CONTRIBUTED PAPER

Revealing migration and reproductive habitat of invasive fish under an active population suppression program

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Abstract

Endemic species face a variety of threats including predation from non-native invaders. In some cases, however, invasive species can be managed by directly suppressing populations, and tracking technologies that allow researchers to identify movement patterns and aggregations representative of the population can facilitate suppression activities. In Yellowstone Lake (Yellowstone National Park, Wyoming), invasive lake trout (*Salvelinus namaycush*) have been the target of a population suppression program for over two decades. For this form of management, the reproductive period is particularly important because fish migrate to and from spawning grounds. From 2011 to 2014, adult lake trout ($n = 317$) in Yellowstone Lake were tracked using acoustic biotelemetry. After controlling for spatial and temporal dependency in the data, total abundance of unique individuals was estimated where migratory trajectories occurred at confirmed spawning sites. Aggregations and migratory trajectories were further estimated at locations where spawning had not previously been observed. Across years, the greatest number of individuals was observed along a migration corridor in the southwestern area of the lake. Novel strategies for analyzing acoustic telemetry data provided insights into the behavior of an invasive fish species. By betraying the positions of conspecifics, tagged fish revealed potentially

important reproductive habitats and migration corridors that warranted further investigation as possible sites for population suppression.

1 | INTRODUCTION

Among the stressors that threaten global ecosystems, invasive species are perhaps the most challenging to manage (Allendorf & Lundquist, 2003; Hauser & McCarthy, 2009; Hulme, 2009). The spread of invasive species is often cryptic, supported by numerous vectors (Meyerson & Mooney, 2007), and the ecological and social aspects of control or eradication can be difficult to reconcile (Epanchin-Niell et al., 2010; Myers, Simberloff, Kuris, & Carey, 2000; Zavaleta, Hobbs, & Mooney, 2001). Negative consequences associated with invasive species are well-documented and particularly evident in isolated freshwater ecosystems (Gutowsky et al., 2019; Johnson, Ricciardi, & Carlton, 2001; Leung & Mandrak, 2007). Although control is not always an option, the costs of inaction can justify management programs to reduce the negative consequences of aquatic invasive species on ecosystems and the economies they support (Homans & Smith, 2013; Horsch & Lewis, 2009; Lovell, Stone, & Fernandez, 2006). In some freshwater systems, invasive species management has been performed through targeted removal during periods when individuals aggregate, including early developmental stages and adult migration (Bajer, Chizinski, & Sorensen, 2011; Holbrook et al., 2016).

Migration occurs when a fraction of a population makes predictable, directed, uninterrupted movement to conditions that are favorable for reproduction, bioenergetics, feeding opportunities, or predator avoidance (Dingle, 2014; Lucas & Baras, 2001; Mehner, 2012). Given these characteristics, migratory populations are invariably vulnerable to threats including over exploitation (Wilcove & Wikelski, 2008). Moreover, movement patterns of migratory invasive species can be used for implementing effective control measures (Britton, Gozlan, & Copp, 2011; Lennox, Blouin-Demers, Rous, & Cooke, 2016; Olson, 2006). For example, tagged "Judas" animals that betray the location of conspecifics, inform population suppression programs, and ultimately aid to conserve native species (Bajer et al., 2011; McIntyre, 1995; Woolnough et al., 2012).

Yellowstone Lake (Yellowstone National Park in Wyoming) supports what is believed to be the largest population of genetically unaltered Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) (Gresswell, Liss, & Larson, 1994). This species is integral to the aquatic ecosystem, economy, and history of Yellowstone National Park (Koel, Bigelow, Doepke, Ertel, & Mahony, 2005; Varley & Schullery, 1995). However, the introduction of invasive lake trout (*Salvelinus namaycush*) and the potential effects of whirling disease have led to large-scale declines in abundance and demographic shifts in the Yellowstone cutthroat trout population (Syslo et al., 2011). For instance, lake trout were estimated to have consumed up to 15 metric tons or 14% of the vulnerable Yellowstone cutthroat trout production in Yellowstone Lake in 1996 (Ruzycki, 2003), and by 2006, the number of Yellowstone cutthroat trout ascending one of the major spawning streams had declined two orders of magnitude from estimates prior to the discovery of lake trout (mean 1977–1992 = 43,580, Gresswell et al., 1994; total 2006 = 471, Koel et al., 2007). Losses in Yellowstone cutthroat trout production has profound effects on the Yellowstone Lake ecosystem and the many species that depend on them as a nutrient resource (Crait & Ben-David, 2006; Koel et al., 2005; Reinhart, Haroldson, & Mattson, 2001; Stapp & Hayward, 2002).

Lake trout are opportunistic life history strategists that are long-lived, large-bodied, iteroparous, and highly fecund with large eggs and independent embryos (Ruzycki, 2003; Winemiller & Rose, 1992). Stocking and a suite of adaptable life history characteristics have allowed lake trout to colonize freshwater environments outside of their native range (Fredenberg et al., 2017; Gray, Fraser, & Grant, 2014; Rosenthal, 2012). In the western United States, invasive lake trout population suppression has been performed on a number of freshwater systems (Fredenberg et al., 2017; Hansen, Horner, Liter, Peterson, & Maiolie, 2008; Martinez et al., 2009; Ng, Fredericks, & Quist, 2016), including Yellowstone Lake (Syslo et al., 2011). Lake trout suppression is a conservation program for Yellowstone cutthroat trout, and more generally to the aquatic and terrestrial ecosystems the subspecies supports (Crait & Ben-David, 2006; Reinhart et al., 2001). Lake trout in Yellowstone Lake have been targeted with population suppression activities for decades (Kaeding, Boltz, & Carty, 1995), and in 2011, an acoustic telemetry program was initiated, in part, to reveal potentially important reproductive habitat (Gresswell, Heredia, Romine, Gutowsky, & Parsley, 2016).

We used data from the multi-year acoustic telemetry program to: (a) identify migration routes of lake trout; (b) estimate spatiotemporal patterns of abundance; and (c) estimate spatiotemporal patterns of residency (Campbell, Watts, Dwyer, & Franklin, 2012; Zeller, 1998). We sought to examine behavior and infer important migratory corridors and areas of possible reproductive activity. The resultant information was intended to further support current and prospective population suppression efforts in Yellowstone Lake (Gresswell et al., 2016; Koel et al., 2015).

2 | METHODS

2.1 | Study site

Yellowstone Lake (44.4605, 110.3333 W) is located at an elevation of 2,357 m in east-central Yellowstone National Park, Wyoming (Figure 1a). The lake has at least 124 tributaries (Gresswell et al., 1994), 239 km of shoreline, and covers 341 km^2 in surface area (Kaplinski, 1991). Mean depth is 48.5 m, and maximum depth is 131 m. Substrate is a mix of boulders, rubble, sand, and clay (Benson, 1961). Approximately 4% (1,341 ha) of the lake is potentially suitable spawning habitat for lake trout (i.e., suitable fetch, slope, depth, and lack of sediment deposition, Bigelow, 2009). As of 2014, the presence of lake trout eggs or fry had been confirmed at Carrington Island in the West Thumb, East West Thumb to Southwest Breeze Channel, Snipe Point, Flat Mountain Arm, and Plover Point ($\sim$ 6 ha, Figure 1a) by snorkel, SCUBA, suction dredge, egg baskets, and fry traps (Gresswell et al., 2015).

