

COMBINATION OF ACOUSTIC TELEMETRY AND SIDE-SCAN SONAR PROVIDES
INSIGHT FOR LAKE TROUT *SALVELINUS NAMAYCUSH*
SUPPRESSION IN A SUBMONTANE LAKE

by

Michael James Siemiantkowski

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of

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in

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TABLE OF CONTENTS

1. COMBINATION OF ACOUSTIC TELEMETRY AND SIDE-SCAN SONAR PROVIDES INSIGHT FOR LAKE TROUT <i>SALVELINUS NAMAYCUSH</i> SUPPRESSION IN A SUBMONTANE LAKE.....	1
Introduction.....	1
Methods.....	4
Study Area	4
Transmitter Allocation	6
Transect and Tracking Design	7
Location Accuracy and Detection Distance.....	8
Tracking Protocol.....	9
Aggregations and Spawning Sites	9
Site Use, Movement Rate, and Nearest Neighbor Distance	10
Spawning Habitat Characteristics	10
Carcass-analog Pellet Embryo Suppression.....	12
Results.....	14
Lake Trout Spawning Sites and Spawning Habitat Description.....	14
Carcass-analog Pellet Embryo Suppression.....	16
Discussion.....	18
Conclusion	25
Tables	27
Figures.....	31
REFERENCES CITED.....	37
APPENDIX.....	47

LIST OF TABLES

Table	Page
1. Number of individual Lake Trout, number of individual relocations, mean individuals per tracking survey, and nearest neighbor distance (m) by lake region (North, Central, South) in Swan Lake, Montana during September, October, and November of 2018 and 2019. Lake Trout relocations were pooled for years. Individuals was calculated as the sum of unique Lake Trout detected during annual tracking efforts for each lake region	27
2. Total number of individual Lake Trout, number of relocations, mean individuals per tracking survey, mean nearest neighbor distance (m), length of stay (days), and individual days for each confirmed and unconfirmed Lake Trout spawning site in Swan Lake, Montana during September, October, and November of 2018 and 2019. Lake Trout locations were pooled for years. Individuals was calculated as the sum of unique individual Lake Trout detected during each year. Individual days was calculated as the product of mean individuals per survey and mean length of stay.....	28
3. Size (m ²) and depth (m) for confirmed and unconfirmed spawning sites in Swan Lake, Montana during September, October, and November of 2018 and 2019. Area of Lake Trout relocations was estimated by summing the total area of Lake Trout locations from kernel density estimates. Spatial error estimate (± 49 m ²) was calculated by squaring the sum of the minimum mapping unit (4 m) and horizontal accuracy of the Lowrance side-scan sonar (3 m).....	29
4. Estimates of total surface area (m ²) for suitable and unsuitable spawning substrate, total amount of pellet material required (kg) to reach an effective level of coverage (1.75 kg/m ²), estimated cost of pellet material (US dollars), and total amount of phosphorous (kg) and nitrogen (kg) nutrient inputs from pellet treatment(s) by spawning site type (confirmed and unconfirmed) and for all locations (total) in Swan Lake, Montana. The spatial error estimate (\pm m ²) for total surface area was calculated by squaring the sum of the minimum mapping unit and horizontal accuracy of side-scan sonar. Uncertainty of quantity of pellets, cost, total phosphorous, and total nitrogen estimates was calculated using the upper and lower bounds of surface area estimates.....	30

LIST OF FIGURES

Figure	Page
1. Map of Swan Lake, Montana. Black lines delineate the three tracking regions (North, Central, and South). Grey line delineates tracking transect. Black circles are nightly starting locations.....	31
2. Kernel-density map of Lake Trout locations during September, October, and November of 2018 and 2019 in Swan Lake, Montana. Relative densities delineate Lake Trout aggregations. Unique spawning sites are numbered (1-10).....	32
3. Map of three confirmed spawning sites (grey with crosshatch) and seven unconfirmed spawning sites (solid grey) in Swan Lake, Montana during September, October, and November of 2018 and 2019. Unique spawning sites are numbered (1-10).....	33
4. Substrate classification map for 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. Unique spawning sites are numbered (1-10).....	34
5. Substrate classification map for site 6 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. Number indicates unique site identifier (see Figure 2).....	35
6. Substrate classification map for site 10 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. Number indicates unique site identifier (see Figure 2).....	36

ABSTRACT

Expansion of an invasive Lake Trout *Salvelinus namaycush* population in Swan Lake, Montana threatens a core area population of Bull Trout *Salvelinus confluentus* in Montana. Given the increased efficacy of suppression using novel embryo suppression methods, there is renewed interest in Lake Trout suppression in Swan Lake. The specific questions of this study were: 1) where are Lake Trout spawning, 2) where are the most used spawning sites, 3) what is the amount of spawning habitat, 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 phosphorous and nitrogen would be added to Swan Lake if carcass-analog pellet treatments were implemented? Acoustic tags were implanted in 85 Lake Trout in July and August of 2018 and 2019. Nightly tracking efforts during September, October, and November of 2018 and 2019 resulted in 1,744 relocations for 49 individual Lake Trout. Kernel-density analysis was used to evaluate Lake Trout aggregation locations identifying 10 distinct spawning sites — corroborating previous studies. Visual observation of Lake Trout embryos confirmed spawning at three sites with the remaining seven sites considered to be unconfirmed spawning sites. All confirmed spawning sites were located in the littoral zone along areas of steep bathymetric relief and were the most used across both spawning seasons. In 2019, side-scan sonar imaging was used to classify and quantify the total area of suitable spawning substrate, which comprised 12.8% of the total surface area estimated for confirmed sites and 11.4% for unconfirmed spawning sites. Simultaneous treatment of all confirmed and unconfirmed spawning sites would require $205,709 \pm 86$ kg of carcass-analog pellet material, resulting in 370.4 ± 0.2 kg of phosphorous 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 for total phosphorous, and from 22.1 to 26.2 for total nitrogen. Based on a TSI threshold value of < 40 for an oligotrophic lake, the use of carcass-analog pellets could be a feasible addition to renewed Lake Trout suppression efforts in Swan Lake.

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Introduction

Introduction of invasive species to freshwater ecosystems is considered the second greatest threat to biodiversity after habitat destruction, and fishes are one of the most widely introduced taxa (Gozlan et al. 2010; Havel et al. 2015; Thomaz et al. 2015). Societal demand for fish as commodities and expanded recreational opportunities are the principal drivers of fish introductions outside of their native range (Gozlan et al. 2008; Gozlan et al. 2010). Lake Trout *Salvelinus namaycush* was one species widely introduced outside of their native range due to their 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 has 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 (Beauchamp et al. 2006; Hansen et al. 2016) and declines in abundance of native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Yellowstone Lake (Koel et al. 2019; Koel et al. 2020a).

