Lake. The solid line is the observed $D(r)$, the dashed line is the expected $D(r)$ under complete spatial randomness, and the gray shaded areas are significance bands from Monte Carlo simulations. A solid line outside of the confidence bands indicates a significant difference in the G-function. A positive $D(r)$ indicates a higher degree of aggregation during the spawning period.

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 $D(r)$ that would be expected under complete spatial randomness and was outside the Monte Carlo significance bands (Figure 4).

In addition to variation in aggregation between seasons, Lake Trout moved considerably less during the summer (median = 124.5 m/d) than during the spawning period (median = 294.4 m/d; Wilcoxon rank-sum test: $W = 1.2 \times 10^5$, $P < 0.01$). Median movement rates of male (118.0 m/d; SE = 126.9) and female (164.0 m/d; SE = 194.2) Lake Trout were highly variable in the summer. During the spawning period, the median movement rate for male Lake Trout (170.8 m/d; SE = 60.1) was less than that for females (310.6 m/d; SE = 101.2), which is consistent with males staying longer at a spawning location.

DISCUSSION

Lake Trout clearly aggregated in the summer and spawning periods, and locations varied by season. Locations used for aggregations during the spawning period (e.g., Flat Mountain Arm, Carrington Island, and Anglers Bluff) were rarely used by Lake Trout during the summer. The patterns observed in Yellowstone Lake were consistent with those of other Lake Trout populations within (Blanchfield et al. 2009; Pinheiro et al. 2017) and outside of (Dux et al. 2011; Fredenberg et al. 2017) their native range. 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). However, some Lake Trout in Yellowstone Lake used South Solution, Breeze Channel, and Breeze Bay during both the summer and the spawning period, suggesting that Lake Trout used these areas throughout the year for feeding and spawning. Lake Trout use of the same locations throughout the year was corroborated by high catch rates in the same region (e.g., West Thumb) during annual summer assessment netting (Arnold et al. 2017) and during suppression netting in both the summer and spawning periods. The locations were deeper than other spawning locations, providing both preferred environmental conditions (e.g., water temperature) in summer and suitable substrate for spawning in autumn.

Lake Trout in Yellowstone Lake were more aggregated during summer than other invasive Lake Trout populations (Dux et al. 2011), probably in response to preferred environmental conditions or prey availability (Olson et al. 1988; Blanchfield et al. 2009; Plumb and Blanchfield 2009). Lake Trout require cold water temperatures (7.5–16.4°C; Challice et al. 2019) 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 seek refugia in the hypolimnion (Dux et al. 2011; Guzzo et al. 2017). However, Lake Trout in some oligotrophic lakes exhibit thermally flexible habitat ranges extending past their maximum preferred temperatures (Challice et al. 2019). 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). The postspawn migration of Lake Trout in Lake Superior was also related to the distribution of their preferred prey (Binder et al. 2018). Amphipod distributions in Lake Superior (Auer et al. 2013) are known to influence the spatial patterns of fishes (Hondorp et al. 2005). When Yellowstone Cutthroat Trout abundance was low, Lake Trout in Yellowstone Lake fed primarily on amphipods during the summer (Syslo et al. 2016), which may cause them to aggregate where amphipod densities are highest.

Understanding seasonal movement patterns is essential for the effective suppression of an established invasive species (Hennen and Brown 2014). For example, understanding the movement patterns of Sea Lamprey *Petromyzon marinus* allowed for identification of areas where traps would be most effective (Holbrook et al. 2016), and exploiting predictable seasonal dispersal patterns resulted in the successful eradication of Common Carp *Cyprinus carpio* from large lacustrine systems in North America (Sorensen and Bajer 2020) and Australia (Donkers et al. 2012; Taylor et al. 2012). In Yellowstone Lake, Lake Trout moved to all confirmed spawning locations and to putative spawning locations that were previously undocumented. The number of individual Lake Trout, relative densities, mean length of stay, and individual days were similar at the confirmed and putative spawning areas, thus providing evidence that Lake Trout probably spawn at the putative spawning locations. However, visual confirmation of embryos is needed to verify these as Lake Trout spawning locations.

Lake Trout in Yellowstone Lake exhibited low spawning site fidelity compared to other Lake Trout populations. In their native range in Lakes Huron and Champlain, nearly 90% and 74% of tagged Lake Trout, respectively, returned to the same spawning location in subsequent years (Binder et al. 2016; Pinheiro et al. 2017). Additionally, for most spawning sites the mean length of stay by an individual Lake Trout was shorter than that observed in other populations. For example, Lake Trout remained on spawning sites between 15 and 30 d/year in Lake Champlain (Pinheiro et al. 2017). The high amount of suppression effort at Lake Trout spawning sites during the spawning period could be causing fishing-induced selection that is altering the behavioral traits of Lake Trout in Yellowstone Lake (Uusi-Heikkilä et al. 2008; Diaz Pauli and Sih 2017), selecting for fish that move more among spawning locations, have shorter stays, 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. 2017; Diaz Pauli 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* that were captured in gill nets moved downstream rapidly after release (Mäkinen et al. 2000). The tendency of salmonids to stray from natal spawning locations, coupled with frequent disruptions from netting operations, 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 as straying from established spawning locations to spawn at recently constructed spawning reefs in Lake Huron (Marsden et al. 2016), and Lake Trout are known to stray to previously unused spawning locations when historical sites are degraded (McAughey and Gunn 1995). More than two decades of gill-net suppression have likely caused net avoidance, increased straying, and pioneering use of novel spawning locations throughout Yellowstone Lake.

Identification of 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 that they are effective at causing high mortality rates (Thomas et al. 2019; Koel et al. 2020c; Poole et al. 2020). The measure of Lake Trout aggregation size at confirmed spawning locations in this study will assist biologists in identifying areas to be targeted with embryo suppression methods. Furthermore, the identification of 12 putative spawning locations provides additional areas that can be targeted in the future if Lake Trout spawning is confirmed. Applying suppression methods that target multiple life stages in an integrated pest management approach may be more effective than a single suppression method (Weber et al. 2011; Simberloff 2014; Lechelt and Bajer 2016). For example, by combining gill nets, trap nets, and incentivized angling, managers were able to reduce Lake Trout abundance in Lake Pend Oreille, Idaho (Dux et al. 2019). Therefore, targeting putative and confirmed spawning locations with gill nets and methods to suppress embryos should increase the efficacy of the Lake Trout suppression program in Yellowstone Lake.

The identification of Lake Trout spawning locations provides insight into areas that could be targeted with gill nets, many of which were not historically targeted. Despite Lake Trout aggregating during the summer and Breeze Channel having the highest individual days during the summer, the movement of Lake Trout during summer was less than that during the spawning period, which reduces the catch rate in a passive gear. Thus, targeting the spawning period and spawning locations is necessary to increase catch rates of adult Lake Trout and improve efficacy of the suppression program (Williams et al. 2020). As of 2019, targeting Lake Trout at confirmed spawning locations in Yellowstone Lake had resulted in the highest numbers of mature fish captured in gill nets (Koel et al. 2020a). Models indicate that focusing suppression effort on adults is the most efficient strategy for suppressing invasive Lake Trout (Hansen et al. 2019a; Syslo et al. 2020). Population growth rates of Lake Trout in Yellowstone Lake are most sensitive to changes in age-0 survival (Syslo et al. 2011); therefore, increasing the removal of adult female Lake Trout, thereby removing their reproductive potential, will increase the efficacy of the suppression program (Syslo et al. 2011, 2020).

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SUPPORTING INFORMATION

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