Yellowstone cutthroat trout and longnose dace (*Rhinichthys cataractae*) are the only fish species endemic to Yellowstone Lake. Introduced fishes include lake trout,
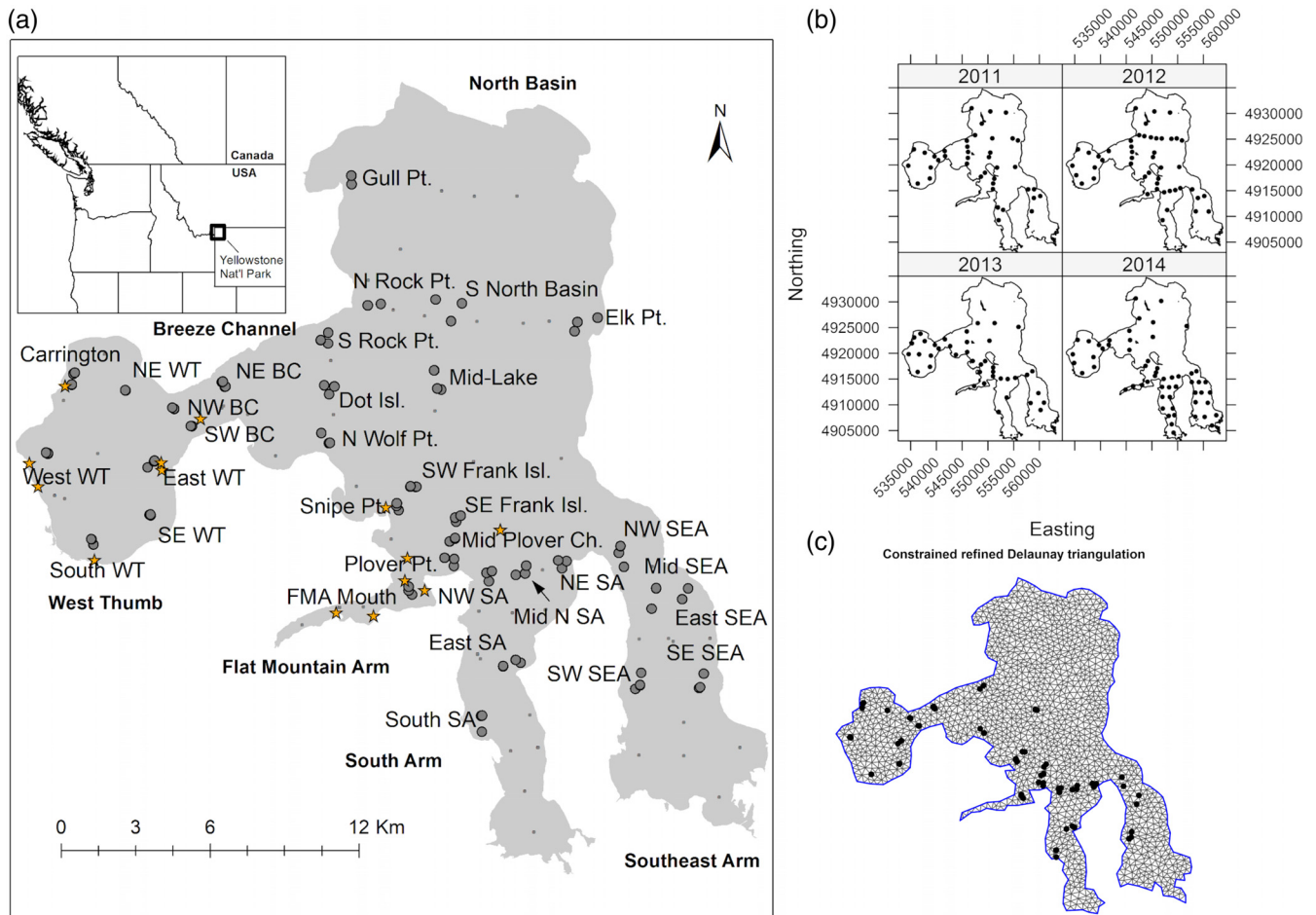

FIGURE 1 (a) Yellowstone Lake with acoustic telemetry receiver groups (black circles). Labels are abbreviated receiver group names and major sections of the lake (in bold). Groups were created for receivers placed within a 1 km area for at least three successive years from 2011 to 2014. Lake islands are excluded to improve legibility. Stars indicate the approximate location of confirmed spawning sites. The inset map shows the location of Yellowstone National Park, Wyoming. (b) Yearly acoustic telemetry array designs for the detection of tagged lake trout in Yellowstone Lake. (c) The mesh (vertices = 1,687) created constrained refined Delaunay triangulation. Black circles show the positions of telemetry receivers that operated for 3–4 years

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longnose sucker (*Catostomus catostomus*), redside shiner (*Richardsonius balteatus*), and lake chub (*Couesius plumbeus*) (Gresswell, 2004). Both Yellowstone cutthroat trout and lake trout occur in the littoral and limnetic zones when the lake is isothermal. As a thermocline develops during summer, lake trout habitat use shifts to mainly the hypolimnetic zone (Sandstrom, Gresswell, Farokhkish, & Parsley, 2014). The reproductive period of lake trout occurs during late summer and autumn when water temperatures are 12°C or lower (Casselman, 1995).

2.2 | Suppression netting

In rapid response to the detection of lake trout, the National Park Service (NPS) began a population suppression program with the goal of removing as many lake trout as possible (McIntyre, 1995; Syslo et al., 2011). Gillnetting has occurred on Yellowstone Lake since 1994 (Kaeding et al., 1995), with effort considerably intensifying in 2012 to target large reproductive fish (Koel et al., 2015). Crews used 25–76 mm bar-mesh nylon gillnets set on bottom at depths typically less than 30 m. Gillnets were a maximum of 3 km long and typically fished for 3 days. From 2012 to 2014, large-mesh gillnets (44–76 mm bar mesh) captured up to 51% of the lake trout biomass removed per year, and the highest catches occurred each year in the West Thumb and Breeze Channel (Appendix S1, Figure S1b, Koel et al., 2015). Areas near Flat Mountain Arm and South of Frank Island also yielded many mature lake trout. Large trap nets were used in 2012 and 2013 to further remove lake trout in near-shore areas where Yellowstone cutthroat trout commonly occur. Trap nets consisted of up to a 275 m guide line to a funnel shaped tunnel leading into a box that was up to 12 m long x 6 m wide x 9 m high woven with heavy mesh. Trap nets were checked 1–2 times per week. In addition to permitting the live-release of Yellowstone cutthroat trout bycatch (Koel et al., 2005), trap nets were also used to live-capture lake trout for research purposes (i.e., acoustic tagging).