Invasive Lake Trout were first discovered in Swan Lake, Montana in 1998 (Rosenthal et al. 2012), likely establishing through illegal introduction(s) or colonization from Flathead Lake (Cox et al. 2013). Once established in an ecosystem, suppression of an invasive species is

typically the most attainable goal to conserve the native ecosystem (Veitch and Clout 2002; Simberloff et al. 2005). Selective removal methods, such as gillnetting, are common suppression 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). For invasive Lake Trout suppression, gillnetting can effectively suppress abundance when a level of effort is achieved capable of recruitment overfishing by overexploitation of spawners and maintaining the lowest density possible given monetary and logistic constraints (Healey 1978; Hansen 1999; Cox 2010; Syslo et al. 2011; Syslo et al. 2013; Hansen et al. 2019). Gillnetting was initiated in Swan Lake, Montana in 2009 to suppress an invasive Lake Trout population and conserve native Bull Trout (Rosenthal et al. 2012). Gillnetting efforts removed 56,974 juvenile and 2,778 adult Lake Trout from 2009 to 2016. However, the gillnetting effort was suspended in 2017 because of financial costs and incidental bycatch of Bull Trout (Rosenthal et al. 2017).

Gillnetting bycatch is especially concerning when a threatened or endangered species is susceptible to incidental capture (Hall et al. 2000; Raby et al. 2011), such as the federally listed Bull Trout in Swan Lake (Rosenthal and Fredenberg 2017). Mitigating Bull Trout bycatch is of paramount importance for renewed suppression of Lake Trout in Swan Lake. Fortunately, complementary techniques to gillnetting exist which are capable of avoiding bycatch and improving suppression efficacy. A combination of complementary techniques under an Integrated Pest Management (IPM) framework presents renewed opportunity for Lake Trout suppression in Swan Lake.

Use of complementary suppression techniques under an 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). Acoustic

telemetry is one complementary technique to gillnetting capable of identifying aggregation locations 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 determine the spawning sites of Lake Trout (Flavelle et al. 2002; Cox 2010; Dux et al. 2011; Fredenberg et al. 2017; Binder et al. 2018; Williams et al. 2021) allowing for targeted gillnetting efforts and the use of novel embryo suppression techniques. Thus, given the potential benefits of using an IPM approach for Lake Trout suppression, agencies such as the National Park Service in Yellowstone National Park have invested in complementary techniques and the development of novel suppression methods (Doepke et al. 2017).

In Yellowstone Lake, novel embryo suppression using carcass-analog pellets has shown promise as another complementary suppression technique to gill netting (Poole 2019; Thomas et al. 2019; Koel et al. 2020b). Carcass-analog pellets are a highly effective method for embryo suppression (Thomas et al. 2019; Koel et al. 2020b). However, implementation of carcass-analog pellet treatments for embryo suppression requires detailed information on the location and area of suitable spawning substrate within spawning season aggregation locations. Therefore, the sole use of telemetry to define spawning sites could misrepresent the area of suitable spawning substrate requiring pellet treatment for embryo suppression. The novel combination of acoustic telemetry and side-scan sonar imaging could accurately estimate suitable spawning substrate within spawning season aggregations, which can be used to inform carcass-analog suppression techniques.

Increased nutrient inputs are the principal concern with the use of carcass-analog pellets because the pellets contain phosphorous and nitrogen, the primary limiting nutrients for

productivity in aquatic systems (Guildford and Hecky 2000; Sondergaard et al. 2017; Fink et al. 2018). Therefore, the large-scale use of carcass-analog pellets for embryo suppression will result in additional nutrient inputs to Swan Lake. Mitigation of the effects of the additional nutrients might be necessary and can be achieved by judicious use of pellet material by obtaining accurate and precise estimates of suitable spawning substrate area and prioritizing treatments by spawning site use. Additionally, phosphorous and nitrogen concentrations can be reduced in Swan Lake by removing Lake Trout, further offsetting the nutrient inputs from carcass-analog pellet treatments. 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) where are the most used spawning sites, 3) what is the amount of spawning habitat, 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 phosphorous 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 situated at an elevation of 940 m in the Flathead River drainage of northwest Montana, USA. Swan Lake has an average depth of 16 m and maximum depth of 43 m, with two basins greater than 30 m at the north and south ends, connected by a shallow mid lake section (Figure 1). Swan Lake is a dimictic lake, and the thermocline is commonly at 18 m during summer months (Cox 2010). The substrate in Swan Lake is characterized by sand and silt below the littoral zone and 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 other glacially formed lakes in northwest Montana, such as Lindbergh, McDonald, and Quartz lakes, where Lake Trout spawning has been documented (Dux et al. 2011; Curtis and Koopal 2012; D'Angelo et al. 2013; Fredenberg et al. 2017).

Swan Lake is an oligotrophic lake typified by high dissolved oxygen (DO) concentrations, low nutrient inputs, and low productivity (Koopal 2014). However, hypoxic conditions persist annually in the hypolimnion of the northern and southern basins, with the lowest concentration (i.e., < 0.1% DO saturation) in the southern basin attributed to nutrient inputs from historic logging and road construction in the watershed (Butler et al. 1995; Koopal 2014). Nutrient levels and productivity in Swan Lake are typical for an oligotrophic lake with average total phosphorous (TP) concentrations of 3.4 µg/L, total nitrogen (TN) concentrations of 105.8 µg/L, and chlorophyll-a concentrations of 1.06 mg/m³ (Koopal 2014).

Hydraulic residence time for Swan Lake averages 70 days, resulting in complete cycling of lake water 5.2 times per year (Butler et al. 1995). The residence time of water in Swan Lake contributes to maintenance of the oligotrophic trophic state essential for persistence of native species (Butler et al. 1995; Koopal 2014). Native species in Swan Lake include Westslope Cutthroat Trout *Oncorhynchus clarkia lewisi*, Bull Trout, Mountain Whitefish *Prosopium williamsoni*, Pygmy Whitefish *Prosopium coulterii*, Northern Pikeminnow *Ptychocheilus oregonensis*, Peamouth *Mylocheilus caurinus*, Redside Shiner *Richardsonius balteatus*, Longnose Sucker *Catostomus catostomus*, Largescale Sucker *Catostomus macrocheilus*, and Columbia Slimy Sculpin *Uranidea cognata*. Nonnative species in Swan Lake include Lake Trout, Kokanee *Oncorhynchus nerka*, Rainbow Trout *Oncorhynchus mykiss*, Brook Trout

Salvelinus fontinalis, Northern Pike *Esox lucius*, Brook Stickleback *Culaea inconstans*, and Central Mudminnow *Umbra limi* (Cox 2010; Guy et al. 2011). Additionally, nonnative Opossum shrimp *Mysis relicta* are in Swan Lake providing an abundant food source and competitive advantage for invasive Lake Trout (Rosenthal and Fredenberg 2017).

