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REVIEW

Combination of Acoustic Telemetry and Side-Scan Sonar Advances Suppression Efforts for Invasive Lake Trout in a Submontane Lake

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Abstract
Expansion of an invasive Lake Trout *Salvelinus namaycush* population in Swan Lake, Montana, threatens a core area population of Bull Trout *S. confluentus*. Given the recent development of novel suppression methods, such as use of carcass analog pellets to cause high mortality of embryos, there was a need to quantify spawning season aggregation sites, site use, and spawning habitat for Lake Trout in Swan Lake. Acoustic tags were implanted in 85 Lake Trout during the summer in 2018 and 2019. Nightly tracking efforts during autumn in both years resulted in 1,744 relocations for 49 individual Lake Trout. Kernel density analysis was used to evaluate Lake Trout aggregation sites, identifying 10 distinct sites. All spawning sites were located in the littoral zone along areas of steep bathymetric relief, and these sites composed 48% of total relocations during both spawning seasons. In 2019, side-scan sonar imaging was used to classify and quantify the total area of spawning substrate, which constituted 12.8% of the total surface area estimated for spawning sites 1, 6, and 9 and 11.4% of the total surface area for aggregation sites 2–5, 7, 8, and 10. Simultaneous treatment of all spawning sites would require 205,709 $\pm$ 86 kg of carcass analog pellet material, resulting in 370.4 $\pm$ 0.2 kg of phosphorus inputs and 7,487.9 $\pm$ 3.1 kg of nitrogen inputs to Swan Lake. Thus, pellet treatment would increase the Carlson's trophic state index (TSI) values from 20.8 to 27.7

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for total phosphorus and from 22.1 to 26.2 for total nitrogen. Based on a TSI threshold of less than 40 for an oligotrophic lake, the use of carcass analog pellets could be feasible for supplementing the gill-netting suppression of Lake Trout in Swan Lake.

Introduction of invasive species into freshwater ecosystems is considered the second-greatest threat to biodiversity after habitat destruction, and fishes are among the most widely introduced taxa (Gozlan et al. 2010; Havel et al. 2015; Thomaz et al. 2015). Societal demands for fish as commodities and for expanded recreational opportunities are the principal drivers of fish introductions outside of their native ranges (Gozlan 2008; Gozlan et al. 2010). The Lake Trout *Salvelinus namaycush* is one species that has been widely introduced outside of its native range due to its ability to support valuable commercial and recreational fisheries (Healey 1978; Crossman 1995; Eshenroder et al. 1995; Mackenzie-Grieve and Post 2005). Unfortunately, the introduction and establishment of invasive Lake Trout populations have contributed to declines in abundance of native salmonid populations through competition, predation, or both (Donald and Alger 1993; Fredenberg 2002; Koel et al. 2005; Guy et al. 2011; Cox et al. 2013; Fredenberg et al. 2017). For example, invasive Lake Trout contributed to the collapse of the native Bull Trout *Salvelinus confluentus* population in Flathead Lake, Montana (Beauchamp et al. 2006; Hansen et al. 2016), and to declines in abundance of native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Yellowstone Lake, Wyoming (Koel et al. 2019, 2020a).

Once an invasive species has become established, the suppression of that species is typically the most common approach to conserve the native ecosystem (Veitch and Clout 2002; Simberloff et al. 2005). Selective removal methods, such as gill netting, are common techniques for large-scale fish suppression programs in lentic ecosystems (Britton et al. 2011; Franssen et al. 2014; Dux et al. 2019; Koel et al. 2020a). Gill netting of an invasive population can effectively suppress abundance when a level of effort leading to recruitment overfishing (i.e., level of fishing mortality that results in a sharp decrease in recruitment at equilibrium; Quinn and Deriso 1999) is achieved. For Lake Trout, recruitment overfishing can be achieved by overexploiting mature fish and maintaining the lowest density possible given monetary and logistical constraints (Healey 1978; Hansen et al. 1999; Cox 2010; Syslo et al. 2011, 2013; Hansen et al. 2019). However, gill-net bycatch can be a concern when a threatened or endangered species is susceptible to overharvest, which could result in negative population effects (Hall et al. 2000; Raby et al. 2011).

Invasive Lake Trout were first discovered in Swan Lake, Montana, in 1998 (Rosenthal et al. 2012); they likely entered the lake through illegal introduction(s) or colonization from Flathead Lake (Cox et al. 2013). Gill netting was initiated in Swan Lake in 2009 to suppress the invasive Lake Trout population and conserve native Bull Trout (Rosenthal et al. 2012). Gill-netting efforts removed 56,974 juvenile Lake Trout, 2,778 adult Lake Trout, and 1,461 Bull Trout from 2009 through 2016. However, gill-netting efforts were suspended in 2017 because the effort did not increase the total annual mortality rate to a level capable of achieving overexploitation for Lake Trout, funding resources were exhausted, and Bull Trout bycatch was a concern (Rosenthal and Fredenberg 2017). Fortunately, potential complementary alternatives to gill-netting suppression have been developed that avoid bycatch and improve suppression efficacy (Thomas et al. 2019; Koel et al. 2020b; Poole et al. 2020).

Use of complementary methods to traditional gill netting under an integrated pest management (IPM) framework can aid in maximizing the efficacy and cost-effectiveness of a suppression program (Sawyer 1980; Christie and Goddard 2003; Jones et al. 2009; Thresher et al. 2014; Lechelt and Bajer 2016). One technique that is complementary to gill netting is acoustic telemetry, which is capable of identifying aggregation sites that can then be targeted to increase suppression efficacy and reduce bycatch (Lechelt and Bajer 2016; Lennox et al. 2016; Crossin et al. 2017; Rust et al. 2018; Bouwens et al. 2019; Williams et al. 2020). Furthermore, acoustic telemetry can efficiently identify the location of Lake Trout spawning sites (Flavelle et al. 2002; Cox 2010; Dux et al. 2011; Fredenberg et al. 2017; Binder et al. 2018; Williams et al. 2022), allowing for the use of targeted gill-net sets and novel embryo suppression techniques.