2.3 | Fish capture and surgical procedures

Lake trout were captured by trap nets, short-set (2 hr) gill nets, and angling (Sandstrom et al., 2014). Anesthesia and surgery were performed on one animal at a time. Transmitters (V13-1 L or V13P-1 L, Vemco Inc., Halifax, Nova Scotia, Canada) were 36 mm long, 13 mm wide, and weighed 11 g in air (6 g in water), and each randomly transmitted a uniquely-coded identification (ID) every 60–180 s. Pings were decoded by a hydrophone (i.e., underwater microphone located in a plastic housing) and recorded in its onboard computer. Expected battery life for transmitters was ~1,100 days. Only those lake trout estimated to be >500 g were used in this study to achieve a tag burden of less than 2% in water (Table 1, Brown, Cooke, Anderson, & McKinley, 1999).

Fish were anesthetized with 100 mg/L MS-222 buffered with 200 mg/L NaHCO3 or 20 mg/L of AQUI-S 20E Aquatic Anesthetic (10% Eugenol). After reaching stage-four anesthesia (total loss of muscle tone and equilibrium; slow but regular opercular rate; loss of spinal reflexes), length (nearest mm, total length) was obtained from each fish. Weights were estimated from a length-weight power function (1):

$$W = a*L^b \qquad (1)$$

Where W is weight, a is the constant intercept (a = 3.1×10^{-6}), L is total length, and b is the constant slope (b = 3.19) converted from a $\log_{10}$-W vs $\log_{10}$-L regression. Coefficients were generated from a sample of lake trout (n = 931) captured by suppression netting in 2011 and 2012. During surgery, a water-recirculation pump and hose was used to constantly flush gills with anesthetic (Summerfelt & Smith, 1990). To verify that transmitters were functioning properly prior to implantation, signal transmission was confirmed with a VR-100 portable receiver (Vemco Inc., Halifax, Nova Scotia, Canada).

All surgical instruments and transmitters were disinfected in a Betadine (Povidone-Iodine) bath prior to, and following surgery. Latex surgical gloves were worn by the surgeon and changed frequently. Fish were retrieved from the holding pen and placed supine in a surgical trough where water and anesthetic was washed over the gills. A 15-mm incision was made parallel to and off the midline, anterior to the pelvic girdle, and into the peritoneal cavity using a sterile #10-scalpel blade. Sex was assessed by observing inside the

TABLE 1 Annual summaries of tagged Lake Trout total length (mm), estimated weight (g), and tag burden in water (%)

Year	*n*	Mean TL ± *SD* (mm)	Range TL (mm)	Mean weight ± *SD* (g)	Range weight (g)	Range tag burden (%)
2011	159	571 ± 58	458–878	2006 ± 783	954–7,605	0.08–0.63
2012	119	597 ± 56	469–737	2,295 ± 682	1,029–4,351	0.14–0.58
2013	35	542 ± 78	412–405	1,759 ± 971	680–5,364	0.11–0.88
2014	31	506 ± 60	405–646	1,380 ± 536	644–2,858	0.21–0.93

body for the presence of eggs or sperm; however, subsequent pilot studies suggested this method of sex determination to be unreliable for lake trout on Yellowstone Lake during early summer. A transmitter was placed inside the body cavity, and two sutures (Mono-Dox absorbable synthetic monofilament 3/0 NFS-1, CP Medical, Portland, Oregon), each consisting of two knots and four double throws, was used to close the incision (Summerfelt & Smith, 1990). During the post-surgery recovery phase, fish were retained in the holding pen for up to 30 min. Lake trout were released once ventilation rates were regular and body orientation was prone and at equilibrium. Acoustic transmitter implantation occurred in 2011 ($n = 159$), 2012 ($n = 119$), 2013 ($n = 35$), and 2014 ($n = 31$). High rates of transmitter code collisions, especially during winter when fish remained relatively immobile (Sandstrom et al., 2014), led to the decision to tag fewer lake trout following 2012. All fish were handled according to Montana State University Institutional Animal Care and Use Protocols (2011-48 and 2014-43) and by Carleton University under the protocol "Intracoelomic implantation of electronic tags in fish".

2.4 | Receiver deployment

Acoustic receivers (VEMCO VR2W receivers operating at 69 kHz) were fixed to polypropylene rope between an anchor point and buoy. In October of each year, buoys were submerged 3–4 m to avoid ice and were subsequently relocated and refloated after ice-out in June. From 2011 to 2014, receivers were consistently stationed in some locations, for example the West Thumb Geyser Basin, to gather data from known spawning locations or migration corridors (herein referred to as corridors). However, many receiver locations seasonally or annually changed to identify other potentially important areas to lake trout (Figure 1b).

Receiver locations were both independently examined across years and grouped based on locations where the receiver listening footprint (assumed to be up to ~3 km², Shroyer & Logsdon, 2009) was consistent across 3–4 years (Figure 1c). Because acoustic receivers were removed, downloaded, replaced, or moved within a single year, these inconsistencies in the receiver listening area and listening duration were controlled statistically when appropriate, and we assumed that receiver listening areas and receiver detection efficiencies were each similar among locations.

2.5 | Data processing

Raw biotelemetry data were filtered for incomplete tag-to-receiver transmission that can result from environmental noise and code collisions (Heupel, Semmens, & Hobday, 2006). Coded transmissions were considered valid if the

animal was detected at least twice within 30 min a receiver. Individual receiver clock-drift was corrected using the software program VUE (VEMCO Division, AMIRIX Systems). All data were checked for outliers using various plotting functions in R (R Core Team, 2018). Data from fish believed to have died in the lake during the study ($n = 14$) were removed after movements ceased, that is, were continuously recorded at a receiver or records stopped without tag return from the fishery.

Quality controlled data were compiled in the R package VTrack (Campbell et al., 2012). This package is useful for summarizing acoustic telemetry data, such as animal counts, residency duration (i.e., time at each receiver station, Zeller, 1998), and movements among receiver stations. Here, residency began when a tagged animal was recorded two or more times, and residency was terminated when 30 min passed without a detection at the same receiver, or the animal was detected on another receiver. Compiled data were used as the basis for analyses.