Transmitter Allocation

Swan Lake was divided into three regions (North, Central, and South) to facilitate nightly tracking efforts and provide equal representation of telemetered Lake Trout throughout Swan Lake (Figure 1). Gill nets were used to sample Lake Trout within each lake region during July and August of 2018 and 2019 when mature Bull Trout had migrated out of Swan Lake to spawn, which minimized Bull Trout by-catch. Gill nets were 91-m long by 2-m height, with mesh sizes of 57-mm and 65-mm bar measure constructed out of 0.2-mm diameter clear monofilament. Gill nets were set twice daily and pulled after 2-3 h to reduce stress to Lake Trout and by-catch species. Mature male Lake Trout ≥ 500 mm (total length) were implanted with Lotek MAP (MM-M-16-50; 80-mm long, 16-mm diameter, weight 35 g) series acoustic transmitters (Lotek Wireless, Inc., Newmarket, ON, Canada). Tagging efforts were focused on mature male Lake Trout because they are known to stay at spawning sites longer than females allowing for more accurate and precise description of spawning sites (Martin and Olver 1980; Muir et al. 2021). Mature female Lake Trout were implanted with transmitters when catch of mature male Lake Trout was insufficient to deploy all transmitters.

Once captured, Lake Trout were anesthetized using AQUI-S 20E (25 mg/L) and Lotek MAP transmitters were implanted using standard surgical procedures for internal tagging of fish (Jepsen 2002; Jepsen 2008; Wagner 2011). Sex and stage of maturity were determined by visual

observation of the gonads through the surgical incision (Williams et al. 2021). Lake Trout selected for transmitter implantation had testes or ovaries easily identifiable as mature — immature Lake Trout were not tagged. Tagged Lake Trout were held in a 114-L oxygenated tank for a minimum of 15 minutes to recover, followed by release after a return to normal respiration rates and maintaining equilibrium.

Eighty-five Lake Trout ≥ 500 mm (mean TL = 669.7 mm; SE = 7.0) were implanted with transmitters — 71 male Lake Trout (mean TL = 655.9; SE = 6.8) and 14 female Lake Trout (mean TL = 740.0; SE = 14.1). Transmitter allocation was unequal among lake regions because of varying catch rates. Three male Lake Trout were tagged in the North Region; 38 male Lake Trout and six female Lake Trout were tagged in the Central Region; and 30 male Lake Trout and eight female Lake Trout were tagged in the South Region.

Transect and Tracking Design

Tracking was conducted during the spawning period (28 September to 2 November in 2018, and 29 September to 2 November in 2019). The spawning period was determined through previous suppression-netting-catch data of ripe male and female Lake Trout from 2009 to 2017 (Rosenthal and Fredenberg 2017). In general, Lake Trout spawning activity occurs at night between dusk and midnight (Esteve et al. 2008); thus, tracking was initiated one hour before sunset and continued for six hours.

A tracking map with transects delineated was constructed in ArcMap 10.6.1 (ESRI 2019). Transects were parallel to and ≤ 500 m from shore or adjacent transects and divided among lake regions with starting locations located at opposing ends of each transect region. Transect methods were similar to methods used by Melnychuk and Christensen (2009) and Williams et

al. (2021). Tracking was conducted 29 nights in 2018, and 27 nights in 2019 from September 28 to November 2 encompassing the Lake Trout spawning period. Nightly tracking efforts began from randomized starting locations for the Central and South regions on night one, followed by the North and Central regions on night two. Alternating tracking among lake regions and starting locations ensured equal representation of tracking effort for each lake region.

Location Accuracy and Detection Distance

Location accuracy testing was conducted concurrently with detection distance testing during two time periods: pre-spawn and post-spawn. The test-tag setup used to determine location accuracy and maximum detection distance consisted of a single Lotek Map series transmitter suspended 0.5 m from the lake substrate, attached to an anchored line. The anchored line was deployed at depths of 10 m for pre-spawn testing, and at 5 m for post-spawn testing to simulate seasonal locations of Lake Trout (Muir et al. 2021; Williams et al. 2021). The anchored line was extended and secured to shore allowing for the absence of a surface buoy enabling blind trials. Blind trials were conducted following the same tracking protocols as tracking Lake Trout (see below). Difference between estimated UTM location from the true UTM location provided an estimate of location accuracy. Similarly, difference between the UTM location of the point of first detection and the true UTM location provided an estimate of detection distance. 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.

Tracking Protocol

Lake Trout locations were estimated using a Lotek MAP RT series acoustic receiver equipped with two Lotek LHP_1 directional hydrophones and Lotek MapHost software (Lotek Wireless, Inc., Newmarket, ON, Canada). Universal Transverse Mercator (UTM) coordinates were recorded using an on-board Lowrance HDS 9 Carbon GPS chartplotter, with horizontal location accuracy reported at 3 m (Lowrance 2018). Protocols developed for tracking and estimating the location of Lake Trout in Yellowstone Lake, Yellowstone National Park (Williams et al. 2021) were used in Swan Lake.

Aggregations and Spawning Sites

Location data from 49 individual Lake Trout (mean TL = 687.1 mm; SE = 8.7) were used with ArcMap 10.6.1 (ESRI 2019) to delineate aggregation locations. Lake Trout location data did not include Lake Trout considered to be mortalities. Lake Trout were considered mortalities following methods by Williams et al. (2021) when mean movement distance during the study period was < 500 m. Kernel density estimation (KDE) in ArcMap 10.6.1 (ESRI 2019) was used to determine Lake Trout aggregations. Relative density estimates from 0 to 1 were calculated using KDE and Lake Trout point-location data. Aggregation locations were determined using all positive bandwidths surrounding areas with a minimum relative density of 0.25, indicating an aggregation of four or more Lake Trout.

Polygons were constructed in ArcMap 10.6.1 (ESRI 2019) using relative density values ≥ 0.25 to identify the spatial extent of Lake Trout aggregations. Confirmation of spawning at aggregation locations was conducted post-tracking using an Aqua-Vu underwater camera and SCUBA divers to detect the presence or absence of Lake Trout embryos within in-situ suitable

spawning substrate. Aggregation locations were designated as confirmed spawning sites if Lake Trout embryos were present, or unconfirmed if no embryos were observed. Confirmed and unconfirmed spawning sites were designated as individual sites (1-10) with sites numbered counter-clockwise from south to north.

Site Use, Movement Rate, and Nearest Neighbor Distance

Mean, minimum, and maximum lake depth was calculated for each confirmed and unconfirmed spawning site. Number of Lake Trout present; mean number of individuals present; and mean, minimum, and maximum residence time were calculated for each confirmed and unconfirmed spawning site. Residence time at confirmed and unconfirmed spawning sites was defined as the number of days between the first and last day a Lake Trout was detected at a location. Mean residence time at confirmed and unconfirmed spawning sites was calculated as the product of mean individuals present and the mean time at a location.

Total movement was calculated for each Lake Trout using the Euclidian distance between sequential relocations. Daily movement rate (m) for each individual was estimated by dividing total distance by total number of days between sequential relocations. Mean, minimum, and maximum nearest-neighbor distance was calculated using the Euclidian distance between point locations of individual Lake Trout. All descriptive statistics were conducted in R (R Core Team 2018).