Carcass analog pellets developed for use in Yellowstone Lake were found to be an effective method for causing high mortality of Lake Trout embryos (Thomas et al. 2019; Koel et al. 2020b; Poole et al. 2020). Hence, this method has promise for increasing Lake Trout embryo mortality in Swan Lake and may be a useful tool in the IPM approach to Lake Trout suppression. However, implementation of carcass analog pellet treatments for embryo suppression requires fine-scale information on the location and area of spawning substrate within spawning season aggregations that are identified by telemetry. Therefore, the sole use of telemetry to define spawning sites could misrepresent the area of spawning substrate requiring pellet treatment.

The combination of acoustic telemetry and side-scan sonar imaging could permit accurate estimation of spawning substrate (defined as cobble and rubble substrates from 65 to 999 mm, as suggested by Marsden et al. 1995) within the region of spawning season aggregations, which could be used to inform carcass analog suppression techniques. Given the importance of accurately estimating the spawning habitat area in Swan Lake for Lake Trout suppression, we addressed the following questions: (1) "Where are Lake Trout spawning?"; (2) "Which spawning sites have the highest use?"; (3) "What is the surface area of spawning habitat within spawning sites?"; (4) "Does the estimated spawning area differ between estimates from telemetry locations and side-scan sonar imagery of suitable spawning substrate?"; and (5) "How much phosphorus and nitrogen would be added to Swan Lake if carcass analog pellet treatments were implemented?"

METHODS

Study area.— Swan Lake is a 1,335-ha, glacially formed lake that is situated at an elevation of 940 m in the Flathead River drainage of northwestern Montana, USA. Swan Lake has an average depth of 16 m and a maximum depth of 43 m, with two deeper basins at the north and south ends connected by a shallow mid-lake section (Figure 1). The substrate in Swan Lake is characterized by sand and silt below the littoral zone, larger cobble and boulder substrates scattered on multiple reefs, glacial till in the upper and middle littoral zone, and large angular cobble and boulders in the upper and middle littoral zone where Montana Highway 83 approaches the shoreline (Cox 2010). The substrate of Swan Lake is similar to that of other glacially formed lakes in northwestern Montana, such as Lindbergh Lake, Lake McDonald, and Quartz Lake, where Lake Trout spawning and recruitment have been documented (Dux et al. 2011; Curtis and Koopal 2012; D'Angelo et al. 2013; Fredenberg et al. 2017).

Swan Lake is assumed to be oligotrophic based on its high dissolved oxygen concentrations and low nutrient inputs and concentrations (Koopal 2014). However, hypoxic conditions persist annually in the hypolimnion of the northern and southern basins, with the lowest concentration (i.e., <0.1% dissolved oxygen saturation) in the southern basin being attributed to nutrient inputs from historical logging and road construction in the watershed (Butler et al. 1995; Koopal 2014). Nutrient concentrations in Swan Lake are typical for an oligotrophic lake, with average concentrations of 3.4 μg/L for total phosphorus (TP), 105.8 μg/L for total nitrogen (TN), and 1.06 mg/m^3 for chlorophyll *a* (Koopal 2014). Hydraulic residence time for Swan Lake averages 70 d, contributing to the maintenance of the oligotrophic state that is essential for persistence of native species (Butler et al. 1995; Koopal 2014).

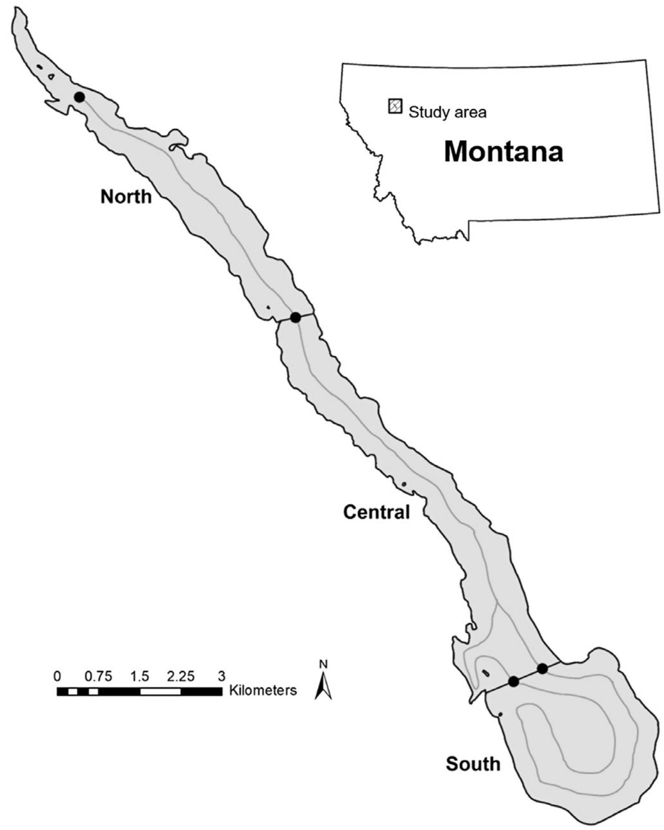

FIGURE 1. Map of Swan Lake, Montana. Black lines delineate the three Lake Trout tracking regions (North, Central, and South). The gray line delineates the tracking transect. Black circles represent the nightly starting locations.

Transmitter allocation.— Gill nets set for short duration (<2 h) were used to capture Lake Trout larger than 500 mm TL during July and August of 2018 and 2019. Capture of Lake Trout occurred when mature Bull Trout had out-migrated from Swan Lake to spawn in streams, thus minimizing Bull Trout bycatch. Lake Trout were anesthetized using AQUI-S 20 E (25 mg/L), and Lotek MAP series (MM-M-16-50; length = 80 mm; diameter = 16 mm; weight = 35 g) acoustic transmitters (Lotek Wireless, Newmarket, Ontario) were implanted using standard surgical procedures for the internal tagging of fish (Jepsen et al. 2002, 2008; Wagner et al. 2011). Sex and stage of maturity were determined by visual observation of the gonads through the surgical incision (Williams et al. 2022). Lake Trout selected for transmitter implantation had testes or ovaries that were easily identifiable as mature; immature Lake Trout were not tagged. Transmitters were implanted into 85 Lake Trout (mean TL = 669.7 mm; SE = 7.0): 71 males (mean TL = 655.9 mm; SE = 6.8) and 14 females (mean TL = 740.0 mm; SE = 14.1). Tagged Lake Trout were held in a 114-L oxygenated tank for a minimum of 15 min to recover, followed by release after the fish returned to normal respiration rates and were able to maintain equilibrium. Tagging efforts were focused on mature male Lake Trout because they are known to stay at spawning sites longer than females, thereby allowing for a more accurate and precise description of spawning sites (Martin and Olver 1980; Binder et al. 2021).