3 | DATA ANALYSIS

3.1 | Migratory trajectories

To identify lake trout migration routes, we initially determined locations with the greatest daily abundance of individuals during the spawning season (15 August–15 October) using plotting techniques in R (Appendix S2: Figures S1 and S2). Results from previous studies suggest that detections made across time during the reproductive period were expected to show an increase and decrease in abundance at any point along a corridor, including the final destination (Figure 2; Achord, Matthews, Johnson, & Marsh, 1996, Baril & Magnan, 2002, Boatright, Quinn, & Hilborn, 2004, Sinnatamby et al., 2018). Preliminary data exploration confirmed that previously identified lake trout spawning sites could be characterized by such patterns of increased (gradual to pronounced) and decreased abundance; thus, we used nonlinear relationships to estimate lake trout abundance through time. Lake trout abundance was modeled using generalized additive models (GAM) with date as the spline smoother. The spline was fitted in the R package mgcv, which uses cross-validation to automatically determine the optimal amount of smoothing (Wood, 2006; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The amount of smoothing is defined by the effective degrees of freedom (edf), where an edf of one is linear and higher values indicate a more nonlinear function (Zuur, Saveliev, & Ieno, 2014). Here, we considered models with an edf ≤ 1.5 to be an approximately linear pattern of estimated abundance, whereas those with edf > 1.5 were considered nonlinear. We specified models for individual receiver locations by year
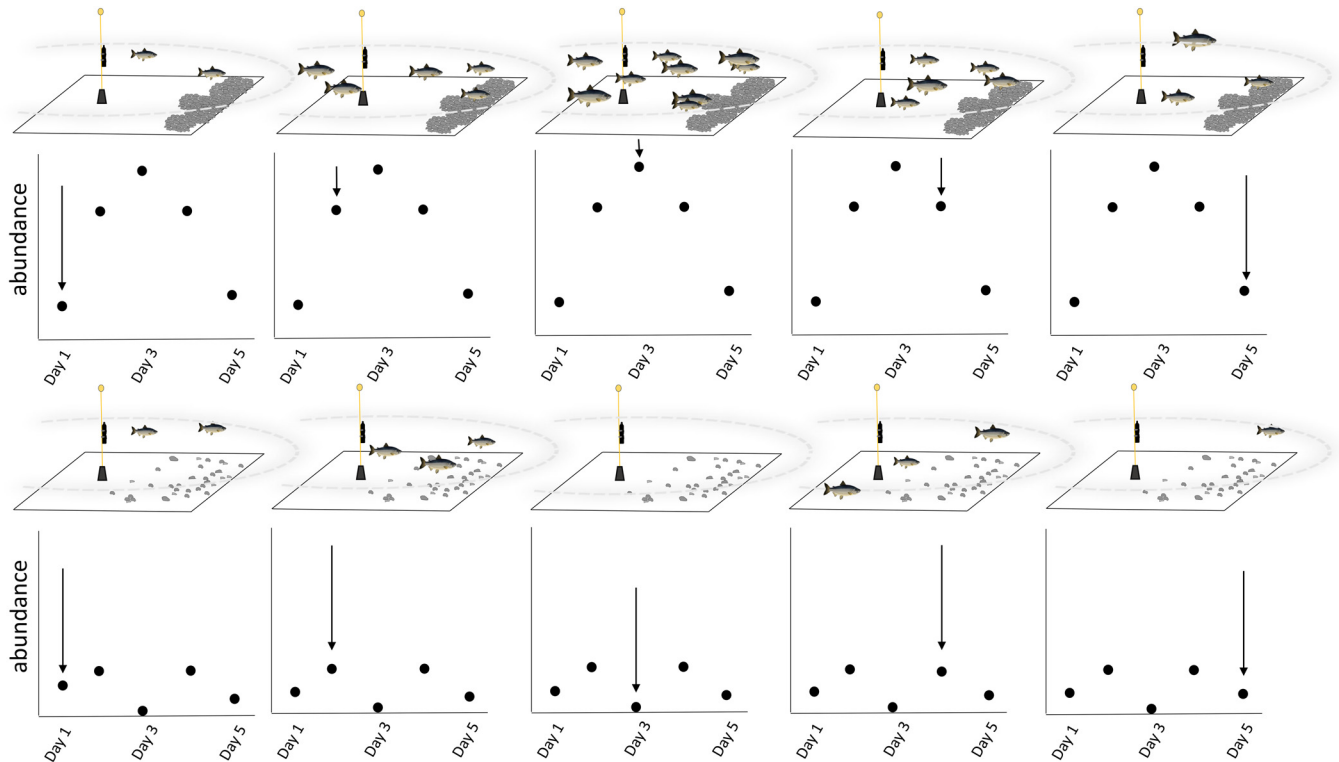
FIGURE 2 Conceptual illustration of migration as detected by an acoustic telemetry receiver. (a) Spawning sites or those along corridors are characterized by a nonlinear uni- or multimodal curve in daily abundance within the listening area of a telemetry receiver (shown with a gray halo). (b) Nonreproductive or relatively less important sites are characterized by linear patterns in abundance. Receiver listening areas are shown as a gray hashed line encircling an anchored receiver

($n = 158$). Linear patterns where daily abundance remained high over the entire listening period (e.g., 4–5 animals per day) was further examined qualitatively (Appendix S2).

Given a window of time that covered the known spawning season, nonlinear patterns estimated by GAM were used to identify migratory pulses of abundance, and therefore, could indicate corridors or spawning sites. Qualitative comparisons were considered valid because smoothers were generated based on the same unit of time (i.e., day). Results were examined in relation to the number of listening days, which was expected to influence the shape of smoothers. Receiver sites were categorized as overlapping (within the approximate receiver listening area; ~ 1 km diameter) a "confirmed" or "unconfirmed" spawning site during the sampling year. Maximum estimated abundance at unconfirmed spawning sites with nonlinear abundance patterns were plotted in GIS (ArcMap version 10.3.1, ESRI, Redlands CA) to identify locations possibly important for lake trout.

3.2 | Assumptions

We made a number of assumptions including that (1) day (24 hours) is a sufficient base temporal resolution to observe migration over the spawning season; (2) the increase and decrease in instrumented lake trout abundance is representative of migration; (3) counts are made over the full breadth of the reproductive period including pre-spawn and post-spawn periods; (4) tagged lake trout behavior is similar to that of untagged lake trout; (5) all transmitters were retained and functioned properly during the study period and; (6) the relative abundance of detected instrumented lake trout is proportional to the lake population. Preliminary analyses indicated that daily abundance (assumption 1) revealed the expected patterns (assumption 2) at confirmed spawning sites. Daily abundance is commonly used in telemetry studies showing migratory behavior (Baril & Magnan, 2002; Rakowitz, Berger, Kubecka, & Keckeis, 2008; Sinnatamby et al., 2018). Based on the known reproductive timing of lake trout in Yellowstone Lake (Gresswell et al., 2015), assumption 3 likely holds for receivers remaining in place from 15 August to 15 October. A violation of assumption 3 was addressed by including the number of listening days into models to account for sparse data collected by receivers removed prior to 15 October or installed after 15 August. Therefore, we could generate predicted values for a given number of receiver listening days. Assumption 4 is expected to hold true given that tag burden was below 2% (Table 1). Except for lake trout captured in fisheries, most instrumented fish should have retained their transmitters for

the duration of the study (Assumption 5). Guaranteed transmitter life (1,100 days) was sufficient to cover the 3-year study period. Finally, we observed a positive relationship between instrumented lake trout abundance and gillnet catches across lake sections (Assumption 6; Appendix S1).