Spawning Habitat Characteristics

Polygons constructed in ArcMap 10.6.1 (ESRI 2019), using the KDE map for Lake Trout aggregations, were used to facilitate placement of transects for sonar imaging of the substrate. A boat-mounted Lowrance side-scan sonar transducer was used to acquire images of substrate

contained within confirmed and unconfirmed spawning sites. Parallel transects were at 25-m intervals to achieve optimal sonar image resolution (Cummings 2015; Richter et al. 2016; Dow 2018). Side-scan sonar imaging was conducted along each transect while operating the vessel at 4.5 km/h, with the transducer operating frequency set to 455 kHz. Additional sonar settings followed methods used by Richter et al. (2016) and Dow (2018). Side-scan images (Figure A.1) were collected until total coverage was achieved for confirmed and unconfirmed spawning sites. Images were used to evaluate for substrate type, quantity (km²), and location.

Substrate maps (Figures A.2, A.3, A.4, A.5) were created by compiling georeferenced side-scan sonar imagery in ArcMap 10.6.1 (ESRI 2019). Side-scan sonar images were converted to an ArcMap 10.6.1 (ESRI 2019) compatible format using the software program SonarTRX[®] (Leraand Engineering Inc., Honolulu, Hawaii). Sonar raster files were georeferenced and processed in ArcMap 10.6.1 (ESRI 2019) to generate mosaic images for each confirmed and unconfirmed spawning site. Polygons were constructed in ArcMap 10.6.1 (ESRI 2019) using the side-scan sonar imagery to assign substrate type. Satellite orthophoto files were used to delineate shoreline boundaries and substrate in ArcMap 10.6.1 (ESRI 2019). A shapefile (.shp) of Swan Lake was used in ArcMap 10.6.1 (ESRI 2019) for generating figures due to computational power limitations. A minimum mapping unit (MMU) was determined using the smallest size polygon for a substrate category. The MMU was used to define areas of uniform sonar signature as representative of a predominant substrate type and provide an error estimate for substrate classification (Kaesler and Litts 2010). Thus, the spatial error estimate ($\pm 49 \text{ m}^2$) used for surface area estimates was calculated by squaring the sum of the MMU (4 m) and horizontal accuracy of the Lowrance side-scan sonar (3 m).

Substrate polygons provided estimates of surface area (km²) of suitable and unsuitable spawning substrate. Suitable spawning substrate is defined as rubble and cobble substrates ≥ 65 mm and ≤ 999 mm, and unsuitable spawning substrate is defined as organic, sand, gravel, and boulder substrates ≤ 64 mm and ≥ 1000 mm in size (modified from Marsden et al. 1995). Total area for each substrate type was calculated by summing the areas for each unique substrate polygon within confirmed and unconfirmed 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). Reference sonar images were visually verified by underwater camera and targeted SCUBA dives at 22 locations within Lake Trout aggregations. SCUBA dive locations were marked with buoys directing dive teams to the target area of substrate where photographs and measurements were collected to verify substrate type.

An error matrix was used to assess the accuracy of substrate type assignment using side-scan sonar imagery. The error matrix was constructed using the assigned substrate types from side-scan sonar imagery and the verified substrate types. Total substrate classifications assigned using the side-scan sonar imagery was divided by the total verified classifications to provide an estimate of total percent accuracy for substrate classification using sonar imagery (Congalton and Green 1999; Richter et al. 2016; Dow 2018).

Carcass-analog Pellet Embryo Suppression

Total phosphorous (TP) and total nitrogen (TN) quantities were estimated to assess the potential for nutrient loading in Swan Lake if carcass-analog pellets were used on spawning sites. Total phosphorous and TN of carcass-analog pellets were determined using the total

Kjeldahl method by Energy Laboratories, Billings, Montana. Treatment of spawning substrate using carcass-analog pellets at 1.75 kg/m² was found to induce >75% mortality on Lake Trout embryos in Yellowstone Lake (Koel et al. 2020b). Therefore, estimates of required pellet quantity and TP and TN contributions for Swan Lake were calculated using a coverage amount of 1.75 kg/m² on suitable spawning substrate within confirmed and unconfirmed spawning sites. Carlson's trophic state index (TSI) reference values from Koopal (2014) were used to describe the effect of the net increase in TP and TN concentrations on the current oligotrophic trophic state assignment for Swan Lake.

Carcass-analog pellet material quantities (kg/m²) required to induce mortality on Lake Trout embryos were calculated using the surface area estimates for suitable spawning substrate. Carcass-analog pellet production cost (US dollars/kg pellets) from 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 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/kg TP and 0.0364 kg/kg TN for pellet material. Carlson's trophic state index values were calculated for the additional TP and TN expected from pellet treatments. Background values for TSI for TP and TN were obtained from Koopal (2014). Carlson's trophic state index values were calculated for the additional TP and TN expected from pellet treatments using equations by Carlson and Simpson (1996). Background TSI values and pellet treatment TSI values for TP and TN were summed to determine total TSI values for TP and TN in Swan Lake. Total TSI values were compared to threshold values for TP and TN reported by Carlson and Simpson (1996) to estimate trophic state assignment.

Results

Lake Trout Spawning Sites and Spawning Habitat Description

Tracking during the spawning period resulted in 1,744 locations for Lake Trout. Mean movement rate for tracked Lake Trout was 734.9 m/day (SE = 33.5) and mean nearest neighbor distance was 39.6 m (SE = 1.6). The central region of Swan Lake had the greatest number of individuals, number of individual relocations, mean individuals per tracking survey, and closest nearest neighbor distance for lake regions (Table 1). Furthermore, the north region of Swan Lake had the lowest number of individuals, number of individual relocations, and mean individuals per tracking survey for the three defined lake regions (Table 1).

Lake Trout were aggregated in ten distinct locations (Figure 2), and 64% of all individual relocations occurred within these locations. The highest relative density values were at sites 1, 6, and 9, which contained values of ≥ 0.50 (Figure 2). Visual observation of Lake Trout embryos confirmed spawning at sites 1, 6, and 9. The remaining seven sites (i.e., 2, 3, 4, 5, 7, 8, 10) were unconfirmed spawning sites (Figure 3). Confirmed spawning sites 1, 6, and 9 comprised 48% of individual relocations among the ten locations. Site 6 was the most used of the confirmed spawning sites and had 6.9 times more relocations than site 9 and 1.8 times more relocations than sites 1 and 9 combined (Table 2). Furthermore, site 6 had 2.0 times more relocations than all seven unconfirmed spawning sites combined (Table 2). Confirmed spawning sites comprised 77% of individual days spent within confirmed and unconfirmed spawning sites. Site use among confirmed spawning sites was greatest for sites 6 and 1, and those sites comprised 109 of 120 individual days and had an average length of stay of 8.5 days (Table 2). Site 6 also had the greatest number of returning individuals for both spawning seasons (N = 40).