Tracking design and protocol.— A tracking map with delineated transects was constructed in ArcMap version 10.6.1 (hereafter, ArcMap; ESRI 2019), similar to methods used by Melnychuk and Christensen (2009) and Williams et al. (2022). Swan Lake was divided into three regions (North, Central, and South) to facilitate tracking efforts and provide equal representation of telemetered Lake Trout throughout the lake (Figure 1). Tracking efforts began from randomized starting locations for the Central and South regions on night 1, followed by the North and Central regions on night 2. Alternating tracking among lake regions and starting locations ensured an equal representation of tracking effort across lake regions. Tracking was conducted during the spawning period (Rosenthal and Fredenberg 2017) from September 28 to November 2, 2018, and from September 29 to November 2, 2019. In general, Lake Trout spawning activity occurs at night between dusk and midnight (Esteve et al. 2008; Binder et al. 2021); thus, tracking was conducted nightly, was initiated 1 h before sunset, and continued for 6 h.

Lake Trout locations were estimated using a Lotek MAP RT series acoustic receiver equipped with two Lotek LHP_1 directional hydrophones, Lotek MapHost software, and Universal Transverse Mercator coordinates. Protocols developed by Williams et al. (2022) for tracking and estimating the location of Lake Trout were used in Swan Lake. Additionally, the location accuracy and detection distance of acoustic transmitters were estimated via the methods described by Williams (2019). Location accuracy for transmitters during the study period was 13.5 m (SE = 5.1). Maximum detection distance during the study period was 946 m (SE = 99.8). Overall detection probability for the test tags was 1.0.

Aggregations and spawning sites.— Location data from 49 individual Lake Trout (mean TL = 687.1 mm; SE = 8.7) were used with ArcMap to delineate aggregation sites (Figure S1 available in the Supplement in the online version of this article). Location data did not include Lake Trout that were considered to be mortalities. Following the methods of Williams et al. (2022), Lake Trout were considered mortalities when mean movement distance during the study period was less than 500 m. Kernel density estimation (KDE) in ArcMap was used to determine Lake Trout aggregations, with the search radius set to the mean nearest neighbor distance for all Lake Trout relocations. Nearest neighbor distance was calculated in R (R Core Team 2018) as the mean Euclidian distance between all point locations of individual Lake Trout. Relative density estimates from 0 to 1 were calculated using KDE with a search radius of 90 m and Lake Trout point location data.

Polygons were constructed in ArcMap to determine aggregation sites using all bandwidth values with a relative density of at least 0.25, indicating an aggregation of four or more Lake Trout. Confirmation of spawning at aggregation sites was conducted after tracking by using an Aqua-Vu underwater camera and SCUBA divers to detect the presence or absence of Lake Trout embryos within in situ spawning substrate. Aggregation sites were designated as individual spawning sites (1–10), with sites numbered counterclockwise from south to north.

Site use and nearest neighbor distance.— Mean, minimum, and maximum lake depths were calculated for each individual spawning site. Number of Lake Trout present; mean number of individuals present; and mean, minimum, and maximum residence times were calculated for each defined spawning site. Minimum and maximum residence times at each spawning site were defined as the number of days between the first and last dates on which a Lake Trout was detected at the site. Mean residence time was defined as the mean number of days for which individual Lake Trout were detected at a spawning site. Mean residence time was calculated as the product of the mean number of individuals present and the mean time at a spawning site.

Mean, minimum, and maximum values of nearest neighbor distance for individual spawning sites were calculated using the Euclidian distance between point locations of individual Lake Trout contained within each spawning site. All descriptive statistics were calculated in R (R Core Team 2018).

Spawning habitat characteristics.— Polygons that were constructed in ArcMap using the KDE map for Lake Trout aggregations were used to facilitate placement of transects for sonar imaging of the substrate. Parallel transects were placed at 25-m intervals to achieve optimal sonar image resolution (Cummings 2015; Richter et al. 2016; Dow 2018). Side-scan sonar imaging was conducted via protocols developed by Richter et al. (2016) and Dow (2018). Side-scan images (Figure 2) were collected using a Lowrance HDS 9 side-scan transducer until total coverage was achieved for spawning sites. Images were used to evaluate for substrate type, quantity (km^2), and location.

Substrate maps (Figures 2, S2–S7) were created by compiling georeferenced side-scan sonar imagery and constructing polygons in ArcMap to assign substrate type following the methods described by Siemiantkowski (2021). A minimum mapping unit was used to define areas of uniform sonar signature as representative of a predominant substrate type and to provide an error estimate for

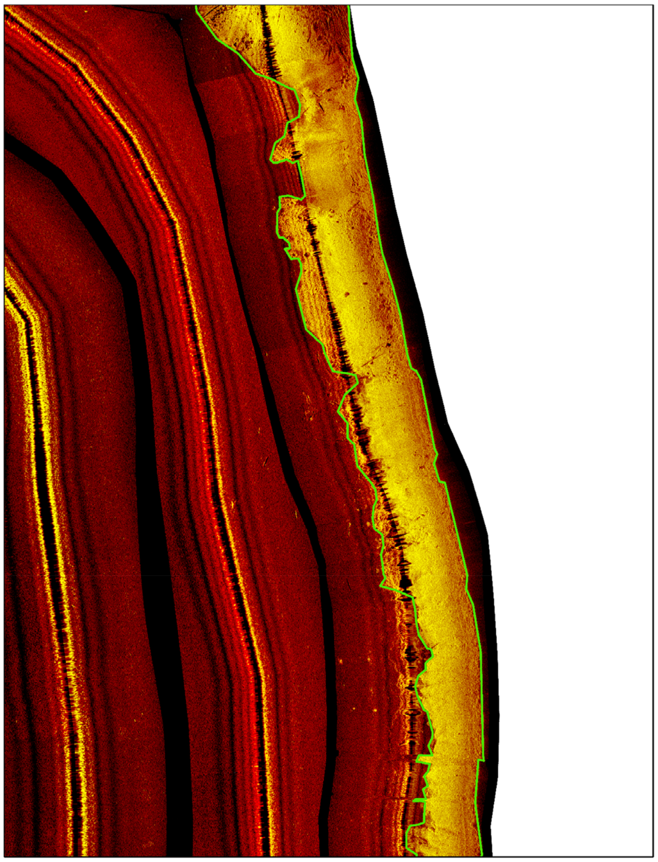

FIGURE 2. Side-scan sonar imagery used to delineate spawning substrate in an area informed by kernel density estimation of Lake Trout relocations during September–November of 2018 and 2019. The green line delineates the area considered to be spawning substrate.