3.3 | Spatiotemporal patterns of lake trout total abundance and residency

We used Integrated Nested Laplace approximation (INLA; R-INLA package http://www.r-inla.org) to model clustering and spatiotemporal dependency expected in total abundance (i.e., the number of unique fish detected at a receiver site during the listening period). This approach approximates Bayesian inference via a second-order Taylor expansion around the mode and computing the integral analytically (Rue et al., 2016). With the specification of non-informative priors, INLA will generate estimates comparable to frequentist methods and provide the means for users to specify the complex spatial and temporal dependencies similar to those available with Markov Chain Monte Carlo simulations (Zheng & Zhu, 2008). Specifically, nesting and modern numerical techniques allow INLA to generate approximate Bayesian inference for latent Gaussian models (Bivand, Gomes-Rubio, & Rue, 2015; Rue et al., 2016). Models contain a response and explanatory variables in addition to hyperparameters, for example, random effects.

To estimate spatiotemporal patterns of tagged lake trout abundance and residency, the total number of unique individuals per site and residency per site were modeled as a function of site (confirmed vs unconfirmed spawning activity) and estimated trajectory (linear vs. nonlinear) from the GAMs. Fish ID was included as a random intercept for the model of residency. Spatial and temporal random effects were specified based on receiver location and sampling year.

The model for total abundance was specified as [2]:

$$total\ abundance_{tj} \sim Poisson(\mu_{tj})$$

$$E(total\ abundance_{tj}) = \mu_{tj}\ and\ var(total\ abundance_{tj}) = \mu_{tj}$$

$$llog(\mu_{tj}) = \alpha + \beta_1 \times Site_{tj} + \beta_2 \times Trajectory_{tj} + \beta_3 \\ \times Site_{tj} \times Trajectory_{tj} + offset(LTK_t) + v_{tj} + \varepsilon_{tj} \tag{2}$$

$$v_{tj} = \phi \times v_{t-1,j} + u_{tj}$$

$$u_{tj} \sim GMRF(0, \Omega)$$

Where total abundance at the jth observation and tth year is poisson distributed with an expected value μ_{tj} and variance

μ_{tj}. μ_{tj} varies with a set of fixed covariates, and offset to account for the number of lake trout killed per year (LTK), a spatiotemporal correlation structure v_{tj}, and random noise ε_{tj}. The autoregressive expression v_{tj} varies according to the correlation ϕ. The normally distributed spatially-dependent random intercept u_{tj} has a mean of zero and covariance matrix Ω, that is estimated by a Matérn correlation function using the continuous domain stochastic partial differential equation (SPDE) approach (Lindgren, Rue, & Lindström, 2011).

The model for estimating spatiotemporal patterns of lake trout residency was specified as [3]:

$$Residency_{tji} \sim N(\mu_{tji}, \sigma^2)$$

$$E(Residency_{tji}) = \mu_{tji}\ and\ var(Residency_{tji}) = \sigma^2$$

$$\mu_{tji} = \alpha + \beta_1 \times Site_{tji} + \beta_2 \times Trajectory_{tji} + \beta_3 \times Site_{tji} \times Trajectory_{tji} + a_{ti} + v_{tji} + \varepsilon_{tji} \tag{3}$$

$$a_{ti} \sim N(0, \sigma^2_{FISH})$$

$$v_{tji} = \phi \times v_{t-1,ji} + u_{tji}$$

$$u_{tji} \sim GMRF(0, \Omega)$$

Where residency at the jth observation, tth year, and ith fish is normally distributed, with an expected value μ_{tj} and variance σ^2. All other terms in the expression are the same as model (1) with the exception that no offset is included, and there is a random intercept fish, a_{tj}, which is normally distributed with a mean of zero and variance σ^2_{FISH}.

To specify the spatial sampling grid, a mesh with 1,687 vertices was created from the 21–25 locations/year (Figure 1c). The mesh is a discrete index, divided into non-overlapping triangles (lines and vertices), on which to evaluate a continuous Gaussian Markovian random field (GRF; Bivand et al., 2015). A stochastic partial differential equation (SPDE) model (Lindgren et al., 2011), with year as a grouping factor, and non-informative priors was applied to the mesh to generate a GRF by year (see Appendix S3). The temporal random effect was specified with an autoregressive correlation structure such that high values of ϕ (e.g., $\phi = 0.9$) indicate the response changes little from 1 year to the next (Zuur, Ieno, & Saveliev, 2017).

4 | RESULTS

Processing the raw receiver data resulted in 119,323 residency events from 317 individual lake trout (LT) during the spawning seasons of 2011 ($n_{LT} = 150$), 2012 ($n_{LT} = 200$),

2013 (n_{LT} = 132), and 2014 (n_{LT} = 120). The mean total length was 566 mm ± 64 SD (range: 405–878 mm). Mean tag burden, based on estimated weight, was 0.42% (Table 1). The number of listening days per receiver was positively correlated with number of tagged fish (r = 0.52, df = 183, p < .001), and an exploratory comparison with gillnet catch confirmed that tagged fish betrayed the population (Appendix S1). A large number of transmitters were recovered from lake trout captured in gillnets (n = 138). The detected proportion of animals of a given tagging year declined sharply over time. The 2011 tagging year class dropped from 97% detected in 2011 to 28% detected by 2014 (r = −0.99, n = 4). Similar trends occurred for the 2012 and 2013 tagging year classes (Appendix S4: Figure S1).

4.1 | Migratory trajectories

Nonlinear patterns (migratory trajectories) in daily lake trout abundance were classified at 71% of confirmed spawning sites during the spawning season (median listening days = 51, 25/35 sites). Linear patterns (presumed to represent unimportant spawning sites or corridors) were observed at 10 confirmed spawning sites (median listening days = 19) and 68 unconfirmed spawning sites (median listening days = 36). Approximately unimodal distributions were observed at a number of sites (Figure 3, Appendix S2: Figures S3 and S4). Based on nonlinear trajectories, potential lake trout spawning sites occured from northwest Breeze Channel to sites on the eastern shores of the South and Southeast Arms (Figure 3).

4.2 | Spatiotemporal patterns of lake trout total abundance

Correlation between fitted values and observed data for the model on total abundance was 0.96. Spatial correlation diminished to less than 0.10 at 18 km, indicating correlation in lake trout total abundance across the receiver network (Table 2). The total number of individual lake trout expected at confirmed spawning sites where migratory patterns were observed was approximately 38 (95% CI: 28–50). Conversely, almost 50% fewer lake trout were expected at sites where spawning has not been confirmed and migratory patterns were absent. At these sites, there was a 95% probability that the number of lake trout would be between 18 and 25 (mean: 21, Table 2, Figure 4). Years were correlated (ϕ = 0.87), and patterns in the GRF suggested spatial dependency with a consistent change in abundance between consecutive years (Figure 5; Appendix S3). The strongest effect in the GRF extended from the northwestern part of West Thumb through Breeze Channel to areas near Plover Point (Figure 5). For example, in 2011 when the largest number of

tagged lake trout were freely swimming, the spatial random effect was related to an ∼3.3 times relative increase (exp [1.2]) in abundance along this corridor (Appendix S3).