Unconfirmed spawning sites comprised 16% of total individual relocations with sites 3 and 10 used the most; for example, individual relocations in sites 3 and 10 comprised 58% of all relocations (Table 2). Sites 3 and 10 comprised 86% of individual days spent in an unconfirmed spawning site with site 3 having the longest average length of stay by Lake Trout for all unconfirmed sites. Sites 3 and 10 had the greatest use among the seven sites with 30 total individual days and an average length of stay of 11.5 days (Table 2). Site 10 also had the greatest number of returning individuals ($N = 17$) for both spawning seasons.

Surface area estimates from Lake Trout relocations informed by KDE varied in size (m^2) and depth (m) for confirmed and unconfirmed spawning sites. Surface area estimates for Lake Trout relocations in confirmed spawning sites varied from $46,943 \pm 49 m^2$ to $487,171 \pm 49 m^2$ with depth varying from 2 m to 43 m (mean = 11.1 m; SE = 0.7) (Table 3). Surface area estimates for Lake Trout relocations in unconfirmed spawning sites varied from $25,700 \pm 49 m^2$ to $105,599 \pm 49 m^2$, with depth varying from 2 m to 43 m (mean = 14.0 m; SE = 1.0) (Table 3).

Surface area estimates for spawning sites were overestimated when using only Lake Trout relocations. That is, the total surface area of confirmed spawning sites was $621,919 \pm 49 m^2$ when not considering suitable spawning substrate and $79,534 \pm 49 m^2$ when Lake Trout relocations were coupled with side-scan sonar images of the substrate type (Tables 3 and 4). Similarly, of $333,492 \pm 49 m^2$ represented by all Lake Trout relocations at unconfirmed spawning sites only $38,014 \pm 49 m^2$ was suitable spawning substrate (Tables 3 and 4). Thus, potential spawning area was 87% smaller for confirmed spawning sites, and 89% smaller for unconfirmed spawning sites than the surface area estimates informed by only Lake Trout relocations.

Suitable spawning substrate comprised 12.8% of the total surface area for confirmed spawning sites (Table 4; Figures 4 and 5; Figures A.2 and A.3). For example, of the $487,171 \pm 49 \text{ m}^2$ informed by Lake Trout relocations for site 6 only $63,301 \pm 49 \text{ m}^2$ of substrate is suitable for Lake Trout to spawn (Tables 3 and 4). Relative to aggregation size, site 9 had the greatest proportion of suitable spawning substrate by surface area (29.4%) followed by site 6 (13%), with the lowest proportion at site 1 (2.8%) (Table 4). Site 6 had the greatest quantity of suitable spawning substrate comprising 80% of the suitable substrate found among confirmed spawning sites, 3.9 times more suitable substrate than sites 1 and 9 combined (Table 4). Confirmed spawning sites also contain the greatest quantity of suitable spawning substrate, 2.1 times more than the seven unconfirmed spawning sites (Table 4).

Three of seven locations (site 10, 8, 7) where spawning was unconfirmed contained suitable spawning substrate (Table 4; Figures 4 and 6; Figures A.3, A.4, A.5, and A.6). Relative to aggregation size for unconfirmed spawning sites site 10 had the greatest proportion of suitable substrate for the total surface area (29.1%), 1.1 times more than sites 8 and 7 combined (Table 4). Furthermore, the quantity of suitable substrate in site 10 ($30,691 \pm 49 \text{ m}^2$) was 4.2 times greater than for sites 8 and 7 combined ($7,323 \pm 49 \text{ m}^2$) (Table 4). The remaining four locations described (site 2, 3, 4, 5) had no suitable spawning substrate present within the area informed by Lake Trout relocations (Table 4).

Carcass-analog Pellet Embryo Suppression

The quantity of carcass-analog pellet material required to treat suitable spawning substrate contained within confirmed and unconfirmed spawning sites would be $205,709 \pm 86 \text{ kg}$ (US\$164,567 \pm 68; Table 4). Treatment of the three confirmed spawning sites with carcass-

analog pellets would require $139,185 \pm 86$ kg (US\$111,348 \pm 68) of pellet material (Table 4).

Site 6 had the most suitable spawning substrate for confirmed spawning sites and comprised 80% of the total pellet material required to treat confirmed spawning sites, 3.9 times more than sites 1 and 9 combined (Table 4). Site 9 had the second most suitable spawning substrate and comprised 17% of the total pellet material required for treatment, 5.7 times more than site 1 which contained the least amount of suitable spawning substrate for confirmed sites (Table 4).

Treatment of suitable spawning substrate within unconfirmed spawning sites would require $66,524 \pm 86$ kg (US\$53,219 \pm 68) of pellet material. Site 10 had the most suitable spawning substrate for unconfirmed locations and comprised 81% of the total pellet material required to treat unconfirmed spawning sites, 4.2 times more than sites 7 and 8 combined (Table 4).

Nutrient inputs of TP and TN from carcass-analog pellet treatments of confirmed and unconfirmed spawning sites would be 370.4 ± 0.2 kg TP and $7,487.9 \pm 3.1$ kg TN. Treatment of the three confirmed spawning sites would result in 250.6 ± 0.2 kg TP and $5,066.4 \pm 3.1$ kg TN added to Swan Lake (Table 4). Site 6 would require the greatest quantity of carcass-analog pellet material to treat and would comprise 80% of the nutrient inputs from treatment of confirmed spawning sites (Table 4). Treatment of suitable spawning substrate at three unconfirmed sites would contribute 119.8 ± 0.2 kg TP and $2,421.5 \pm 3.1$ kg TN (Table 4). Site 10 would require the greatest quantity of pellet material, and would comprise 81% of nutrient inputs, 4.2 times more than sites 7 and 8 combined (Table 4).

Carlson's trophic state index background values for Swan Lake reported by Koopal (2014) for TP was 15.7 for the northern basin, and 25.8 for the southern basin. Carlson's trophic state index values reported by Koopal (2014) for TN in Swan Lake was 21.9 for the northern basin, and 22.2 for the southern basin. The basin-wide average for Swan Lake using values from

Koopal (2014) was 20.8 (SD = 5.1) for TP and 22.1 (SD = 0.1) for TN. Simultaneous treatment of all confirmed and unconfirmed spawning sites would result in an estimated increase of basin-wide TSI for TP and TN to 27.7 and 26.2, respectively. Pellet treatment of the largest and most used spawning site (site 6) would result in an estimated increase of basin-wide TSI for TP and TN to 25.2 and 24.5, respectively. Thus, treatment of site 6 alone would account for 59% of the increase in TSI of TP and 64% of the increase in TSI of TN from pellet treatments.