substrate classification (Kaeser and Litts 2010). Thus, the spatial error estimate (±49 m^2) used for surface area estimates was calculated by squaring the sum of the minimum mapping unit (4 m) and the horizontal accuracy of the Lowrance side-scan sonar (3 m; Siemiantkowski 2021).

Substrate polygons provided estimates of the surface area (km^2) of spawning substrate. Spawning substrate was defined as cobble and rubble substrates from 65 to 999 mm, with organic, sand, gravel, and boulder substrates (either ≤64 or ≥1,000 mm in size) considered unsuitable for successful recruitment, as suggested by Marsden et al. (1995). Total area for each substrate type was calculated by summing the areas for each unique substrate polygon within spawning sites. Accuracy of substrate classifications from side-scan sonar imagery was estimated using reference sonar images of known substrate type (Kaeser and Litts 2013; Richter et al. 2016; Dow 2018; Siemiantkowski 2021) and an error matrix (Table S1 available in the Supplement in the online version of this article; Congalton and Green 1999; Richter et al. 2016; Dow 2018; Siemiantkowski 2021).

Embryo suppression with carcass analog pellets.— Total phosphorus and TN concentrations were measured to assess the potential effects of adding nutrients to Swan Lake in the event that carcass analog pellets were used to treat spawning sites. The TP and TN of carcass analog pellets were estimated by Energy Laboratories (Billings, Montana) using the total Kjeldahl method. Treatment of spawning substrate using carcass analog pellets at 1.75 kg/m^2 was found to induce over 75% mortality in Lake Trout embryos within Yellowstone Lake (Koel et al. 2020b). Therefore, estimates of the mass of pellets, production cost, and TP and TN added to Swan Lake were calculated using 1.75 kg/m^2 and the area of spawning sites.

The cost of producing carcass analog pellets (US$1.25 per kilogram of pellets; Koel et al. 2020b) was used to calculate cost estimates for pellet treatments in Swan Lake. Estimated cost for carcass analog pellet material was calculated as the product of production cost and the quantity of pellets required to treat suitable spawning substrate. Net increases in TP and TN concentrations were calculated based on reported values of 0.0018 kg TP/kg and 0.0364 kg TN/kg for the pellet material. Carlson's trophic state index (TSI) values were calculated for the additional TP and TN expected from pellet treatments by using equations from Carlson and Simpson (1996). Background values of TSI for TP and TN were obtained from Koopal (2014). Background TSI values and pellet treatment TSI values for TP and TN were summed to estimate the total TSI values for TP and TN in Swan Lake. To estimate the trophic state assignment, total TSI values were compared to the threshold TP and TN values reported by Carlson and Simpson (1996).

RESULTS

Lake Trout Spawning Sites and Spawning Habitat Description

Tracking during the spawning period resulted in 1,744 locations for Lake Trout. Lake Trout aggregated in 10 distinct locations (Figures 3, S1), and 64% of all individual relocations occurred within these locations. The highest relative density values were at spawning sites 1, 6, and 9, which had values of 0.50 or greater (Figures 3, S1). Visual observation of Lake Trout embryos using the Aqua-Vu camera confirmed spawning at sites 1, 6, and 9. Embryos were not observed at the remaining seven sites (i.e., 2–5, 7, 8, and 10); hence, these sites were considered aggregation sites (Figure 3). Spawning sites 1, 6, and 9 composed 48% of individual relocations among the 10 locations. Spawning site 6 was the most used; site 6 had 6.9 times more relocations than site 9 and 1.8 times more relocations than sites 1 and 9 combined (Table 1). Spawning sites 1, 6, and 9 constituted 70% of individual days

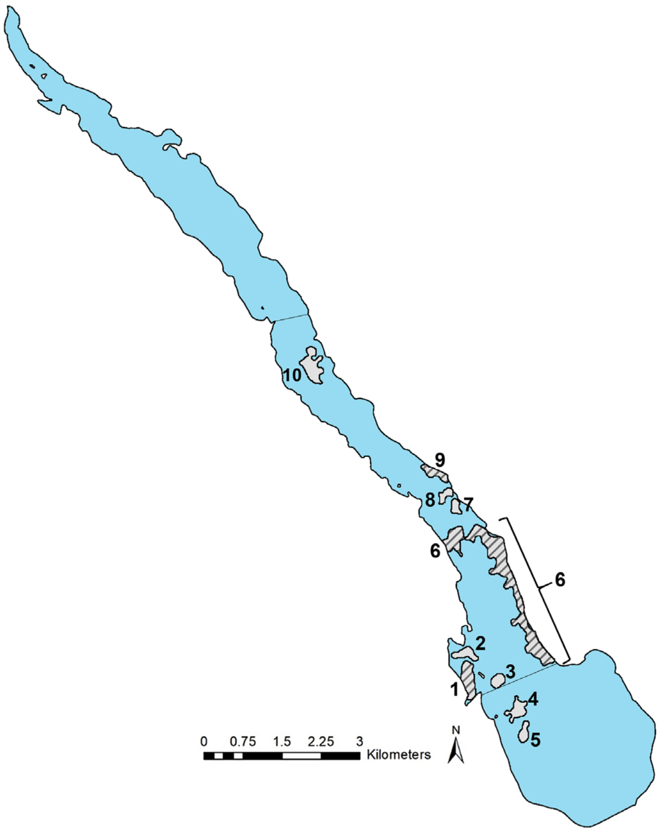

FIGURE 3. Map of three Lake Trout spawning sites (gray with crosshatch) and seven aggregation sites (solid gray) identified in Swan Lake, Montana, during September–November of 2018 and 2019. Unique sites are numbered (1–10).

spent within spawning sites. Site use was greatest for spawning sites 6 and 1, which composed 117 of 131 individual days and had an average length of stay of 8.5 d (Table 1). Site 6 also had the greatest number of individuals returning between spawning seasons ($N = 40$).