4.3 | Spatiotemporal patterns of lake trout residency

The correlation between fitted values and observed data for the model on residency was 0.48. This correlation diminished below 0.10 at 2.7 km, indicating that residency was not strongly correlated among receivers (Table 2). None of the covariates explained lake trout residency (Table 2). Variation in the GRF for residency indicated a possible latent variable that appeared in several locations also highlighted by the GRF for lake trout abundance (Figure 6; Appendix S3). Specifically, the western part of Breeze Channel was characterized by relatively high residencies from 2011 to 2013 (Figure 6). Confirmed spawning sites such as the mouth of Flat Mountain Arm, sites in West Thumb, and Plover Point, and unconfirmed spawning sites such as those in South Arm and Southeast Arm were associated with relatively high residency values suggested by the GRF (Figure 6). Intraclass correlation of fish ID was 0.07 (Table 2). Annual correlation was relatively low (ϕ = 0.43), indicating less similarity in residency for a typical lake trout between successive years.

5 | DISCUSSION

We examined invasive migratory lake trout, under an active population suppression program, to identify corridors and unconfirmed locations of possible reproductive activity. Migratory trajectories, similar to those observed in other salmonids (chinook salmon *Oncorhynchus tshawytscha*, Achord et al., 1996, brook trout *Salvelinus fontinalis*, Baril & Magnan, 2002, bull trout, *Salvelinus confluentus*, Sinnatamby et al., 2018), appeared at receiver locations across Yellowstone Lake. Most known spawning sites and numerous unconfirmed sites were characterized by significant nonlinear patterns in abundance, which may indicate either a corridor or a destination for migrating fish. Although our approach does not provide detailed information such as alternative migration timing for different stocks (Boatright et al., 2004), we can conclude that these broad sites are among the most critical for invasive lake trout during the reproductive period in Yellowstone Lake.

Our approach identified unconfirmed spawning sites characterized by nonlinear patterns that peaked at more than 10 individuals·per day (e.g., Breeze Channel and areas of the West Thumb, Figure 3). Total abundance of unique animals was greatest for nonlinear trajectories in confirmed and unconfirmed spawning areas, and the GRF analysis yielded
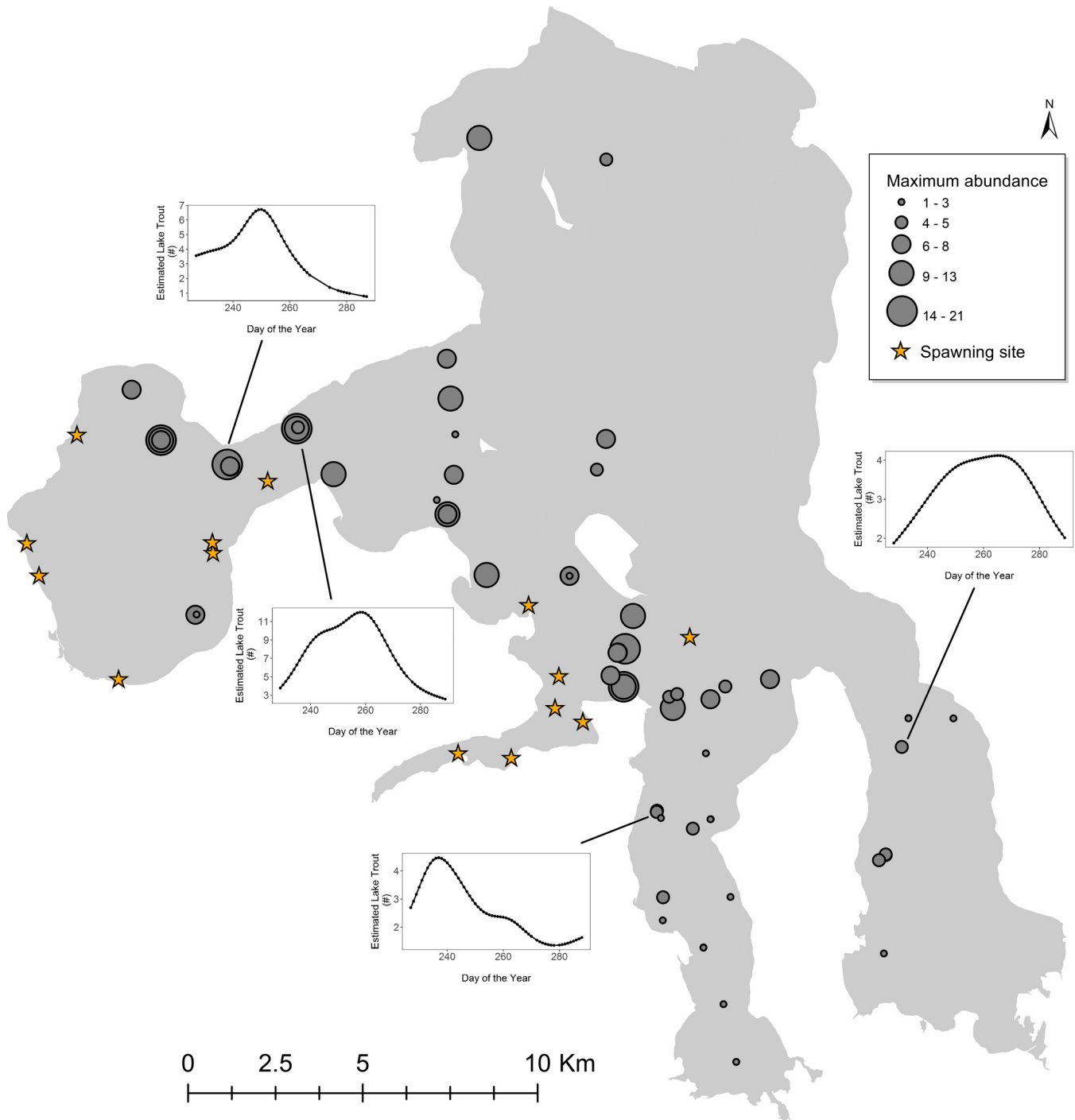
FIGURE 3 Nonlinear smoothers fit to daily abundance estimates where lake trout spawning has not been confirmed. Points are scaled by the maximum daily abundance estimated by modeling (using GAM). Stars indicate the approximate location of confirmed spawning sites. GAM, generalized additive models

spatial and temporal correlation along an extensive corridor (Figures 4 and 5). Specifically, patterns in the GRF suggested relatively high lake trout abundance from the Northwest half of West Thumb to Plover Point that declined in magnitude over time (Figure 5). This pattern is plausible given the annual decline in the number of fish tagged, and mortality related to suppression activities (Appendix S1:

Figure S1b). Previous studies of common carp (*Cyprinus carpio*) and sea lamprey (*Petromyzon marinus*) provide evidence that fish are highly vulnerable to exploitation when migrating or aggregating (Bajer et al., 2011; Holbrook, Jubar, Barber, Tallon, & Hondorp, 2016). Indeed, movement corridors are an important part of invasive fish management, for instance sea lamprey corridors helped narrow the search

TABLE 2 Posterior means and 95% Credible Intervals of parameter estimates for GLMMs. Estimates for the hyperparameters are: $\sigma_u = 0.59$; (Model 1); $\sigma_u = 0.65$; $\sigma_{Fish} = 0.51$ (Model 2)

Model response	Parameters	Mean	$Q_{0.025}$	$Q_{0.975}$
Total abundance	Intercept	**−1.98**	**−2.30**	**−1.66**
	SS.unconfirmed	−0.02	−0.37	0.34
	Nonlinear.yes	**0.57**	**0.34**	**0.80**
	LD	**0.12**	**0.06**	**0.17**
	SS.unconfirmed * nonlinear.yes	−0.23	−0.48	0.21
Residency	Intercept	**5.48**	**4.90**	**6.06**
	SS.unconfirmed	**−0.92**	**−1.47**	**−0.37**
	Nonlinear.yes	0.06	−0.48	0.59
	LD	0.01	0.00	0.02
	SS.unconfirmed * nonlinear.yes	0.10	−0.46	0.67

Note: SS is spawning site (i.e. confirmed vs. unconfirmed). LD is listening days. Bolded intervals do not overlap zero. Parameter estimates for GAMs are not shown.
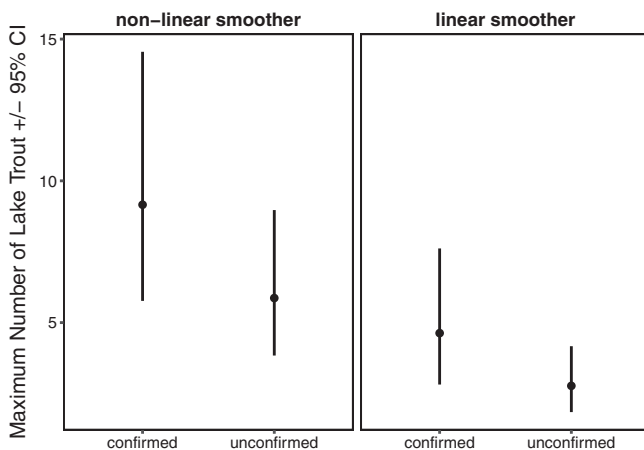

FIGURE 4 Posterior mean fitted values of lake trout total abundance (± 95% Credible Intervals) at confirmed and unconfirmed spawning sites where linear and nonlinear migratory trajectories were detected. Model estimates exclude the influence of the ar1 correlation for year

for spawning locations in the St. Clair-Detroit River System (e.g., Holbrook, Jubar, et al., 2016). Although telemetry receivers were widely spaced in Yellowstone Lake and only a large continuous corridor was highlighted by the GRF, agreement with gill-netting harvest data underscores the utility of this approach for evaluating fish behavior via discrete detection data (Whoriskey et al., 2019).

The amount of time spent near a receiver station was expected to indicate important habitats for reproduction; however, neither migratory trajectory nor spawning site

characterization explained residency. We believe that the inclusion of sex as a fixed effect would have offered a more parsimonious explanation for residence time, because compared with females, males are often observed early and for longer periods near spawning sites during the reproductive season (Binder et al., 2015; Marsden et al., 1995; Pinheiro, Stockwell, & Marsden, 2017). Unfortunately, sex determination of fish recaptured and killed in suppression gill nets showed that initial sex determination was unreliable, perhaps because gonads were undeveloped when transmitters were being implanted. Additional information about substrate composition would also be useful, but benthic habitat of Yellowstone Lake has not been assessed in detail. Furthermore, the receiver listening footprint ($\sim$785,000 m^2) covers a large area that overlaps habitats in pelagic and littoral zones, making it difficult to distinguish sites. One alternative strategy is to evaluate lake trout behavior using over-lapping receivers where fish positions can be triangulated (Niezgoda, Benfield, Sisak, & Anson, 2002). This approach has been successfully used to document spawning behavior of lake trout (Marsden et al., 2016; Riley et al., 2014) and for other species such as Atlantic cod (*Gadus morhua*, Dean, Hoffman, & Armstrong, 2012) and red snapper (*Lutjanus campechanus*, Williams-Grove & Szedlmayer, 2017). In Yellowstone Lake, a complementary fine-scale telemetry study is currently being evaluated to further inform resource managers by identifying previously undocumented patterns in lake trout behavior (Gresswell et al., 2015).

Fish ID and spatial correlation provided some insights into the patterns of lake trout residency. Random effects control for the unexplained variation of confounding factors (Bolker et al., 2009; Nakagawa & Schielzeth, 2010; Whoriskey et al., 2019) and offer ecological insights including measures of repeatability (Fieberg, Rieger, Zicus, & Schildcrout, 2009; Nakagawa & Schielzeth, 2010; Thorson & Minto, 2014). For example, the freshwater gadoid, burbot (*Lota lota*), exhibit repeatable behavior associated with migration and personality in the wild (Cott, Guzzo, Chapelsky, Milne, & Blanchfield, 2015; Harrison et al., 2014). The large variance and small intraclass correlation for Fish ID, used as a random intercept in the current study, suggested that residency of individual lake trout differed markedly across the receiver array. In other words, lake trout residency was largely dependent on the individual, whereas a population-level effect of the fixed factors was not detected. The spatially correlated random effect indicated several "hot spots" near confirmed spawning areas and several unconfirmed sites in the South and Southeast arms. We believe that latent processes (Zuur et al., 2017), possibly resulting from site-specific habitat characteristics (Binder et al., 2018; Marsden et al., 2016), further influence spatial