Discussion

Lake Trout aggregated at ten locations in Swan Lake during the spawning season and spawning was confirmed at three. Two of the confirmed sites, one near the east shore in the central region and another near the inlet of the Swan River, had the majority of use by Lake Trout. Furthermore, the confirmed site along the eastern shore and the northernmost unconfirmed site contained the majority of suitable spawning substrate found within aggregation locations. All confirmed spawning sites and three of the seven unconfirmed aggregation locations contained suitable spawning substrate; however, the area of suitable spawning substrate was considerably less than the area estimated for Lake Trout aggregations. Suitable spawning substrate within Lake Trout aggregations was accurately 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 oligotrophic to mesotrophic. 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 native Lake Trout populations in Lake

Huron and Lake Champlain (Binder et al. 2016; Pinheiro et al. 2017), and invasive Lake Trout populations in Lake McDonald, Quartz Lake, and Yellowstone Lake (Dux et al. 2011; Fredenberg et al. 2017; Williams et al. 2021). For example, Lake Trout in Swan Lake were found to aggregate around areas of steep bathymetric relief containing suitable spawning substrate (cobble, rubble), similar to native Lake Trout populations in the Laurentian Great Lakes (Binder et al. 2018; Farha et al. 2020; Marsden et al. 2021), and invasive populations in the intermountain west (Schoby et al. 2009; Dux et al. 2011; Fredenberg et al. 2017; Marsden et al. 2021). Lake Trout also aggregated at all previously identified confirmed spawning sites within Swan Lake with spawning activity again confirmed in suitable substrate located along the eastern shore of Swan Lake previously described by Cox (2010), re-affirming the locations as preferred spawning sites.

Duration of spawning site use in Swan Lake varied from 1 to 28 days and was similar to native Lake Trout populations where sites were used for 4 to 25 days in Alexie Lake (Callaghan 2016), 19 to 35 days in Lake Champlain (Pinheiro et al. 2017), and 8 to 19 days for an invasive population in Yellowstone Lake (Williams et al. 2021). Interestingly, the spawning site use was found to be similar to patterns observed during the day by Callaghan (2016), Pinheiro et al. (2017), and Williams et al. (2021). However, tracking at night during this study likely resulted in increased resolution of preferred spawning locations within spawning-season aggregations. Lake Trout in Swan Lake also used multiple spawning sites per year similar to spawning behavior in Alexie Lake (Callaghan et al. 2016), Lake Champlain (Pinheiro et al. 2017), Thunder Bay (Marsden et al. 2016), and Yellowstone Lake (Williams et al. 2021). The use of multiple spawning sites per year by Lake Trout is attributed to a “bet-hedging” strategy of broadcasting eggs 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 an individual Lake Trout will use multiple spawning sites per year increases as the size of the lake and the distance between spawning sites decreases (Muir et al. 2021). Thus, due to the relatively small size of Swan Lake and close proximity of spawning sites Lake Trout are likely using this “bet-hedging” spawning strategy to maximize reproductive success.

Interestingly, 20% of Lake Trout relocations in Swan Lake occurred adjacent to confirmed and unconfirmed spawning sites at depths from 20 m to 43 m, which is deeper than would be expected for spawning activity. For example, Lake Trout populations primarily spawn in water depths less than 12 m within their native range (Scott and Crossman 1973; Martin and Olver 1980), and in depths from 1 m to 18 m for populations outside of their native range (Cox 2010; Dux et al. 2011; Fredenberg et al. 2017; Koel et al. 2020a; Williams et al. 2021).

Movement of Lake Trout to spawning sites in early autumn could be indicative of pre-spawn staging behavior in Swan Lake, similar to pre-spawn behavior for other native and introduced Lake Trout populations (Muir et al. 2021). Furthermore, the use of unconfirmed spawning sites by Lake Trout in Swan Lake could be related to exploratory behavior of new sites for potential colonization (Martinez et al. 2009), that is, Lake Trout were located there while moving to preferred spawning sites (Pinheiro et al. 2017) or a function of competition among spawning Lake Trout at preferred spawning sites causing dispersal (Muir et al 2021).

Understanding 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. 2021). For example, targeting Lake Trout aggregations identified using acoustic telemetry with gill nets 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 target species (Ehler 2006; Velez-Espino et al. 2008; Weber et al. 2011; Simberloff 2014; Yick et al. 2021). Thus, the combination of mechanical (i.e., gillnetting) and chemical (i.e., carcass-analog pellet) suppression techniques using an IPM framework can effectively target Lake Trout life stages from embryo to adult — improving suppression efficacy. Furthermore, the complementary use of traditional gillnetting and carcass-analog pellet treatments could decrease the time required to reach suppression targets. Once this is 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 suitable spawning substrate within spawning season aggregations is critical when considering the use of carcass-analog pellets for embryo suppression. Therefore, we used a novel combination of acoustic telemetry and side-scan sonar in Swan Lake to identify and describe Lake Trout spawning season aggregations and in-situ substrate to inform gillnetting and embryo suppression.

Commonly available side-scan sonar was successfully used to locate and classify substrate within spawning-season aggregations in Swan Lake. Substrate associated with each defined substrate class was identified from side-scan sonar imagery as in similar studies (Kaeser and Litts 2010; Kaeser and Litts 2013; Richter et al. 2016; Glassic and Gaeta 2018). Furthermore, suitable spawning substrate was accurately classified and estimated revealing the area of suitable spawning habitat similar to other studies on Rainbow Trout (Cummings 2015), Walleye *Sander vitreus* (Richter et al. 2016), Lake Trout (Redman et al. 2017), and Bonneville Cutthroat Trout *Oncorhynchus clarkii utah* (Glassic and Gaeta 2018). Suitable spawning substrate was identified in all confirmed spawning sites and was concentrated within the littoral zone along areas of steep bathymetric relief. For example, suitable substrate at site 6 was located adjacent to historic road construction, which resulted in anthropogenic deposition of large

angular cobble and rubble. Suitable spawning substrate was also identified in three unconfirmed spawning sites and was concentrated on mid-lake reefs. However, the area of suitable spawning habitat within spawning season aggregations would have been significantly overestimated by the sole use of Lake Trout relocations. Therefore, the location and area estimates calculated for suitable spawning substrate using side-scan sonar allowed for the feasibility of embryo suppression to be evaluated, and the calculation of estimates for the cost and quantity of carcass-analog pellet material required for treatment.

Embryo suppression has the potential to increase efficacy of suppression efforts for Lake Trout. Lake Trout population growth rates have been found to be susceptible to survival rates of the age-0 year class (Ferreri et al. 1995; Cox et al 2013; Fredenberg et al. 2017). Thus, increasing mortality on Lake Trout embryos should help suppress the Lake Trout population in Swan Lake. Carcass-analog pellets were developed and found to be an effective method for inducing mortality of Lake Trout embryos by reducing dissolved oxygen concentrations below lethal levels (Poole 2019; Koel et al. 2020b). Mortality rates greater than 75% for Lake Trout embryos was achieved using carcass-analog pellets at a coverage of 1.75 kg/m² in Yellowstone Lake (Koel et al. 2020b). Thus, estimates for the required quantity, cost, and P and N nutrient inputs were calculated using the coverage amount of 1.75 kg/m². However, due to the positive relationship between cost (US\$), treatment area (m²), and P and N nutrient inputs the quantity of carcass-analog pellets used for embryo suppression could be a concern. Fortunately, the quantity of carcass-analog pellets required for treatment of spawning sites in Swan Lake can be reduced. For example, spawning sites in Swan Lake could be prioritized for treatment by status (confirmed or unconfirmed), total surface area of suitable spawning substrate, and use by spawning Lake Trout to reduce the quantity and cost of pellet treatments.