Surface area (m^2) and depth (m) varied for spawning sites described using Lake Trout relocations informed by KDE. Surface area estimates for Lake Trout relocations at spawning sites 1, 6, and 9 varied from $46{,}943 \pm 49$ to $487{,}171 \pm 49\ m^2$, with depth varying from 2 to 43 m (mean = 11.1 m; SE = 0.7; Table 2). Surface area estimates for Lake Trout relocations in aggregation sites 2–5, 7, 8, and 10 varied from $25{,}700 \pm 49$ to $105{,}599 \pm 49\ m^2$, with depth varying from 2 to 43 m (mean = 14.0 m; SE = 1.0; Table 2).

Surface area estimates for spawning sites were overestimated when using only Lake Trout relocations: the total surface area of spawning sites 1, 6, and 9 was $621{,}919 \pm 49\ m^2$ when not considering spawning substrate and $79{,}534 \pm 49\ m^2$ when Lake Trout relocations informed by KDE were coupled with side-scan sonar images of the substrate type (Tables 2, 3). Similarly, of the surface area ($333{,}492 \pm 49\ m^2$) represented by all Lake Trout relocations at aggregation sites 2–5, 7, 8, and 10, only $38{,}014 \pm 49\ m^2$ encompassed spawning substrate (Tables 2, 3). Thus, potential spawning area was reduced by 87% for spawning sites 1, 6, and 9 and by 89% for aggregation sites 2–5, 7, 8, and 10 relative to the surface area estimates informed only by Lake Trout relocations.

Spawning substrate composed 12.8% of the total surface area for spawning sites 1, 6, and 9 (Table 3; Figures 4,

TABLE 1. Total number of individual Lake Trout, number of relocations, mean individuals per tracking survey, mean nearest neighbor distance, length of stay, and individual days for each Lake Trout spawning site and aggregation site in Swan Lake, Montana, during September–November of 2018 and 2019. Sites are listed in descending order based on surface area, largest to smallest. Lake Trout locations were pooled among years. "Individuals" were calculated as the sum of unique individual Lake Trout detected during each year. "Individual days" were calculated as the product of mean individuals per survey and mean length of stay.

	Individuals				Length of stay (d)			
Site	Total	Relocations	Per survey	Mean (SE) nearest neighbor distance (m)	Mean	Minimum	Maximum	Individual days
				Spawning sites				
6	54	543	10.2	13.9 (0.5)	7	1	17	71
1	33	219	4.6	7.2 (0.4)	10	2	28	46
9	17	79	3.5	8.9 (1.2)	4	1	8	14
				Aggregation sites				
10	20	108	2.2	14.2 (0.9)	6	1	22	13
3	4	49	2.0	7.3 (1.3)	17	15	18	34
4	17	34	2.3	20.7 (3.1)	1	1	1	2
2	12	29	2.0	23.3 (2.6)	4	1	9	8
5	12	23	2.0	19.8 (2.2)	0	0	0	0
8	9	15	2.1	28.3 (2.9)	0	0	0	0
7	10	14	2.1	18.0 (3.3)	0	0	0	0

TABLE 2. Size (m^2) and depth (m) of Lake Trout spawning sites and aggregation sites in Swan Lake, Montana, during September–November of 2018 and 2019. Sites are listed in descending order based on surface area, largest to smallest. The area of Lake Trout relocations was estimated by summing the total area of Lake Trout locations from kernel density estimates. The spatial error estimate (±49 m^2) was calculated by squaring the sum of the minimum mapping unit (4 m) and the horizontal accuracy of the Lowrance side-scan sonar (3 m); the error estimate is the same for all area calculations.

Site	Area of Lake Trout relocations (m^2)	Depth (m)		
		Mean	Minimum	Maximum
Spawning sites				
6	487,171	9	7	43
1	87,805	10	2	21
9	46,943	14	9	37
Aggregation sites				
10	105,599	12	4	22
4	59,198	19	9	37
2	45,908	10	2	21
3	34,300	20	7	43
5	34,100	14	8	32
8	28,687	13	8	19
7	25,700	9	9	12

S2–S4). For example, of the surface area (487,171 ± 49 m^2) informed by Lake Trout relocations for spawning site 6, only 63,301 ± 49 m^2 comprised spawning substrate for Lake Trout (Tables 2, 3). Relative to aggregation size, spawning site 9 had the greatest proportion of spawning substrate by surface area (29.4%), followed by spawning site 6 (13%), and the lowest proportion occurred at spawning site 1 (2.8%; Table 3). Spawning site 6 had the greatest quantity of spawning substrate, comprising 80% of the spawning substrate found among spawning sites 1, 6, and 9, with 3.9 times more spawning substrate than spawning sites 1 and 9 combined (Table 3). Spawning sites 1, 6, and 9 also contained the greatest total quantity of spawning substrate, with 2.1 times more than aggregation sites 2–5, 7, 8, and 10 (Table 3). Furthermore, aggregation sites 2–5 had no spawning substrate present within the area informed by Lake Trout relocations (Table 3).

Embryo Suppression with Carcass Analog Pellets

The quantity of carcass analog pellet material required to treat spawning substrate contained within all 10 sites (spawning and aggregation sites) was estimated as 205,709 ± 86 kg ($164,567 ± 68; Table 3). Treatment of spawning sites 1, 6, and 9 with carcass analog pellets would require 139,185 ± 86 kg ($111,348 ± 68) of pellet material (Table 3). Spawning site 6 had the most spawning substrate among the spawning sites and constituted 80% of the total pellet material required to treat spawning sites (Table 3; Figure 4). Spawning site 9 had the second-highest amount of spawning substrate and comprised 17% of the total pellet material required for treatment (Table 3). Treatment of spawning substrate within aggregation sites 7, 8, and 10 was estimated to require 66,524 ± 86 kg ($53,219 ± 68) of pellet material, with site 10 having the most spawning substrate and composing 81% of the total

TABLE 3. Estimates of total surface area for spawning substrate and nonspawning substrate, total amount of carcass analog pellet material required to reach an effective level of coverage (1.75 kg/m^2), cost of pellet material, and total amount of phosphorus and nitrogen nutrient inputs from pellet treatment(s) for each spawning or aggregation site and for all 10 locations (Total) in Swan Lake, Montana. Sites are listed in descending order based on surface area, largest to smallest. The spatial error estimate (±49 m^2) for total surface area was calculated by squaring the sum of the minimum mapping unit (4 m) and the horizontal accuracy of the side-scan sonar (3 m). Uncertainty in pellet quantity, pellet cost, total phosphorus, and total nitrogen estimates was calculated using the upper and lower bounds of surface area estimates. No spawning substrate was present at aggregation sites 2–5.