FIGURE 5 Posterior mean values of the Gaussian Markov spatial random field estimated for lake trout total abundance across years. The GRF is used to correct estimates for spatial dependence. From Equation (1): u_{tj} for mean estimates and diagonal elements of Ω for *SD*. The absence of receivers in the northeast resulted in the lack of estimates for this portion of the GRF. GRF, Gaussian Markovian random field
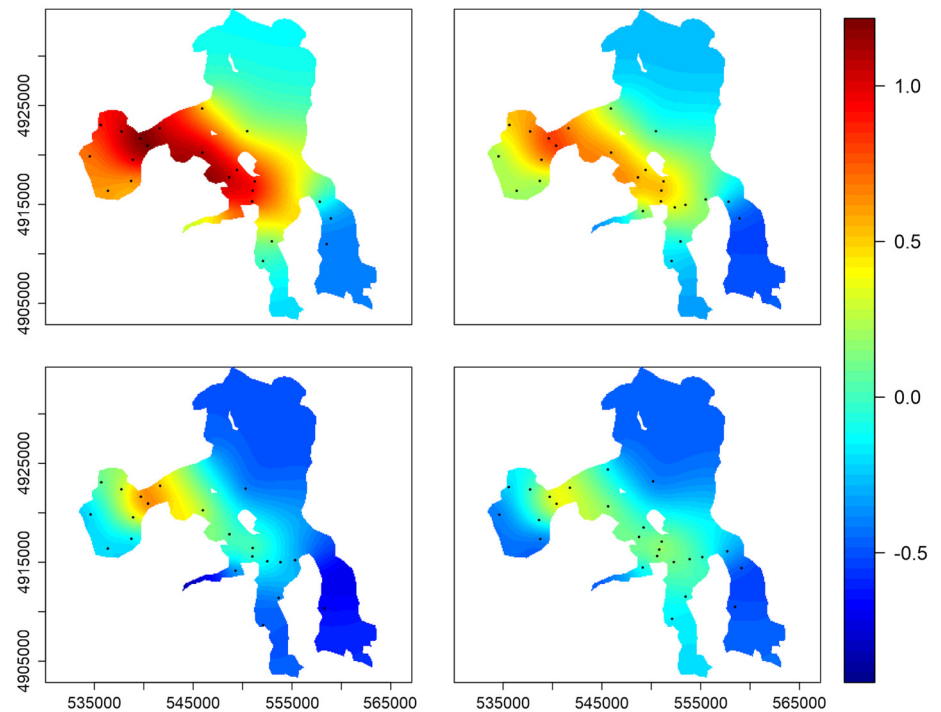

FIGURE 6 Posterior mean values of the Gaussian Markov spatial random fields estimated for lake trout residency across years. The GRF is used to correct estimates for spatial dependence. From Equation (2): u_{tji} for mean estimates and diagonal elements of Ω for standard deviations. The absence of receivers in the northeast resulted in the lack of estimates for this portion of the GRF. GRF, Gaussian Markovian random field
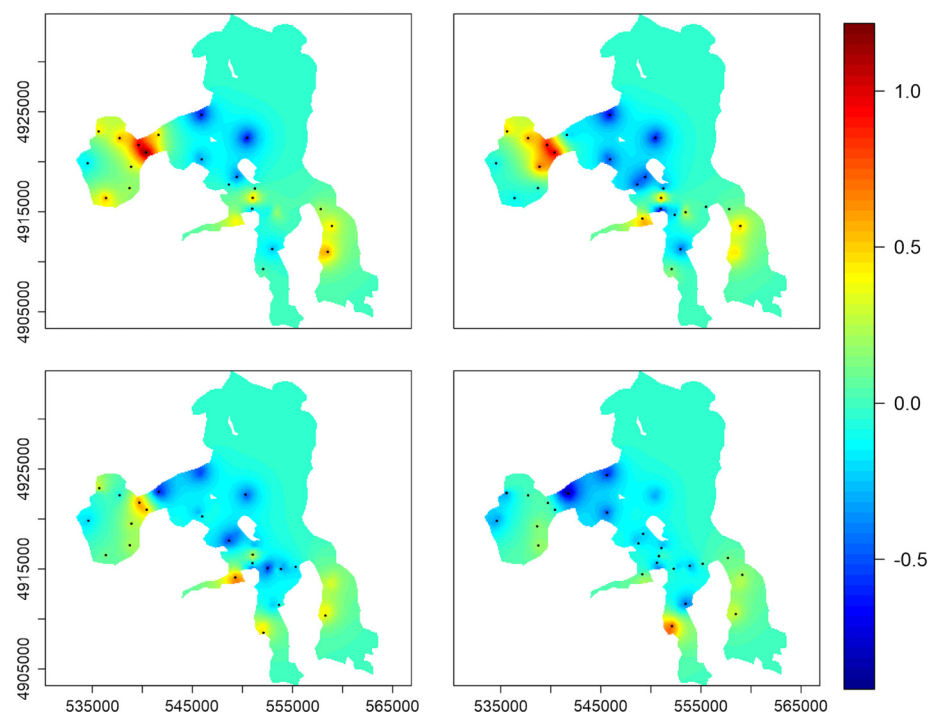
patterns in residency. However, further investigations are required to test this hypothesis.

Although multi-year, broad-scale telemetry programs have benefits in adaptively managed fisheries (Ogburn et al., 2017), these programs can present major logistical and analytical challenges because the configuration of telemetry arrays may need to be modified to meet shifting project objectives (Buckley, 2008) or support may become limited

(e.g., equipment, financial, in-kind, and technical, Crossin et al., 2017). Tagging hundreds of fish may not effectively show the expected behavioral patterns of the population, which, in our study, could partly explain why migratory trajectories were not apparent at several confirmed spawning sites. Importantly, only 30% of these sites had 60 or more receiver listening days, and listening periods at the remaining sites were abbreviated and unevenly implemented

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while showing relatively high numbers of fish. Where telemetry is used to identify reproductive migratory behavior, the extent of the observation period should always be maximized within the window of the reproductive season. In addition, some sites exhibited linear patterns in 1 year and nonlinear in another (e.g., Southwest Frank Island, Appendix S2, Figures S3 and S4), despite similar receiver listening days and similar estimated numbers of animals. In this case, abundance was relatively low, which indicates these are probably low priority sites. We recommend post hoc qualitative evaluations for this type of analysis and in situ investigations to further elucidate interannual variation in habitat selection. Currently, lake trout spawning habitat selection is under investigation in Yellowstone Lake.

Although rocky substrate with clean interstitial spaces is considered prime spawning habitat (Marsden et al., 1995), suction dredge, SCUBA, benthic tow sled sampling, and airborne LIDAR surveys have located embryos, fry, or large-bodied lake trout across a range of habitats in Yellowstone Lake (Roddewig et al., 2018; Simard, 2017). In the current study, instrumented fish revealed migratory trajectories in a number of unconfirmed spawning sites, and highlighted a broad corridor that gillnetters have long considered productive for lake trout. Alternative areas of migratory behavior, abundant lake trout or high residency, such as tributaries in the Southeast Arm, are important to the reproductive life history of cutthroat trout (Gresswell, Liss, Larson, & Bartlein, 1997). Lake trout migratory behavior and high residency could also be related to feeding opportunities, especially as weakened cutthroat trout post-spawners and naive young-of-the-year migrate into the lake. Whether used for reproductive or feeding purposes, the discovery of these novel lake trout habitats is helping to inform invasive species management and conservation in Yellowstone National Park.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHORS' CONTRIBUTIONS

L.F.G.G. authored the manuscript and performed the analyses. J.G.R., N.A.H., S.J.C., and R.E.G. provided input on study design, analyses and writing. P.E.B, M.J.P., P.T.S., C.D.S., A.J.D., S.J.C., and R.E.G. initiated the study, provided funding, performed field work, and contributed writing. All authors reviewed and approved the manuscript.

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ENDNOTE

Abbreviation: GAM, generalized additive models

DATA AVAILABILITY STATEMENT

The telemetry data used in this study are accessible at: https://doi.org/10.5066/P95LNXU7 (Gresswell, Heredia, & Sandstrom, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.