Prioritization of spawning site treatments can also address other primary concerns for the use of carcass-analog pellets such as, the potential for eutrophication from nutrient loading of phosphorous and nitrogen, and negative effects on in-situ benthic communities. Phosphorous 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 P and N have been safely used in fisheries management to enhance productivity of oligotrophic systems without causing eutrophication and 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 phosphorous (Lujan 2020). Changes in chemical composition (i.e., DO concentration), 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, in Yellowstone Lake embryo suppression treatments induced localized changes for macroinvertebrates, except for amphipods, however, due to the small treatment area embryo suppression treatments would have little effect lake-wide (Briggs et al. 2020). However, due to physical and chemical differences between Swan Lake and Yellowstone Lake (i.e., total lake area (m²), basin-wide volume of H₂O, residence time, and average nutrient concentrations) monitoring of water-quality parameters (i.e., phosphorous, nitrogen, and ammonia) and relative abundance estimates for vertebrate and invertebrate species of concern is necessary to assess potential effects of pellet treatments both within Swan Lake and downstream to Flathead Lake. Therefore, the accurate measurement of in-situ suitable spawning substrate will reduce the

negative effects of TP and TN additions and the chance to shift trophic state, which would be unnecessarily increased if an excessive quantity was used.

The trophic state of Swan Lake is currently considered to be oligotrophic based on Carlson's TSI values for TN and TP less than 40 (Koopal 2014). Simultaneous treatment of all confirmed and unconfirmed spawning sites would result in an increase of TP TSI to 27.7, and TN TSI to 26.2 from the use of $205,709 \pm 86$ kg of carcass-analog pellet material. Based on a Carlson's TSI oligotrophic-mesotrophic threshold value of 40 for both TN and TP, treatment of all confirmed and unconfirmed spawning sites containing suitable spawning substrate will not result in eutrophication of Swan Lake. The ability to maintain the oligotrophic state of Swan Lake, given the nutrient additions from pellet treatments, should alleviate concerns of negative effects attributable to nutrient loading of a freshwater lake. However, it is important to acknowledge the potential for error and uncertainty in the results generated by this study given the novel combination of methods used. Therefore, establishing current concentrations for nitrate, ammonium, and soluble phosphorous and phosphate could yield more accurate and precise nutrient concentration estimates from the use of carcass-analog pellets.

Lake Trout spawning activity has been documented on substrate classically considered to be unsuitable for spawning in the Laurentian Great Lakes (Binder et al. 2018; Farha 2018; Farha et al. 2020), Lake Tahoe (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 substrate classes in Swan Lake facilitated the 100% accuracy of substrate classification in spawning season aggregations, which may not be the case for other lakes with Lake Trout populations. However, concentrating suppression efforts on the locations with the highest use and recruitment potential in Swan Lake

could result in the most effective and efficient application of suppression effort. 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 phosphorous and TN are not typically used to assess nutrient concentrations in freshwater lakes because of the rapid uptake of soluble P and N included in measurements of TP and TN (Lusha Tronstad, University of Wyoming, personal communication). The inclusion of soluble P and N would therefore result in overestimating the quantity of P and N added to Swan Lake from the use of carcass-analog pellets. However, given that TSI values for TP and TN after pellet treatment remain below threshold values for an oligotrophic-mesotrophic shift, the inclusion of soluble P and N will not adversely affect the study results.

Conclusion

Expansion of the Lake Trout population in Swan Lake is likely occurring since suppression efforts were suspended in 2017. Suppression of the Lake Trout population in Swan Lake could be accomplished using traditional gillnetting, a common method used for Lake Trout suppression where invasive populations exist (Hansen et al. 2016; Fredenberg et al. 2017; Dux et al. 2019; Hansen et al. 2019; Koel et al. 2020a). However, because of incidental bycatch inherent to gillnetting, increased mortality occurred on native Bull Trout, the species of conservation priority in Swan Lake. Therefore, the sole use of gillnetting for Lake Trout suppression in Swan Lake remains implausible. Additional investigation would be needed to confirm the efficacy of carcass-analog pellets in Swan Lake to the efficacy found in Yellowstone Lake, and to confirm the background levels of TP and TN reported by Koopal (2014) used to estimate the effects of additional nutrient inputs. However, the novel combination of telemetry and side-scan sonar to

inform traditional and alternative suppression techniques presents renewed opportunity for Lake Trout suppression in Swan Lake in a more targeted and effective way.

Tables

Table 1. Number of individual Lake Trout, number of individual relocations, mean individuals per tracking survey, and nearest neighbor distance (m) by lake region (North, Central, South) in Swan Lake, Montana during September, October, and November of 2018 and 2019. Lake Trout relocations were pooled for years. Individuals was calculated as the sum of unique Lake Trout detected during annual tracking efforts for each lake region.

Individuals	Relocations	Mean individuals per survey	Mean nearest neighbor (SE)
		North	
18	106	3.6	73.3 (4.9)
		Central	
67	1,395	24.4	22.0 (0.7)
		South	
41	243	5.1	49.4 (2.6)

Table 2. Total number of individual Lake Trout, number of relocations, mean individuals per tracking survey, mean nearest neighbor distance (m), length of stay (days), and individual days for each confirmed and unconfirmed Lake Trout spawning site in Swan Lake, Montana during September, October, and November of 2018 and 2019. Lake Trout locations were pooled for years. Individuals was calculated as the sum of unique individual Lake Trout detected during each year. Individual days was calculated as the product of mean individuals per survey and mean length of stay.

Site	Individuals			Length of stay			Individual days	
	Total	Relocations	Per survey	Mean nearest neighbor (SE)	Mean	Minimum		Maximum
Confirmed								
6	54	543	10.2	13.9 (0.5)	7	1	17	68
1	33	219	4.6	7.2 (0.4)	10	2	28	41
9	17	79	3.5	8.9 (1.2)	4	1	8	11
Unconfirmed								
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	17
4	17	34	2.3	20.7 (3.1)	1	1	1	1
2	12	29	2.0	23.3 (2.6)	4	1	9	4
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 3. Size (m^2) and depth (m) for confirmed and unconfirmed spawning sites in Swan Lake, Montana during September, October, and November of 2018 and 2019. Area of Lake Trout relocations was estimated by summing the total area of Lake Trout locations from kernel density estimates. Spatial error estimate ($\pm 49 \text{ m}^2$) was calculated by squaring the sum of the minimum mapping unit (4 m) and horizontal accuracy of the Lowrance side-scan sonar (3 m).