Site	Spawning substrate area (m^2)	Nonspawning substrate area (m^2)	Quantity of pellets (kg)	Estimated cost (US$)	Total phosphorus (kg)	Total nitrogen (kg)
Spawning sites						
6	63,301 ± 49	423,870 ± 49	110,777 ± 86	88,622 ± 68	199.4 ± 0.2	4,032.3 ± 3.1
1	2,430 ± 49	85,375 ± 49	4,253 ± 86	3,402 ± 68	7.7 ± 0.2	154.8 ± 3.1
9	13,803 ± 49	33,140 ± 49	24,155 ± 86	19,324 ± 68	43.5 ± 0.2	879.3 ± 3.1
Aggregation sites						
10	30,691 ± 49	74,908 ± 49	53,709 ± 86	42,967 ± 68	96.7 ± 0.2	1,955.0 ± 3.1
8	5,303 ± 49	23,384 ± 49	9,280 ± 86	7,424 ± 68	16.7 ± 0.2	337.8 ± 3.1
7	2,020 ± 49	23,680 ± 49	3,535 ± 86	2,828 ± 68	6.4 ± 0.2	128.7 ± 3.1
4		59,198 ± 49				
2		45,908 ± 49				
3		34,300 ± 49				
5		34,100 ± 49				
Total	117,548 ± 49	837,863 ± 49	205,709 ± 86	164,567 ± 68	370.4 ± 0.2	7,487.9 ± 3.1

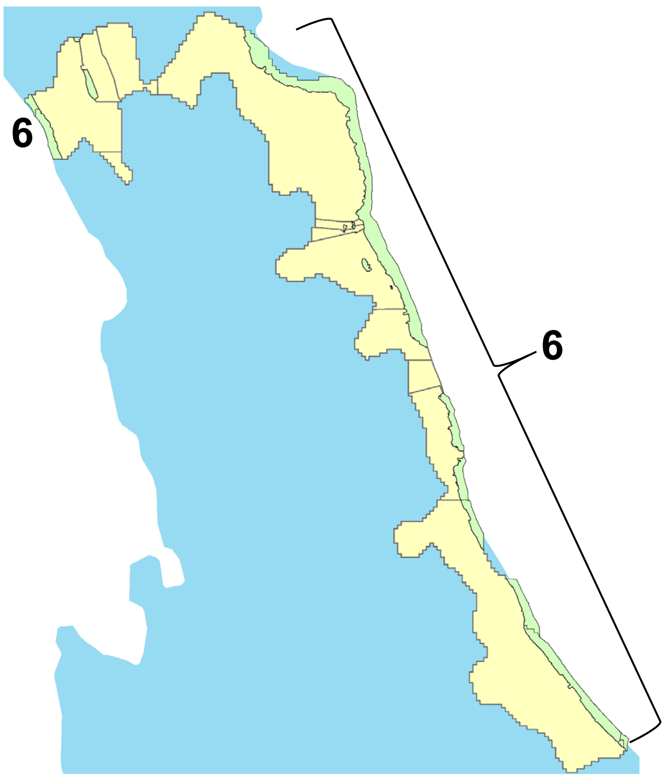

FIGURE 4. Substrate classification map for site 6 (spawning site; see Figure 3) in the Central region of Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Green polygons delineate areas of unique sonar signature corresponding to cobble and rubble substrate categories.

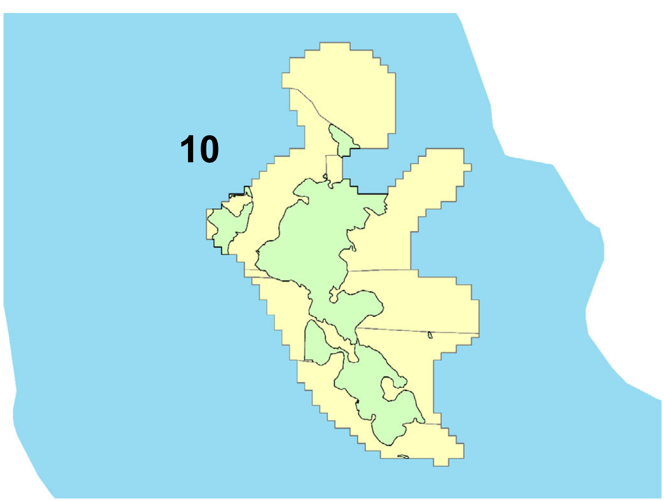

FIGURE 5. Substrate classification map for site 10 (aggregation site; see Figure 3) in the Central region of Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Green polygons delineate areas of unique sonar signature corresponding to cobble and rubble substrate categories.

pellet material required to treat aggregation sites 7, 8, and 10 (Table 3; Figure 5).

Nutrient inputs (TP and TN) from carcass analog pellet treatments of all sites (spawning and aggregation sites) were estimated as 370.4 ± 0.2 kg TP and 7,487.9 ± 3.1 kg TN. Treatment of spawning sites 1, 6, and 9 would result in the addition of 250.6 ± 0.2 kg TP and 5,066.4 ± 3.1 kg TN to Swan Lake (Table 3). The treatment of spawning site 6 would require the greatest quantity of carcass analog pellet material and would comprise 80% of the nutrient inputs from treatment of spawning sites (Table 3). Treatment of spawning substrate at aggregation sites 7, 8, and 10 would contribute 119.8 ± 0.2 kg TP and 2,421.5 ± 3.1 kg TN (Table 3). Among the aggregation sites, site 10 would require the greatest quantity of pellet material, which would comprise 81% of nutrient inputs—4.2 times more than the inputs for aggregation sites 7 and 8 combined (Table 3).

Carlson's TSI background values for TP in Swan Lake were 15.7 for the northern basin and 25.8 for the southern basin. Values of TSI for TN in Swan Lake were 21.9 for the northern basin and 22.2 for the southern basin. The basinwide average TSI for Swan Lake was 20.8 (SD = 5.1) for TP and 22.1 (SD = 0.1) for TN. Simultaneous treatment of all sites that were found to contain spawning substrate (sites 1, 6–9, and 10) would result in an estimated increase of basinwide TSI to 27.7 for TP and 26.2 for TN. Pellet treatment of the largest and most used spawning site (site 6) would result in an estimated increase of basinwide TSI to 25.2 for TP and 24.5 for TN. Thus, treatment of spawning site 6 alone would account for 59% of the increase in TSI for TP and 64% of the increase in TSI for TN from pellet treatments.

DISCUSSION

Lake Trout aggregated at 10 locations in Swan Lake during the spawning season, and spawning was confirmed at three of those locations. Two of the confirmed spawning sites, one near the east shore in the Central region (site 6) and another near the inlet of the Swan River (site 1), had the majority of use by Lake Trout. Furthermore, spawning site 6 and the northernmost aggregation site (site 10) contained the majority of spawning substrate found within aggregation sites. All spawning sites (1, 6, and 9) and three additional aggregation sites (7, 8, and 10) contained spawning substrate, but the area of spawning substrate was considerably less than the area estimated for Lake Trout aggregations based on the defined relative density threshold of 0.25. However, the value selected for the relative density threshold can increase or decrease the estimated area for aggregations. For example, increasing the threshold value to 0.50 would result in smaller aggregation areas aligning more closely with some of the in situ spawning habitat but would miss other areas entirely. Thus, we believe that our use of 0.25 as the defined threshold value accurately represents a conservative estimate of the total area used by Lake Trout, capturing the most effective locations for targeted gill-net sets and the application of carcass analog pellets. Spawning substrate within Lake Trout aggregations was estimated, and embryo suppression using carcass analog pellets would result in increased TP and TN, but the increase would not result in a transition from an oligotrophic state to a mesotrophic state. Thus, carcass analog pellet treatments could be a viable addition to an IPM approach for suppressing Lake Trout in Swan Lake.

Kernel density estimation informed by Lake Trout relocations was successfully used to describe the spatial extent of spawning season aggregations. Spawning season aggregation patterns for Lake Trout in Swan Lake were similar to those of native Lake Trout populations in the Laurentian Great Lakes (Binder et al. 2016, 2018; Farha et al. 2020; Marsden et al. 2021) and Lake Champlain (Pinheiro et al. 2017) and to those of invasive Lake Trout populations in Lake McDonald, Quartz Lake, and Yellowstone Lake (Dux et al. 2011; Fredenberg et al. 2017; Marsden et al. 2021; Williams et al. 2022). Lake Trout in our study also aggregated at all spawning sites that were previously identified by Cox (2010) as hosting spawning activity, confirmed in spawning substrate located along Swan Lake's eastern shore, thus re-affirming the locations as preferred spawning sites.

Spawning site use by Lake Trout in Swan Lake was similar to that of other native and invasive Lake Trout populations. For example, the duration of spawning site use in Swan Lake varied from 1 to 28 d and was similar to durations reported for native Lake Trout populations in Alexie Lake, Northwest Territories, Canada (4–25 d; Callaghan 2016), and Lake Champlain (19–35 d; Pinheiro et al. 2017) and for an invasive population in Yellowstone Lake (8–19 d; Williams et al. 2022). Interestingly, spawning site use in our study was similar to patterns observed during the day by Callaghan (2016), Pinheiro et al. (2017), and Williams et al. (2022). However, tracking at night during the present study likely resulted in increased resolution of preferred spawning sites within spawning season aggregations. Lake Trout in Swan Lake also used multiple spawning sites per year, similar to spawning behavior observed in Alexie Lake (Callaghan et al. 2016); Lake Champlain (Pinheiro et al. 2017); Thunder Bay, Lake Huron (Marsden et al. 2016); and Yellowstone Lake (Williams et al. 2022). The use of multiple spawning sites annually by Lake Trout is attributed to a “bet-hedging” strategy in which eggs are broadcast within and among spawning sites to promote reproductive success (Fitzsimons and Marsden 2014; Callaghan et al. 2016; Marsden et al. 2016; Pinheiro et al. 2017). Additionally, the probability that an individual Lake Trout will use multiple spawning sites per year increases as the size of the lake decreases and as the distance between spawning sites decreases (Binder et al. 2021). Thus, due to the relatively small size of Swan Lake and the close proximity of spawning sites, Lake Trout are likely using this bet-hedging strategy to maximize reproductive success.

An understanding of the spatial distributions and movement patterns of Lake Trout can help to increase the efficacy of suppression efforts (Dux et al. 2011; Koel et al. 2020a; Williams et al. 2022). For example, the use of gill nets to target Lake Trout aggregations that were identified via acoustic telemetry was found to increase catch rates and improve suppression efficacy in Yellowstone Lake (Williams et al. 2020). Suppression efficacy can be increased by targeting multiple life stages of a focal species (Ehler 2006; Velez-Espino et al. 2008; Weber et al. 2011; Simberloff 2014; Yick et al. 2021). Thus, the combination of complementary mechanical (i.e., gill netting) and chemical (i.e., carcass analog pellet) suppression techniques in an IPM framework can effectively target Lake Trout life stages from embryo to adult, thus improving suppression efficacy. Furthermore, the complementary use of traditional gill netting and carcass analog pellet treatments could decrease the time required to reach suppression goals. Once those goals are achieved, Lake Trout can be maintained at a low target abundance with less effort and cost (Hansen et al. 2019). However, a detailed description of the total area and location of spawning substrate within spawning season aggregations is critical when considering the use of carcass analog pellets for embryo suppression.

Commonly available side-scan sonar was successfully used to locate and classify substrate associated with each defined substrate class and was identified from side-scan sonar imagery, as in similar studies (Kaeser and Litts 2010, 2013; Richter et al. 2016; Glassic and Gaeta 2019). Furthermore, spawning substrate was accurately classified and estimated, revealing the area of spawning habitat, similar to other studies on Rainbow Trout *O. mykiss* (Cummings 2015), Walleye *Sander vitreus* (Richter et al. 2016), Lake Trout (Redman et al. 2017), and Bonneville Cutthroat Trout *O. clarkii utah* (Glassic and Gaeta 2019). The area of spawning habitat within spawning season aggregations would have been greatly overestimated by the sole use of Lake Trout relocations. Therefore, the location and area estimates calculated for spawning substrate by using side-scan sonar allowed us to evaluate the feasibility of embryo suppression and to calculate estimates for the cost and quantity of carcass analog pellet material required for treatment. However, due to the positive relationship between cost (US$), treatment area ($m^2$), and nutrient inputs, the quantity of carcass analog pellets used for embryo suppression could be a concern.

Fortunately, the quantity and cost of carcass analog pellets required for treatment of spawning sites in Swan Lake can be reduced by prioritizing sites based on observation of embryos, the total surface area of spawning substrate, and use by spawning Lake Trout.

Prioritization of spawning sites for treatment can also address other primary concerns related to the use of carcass analog pellets, such as the potential for eutrophication from nutrient loading of phosphorus and nitrogen and the negative effects on in situ benthic communities. Phosphorus and nitrogen are the primary limiting nutrients for algal growth in freshwater lakes (Sondergaard et al. 2017; Fink et al. 2018). Thus, nutrient loading could result in eutrophication of an oligotrophic freshwater lake, such as Swan Lake. Fortunately, artificial nutrient additions of phosphorus and nitrogen have been safely used in fisheries management to enhance productivity of oligotrophic ecosystems without causing eutrophication or a shift in trophic state (Budy et al. 1998; Wilson et al. 2018; Benjamin et al. 2020). Furthermore, the addition of carcass analog pellets to Lake Trout spawning sites in Yellowstone Lake was found to suppress algal biomass by limiting the ability of primary producers to use available phosphorus and nitrogen (Lujan et al. 2022).

Changes in chemical composition (i.e., dissolved oxygen concentration) and phytoplankton, macroinvertebrate, and higher-trophic-level species abundance and community structure due to nutrient additions could also have negative effects at the ecosystem level (Beeton 1964; Capblanq 1990; Smith et al. 2006). For example, embryo suppression treatments in Yellowstone Lake induced localized changes in macroinvertebrates except amphipods; however, due to the small treatment area, embryo suppression treatments would have little effect lakewide (Briggs et al. 2020). Monitoring the relative abundances of vertebrate and invertebrate species may be necessary because of the physical differences between Swan and Yellowstone lakes (i.e., total lake area [m^2], basinwide volume of water, and hydraulic residence time). Additionally, chemical differences (e.g., phosphorus and nitrogen concentrations) between Swan and Yellowstone lakes necessitate monitoring of water quality parameters (e.g., phosphorus, nitrogen, and ammonium) to assess potential effects of pellet treatments within Swan Lake and downstream to Flathead Lake. Therefore, the accurate measurement of in situ spawning substrate will reduce the negative effects of TP and TN additions and the probability of shifting the lake's trophic state, which would be increased if an excessive quantity was used.

The trophic state of Swan Lake is currently considered to be oligotrophic based on a TSI threshold value of 40 for TN and TP (Koopal 2014). Simultaneous treatment of sites 1, 6, 7, 8, 9, and 10 would not result in TSI values greater than 40 for either TP or TN. Thus, treatment of all sites containing spawning substrate will not result in the eutrophication of Swan Lake. The ability to maintain the oligotrophic state of Swan Lake despite the nutrient additions from pellet treatments should alleviate concerns about negative effects attributable to nutrient loading in a freshwater lake. However, it is important to acknowledge the potential for error and the uncertainty in the results generated by this study given the novel combination of methods used. Therefore, establishing current concentrations for nitrate, ammonium, soluble reactive phosphorus, and phosphate could yield more accurate and precise nutrient concentration estimates from the use of carcass analog pellets.

Lake Trout spawning activity has also been documented on substrate that was historically considered to be insufficient for the survival of embryos in the Laurentian Great Lakes (Binder et al. 2018; Farha 2018; Farha et al. 2020); Lake Tahoe, California–Nevada (Beauchamp et al. 1992); and Yellowstone Lake (Simard 2017). Thus, the true area of all spawning substrate being used in Swan Lake by Lake Trout could have been underestimated. Furthermore, the stark contrast between homogeneous substrate classes in Swan Lake facilitated the accuracy of substrate classification in spawning season aggregations, which may not be the case for other lakes that contain Lake Trout populations. Concentrating suppression efforts on the spawning sites with the highest use and recruitment potential could result in the most effective and efficient application of suppression effort in Swan Lake.

Another potential source of error is the use of TP and TN to evaluate the effects of nutrient loading from the use of carcass analog pellets. Total phosphorus and TN are often measured to assess nutrient concentrations in freshwater, but these concentrations do not reflect what is readily available to primary producers. Total phosphorus and TN are nutrient pools made up of various molecules, but only some of them are available to algae. Therefore, our estimates of TP and TN likely overestimate the nutrient loading potential from the use of carcass analog pellets. However, given that TSI values for TP and TN after pellet treatment remained below threshold values for an oligotrophic–mesotrophic shift, the inclusion of soluble phosphorus and nitrogen will not adversely affect the study results.

Expansion of the Lake Trout population in Swan Lake is likely occurring because suppression efforts were suspended in 2017. Incidental bycatch of native Bull Trout, the species of conservation priority, remains a principal concern for large-scale use of gill netting in Swan Lake. Therefore, use of gill netting as the sole method for future suppression of Lake Trout in Swan Lake remains unfavorable. Furthermore, live-capture methods (e.g., trap nets or pound nets) that are capable of reducing bycatch mortality cannot be employed at this time due to logistical and financial constraints. Additional investigation is needed to confirm (1) the efficacy of carcass analog pellets in Swan Lake compared to Yellowstone Lake and (2) the background levels of TP and TN used to estimate the effects of additional nutrient inputs. The novel combination of telemetry and side-scan sonar to inform traditional and alternative suppression techniques presents a renewed opportunity for Lake Trout suppression in Swan Lake to be achieved in a more targeted and effective way.

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SUPPORTING INFORMATION

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