Site	Area of Lake Trout relocations (m^2)	Depth (m)		
		Mean	Minimum	Maximum
Confirmed				
6	487,171 \pm 49	9	7	43
1	87,805 \pm 49	10	2	21
9	46,943 \pm 49	14	9	37
Unconfirmed				
10	105,599 \pm 49	12	4	22
4	59,198 \pm 49	19	9	37
2	45,908 \pm 49	10	2	21
3	34,300 \pm 49	20	7	43
5	34,100 \pm 49	14	8	32
8	28,687 \pm 49	13	8	19
7	25,700 \pm 49	9	9	12

Table 4. Estimates of total surface area (m²) for suitable and unsuitable spawning substrate, total amount of pellet material required (kg) to reach an effective level of coverage (1.75 kg/m²), estimated cost of pellet material (US dollars), and total amount of phosphorous (kg) and nitrogen (kg) nutrient inputs from pellet treatment(s) by spawning site type (confirmed and unconfirmed) and for all locations (total) in Swan Lake, Montana. The spatial error estimate (\pm m²) for total surface area was calculated by squaring the sum of the minimum mapping unit and horizontal accuracy of side-scan sonar. Uncertainty of quantity of pellets, cost, total phosphorous, and total nitrogen estimates was calculated using the upper and lower bounds of surface area estimates.

Site	Suitable substrate area (m ²)	Unsuitable substrate area (m ²)	Quantity of pellets (kg)	Estimated cost (US dollars)	Total phosphorous (kg)	Total nitrogen (kg)
Confirmed						
6	63,301 \pm 49	423,870 \pm 49	110,777 \pm 86	88,622 \pm 68	199.4 \pm 0.2	4,032.3 \pm 3.1
1	2,430 \pm 49	85,375 \pm 49	4,253 \pm 86	3,402 \pm 68	7.7 \pm 0.2	154.8 \pm 3.1
9	13,803 \pm 49	33,140 \pm 49	24,155 \pm 86	19,324 \pm 68	43.5 \pm 0.2	879.3 \pm 3.1
Unconfirmed						
10	30,691 \pm 49	74,908 \pm 49	53,709 \pm 86	42,967 \pm 68	96.7 \pm 0.2	1,955.0 \pm 3.1
8	5,303 \pm 49	23,384 \pm 49	9,280 \pm 86	7,424 \pm 68	16.7 \pm 0.2	337.8 \pm 3.1
7	2,020 \pm 49	23,680 \pm 49	3,535 \pm 86	2,828 \pm 68	6.4 \pm 0.2	128.7 \pm 3.1
4	0	59,198 \pm 49	0	0	0	0
2	0	45,908 \pm 49	0	0	0	0
3	0	34,300 \pm 49	0	0	0	0
5	0	34,100 \pm 49	0	0	0	0
Total	117,548 \pm 49	837,863 \pm 49	205,709 \pm 86	164,567 \pm 68	370.4 \pm 0.2	7,487.9 \pm 3.1

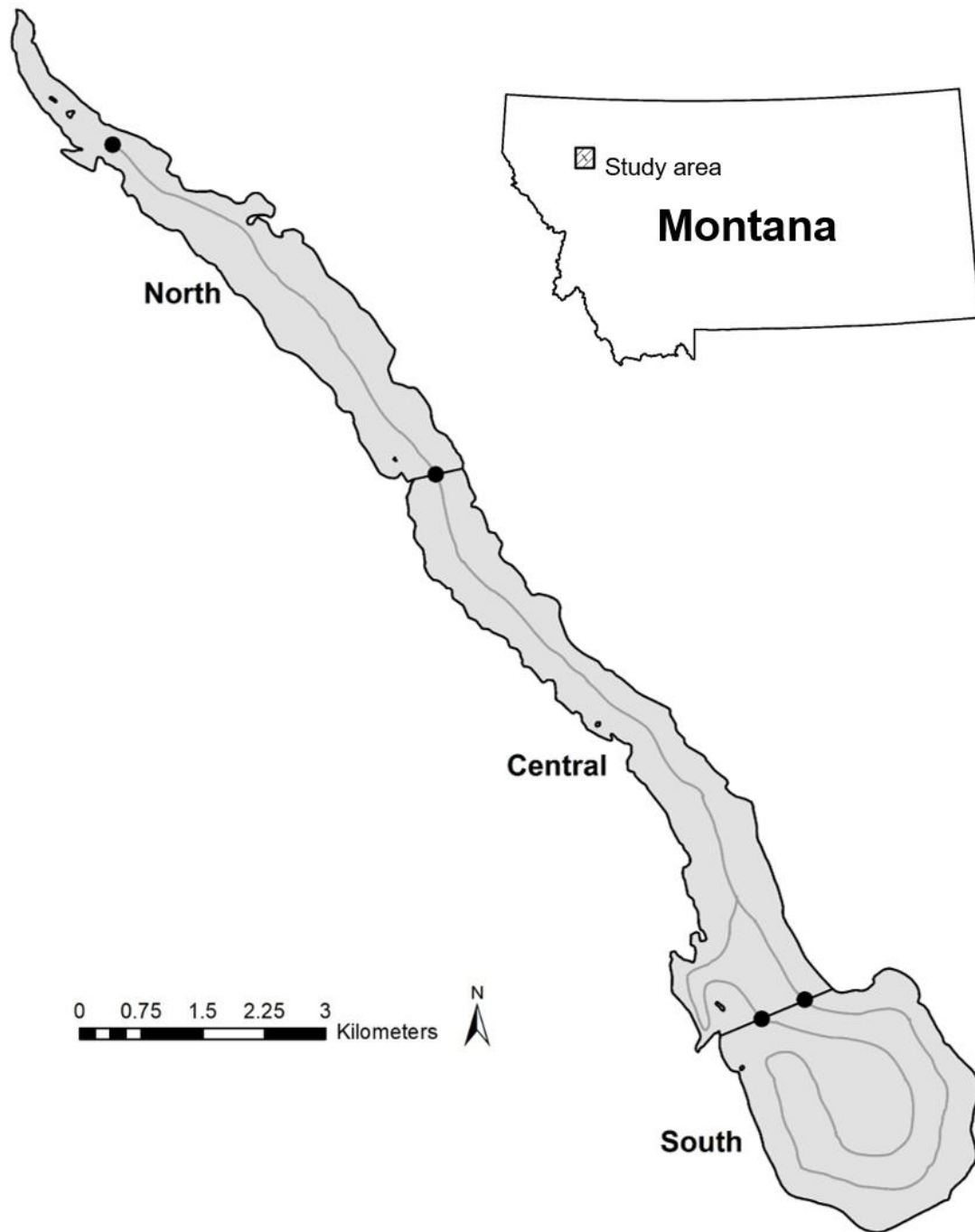
Figures

Figure 1. Map of Swan Lake, Montana. Black lines delineate the three tracking regions (North, Central, and South). Grey line delineates tracking transect. Black circles are nightly starting locations.

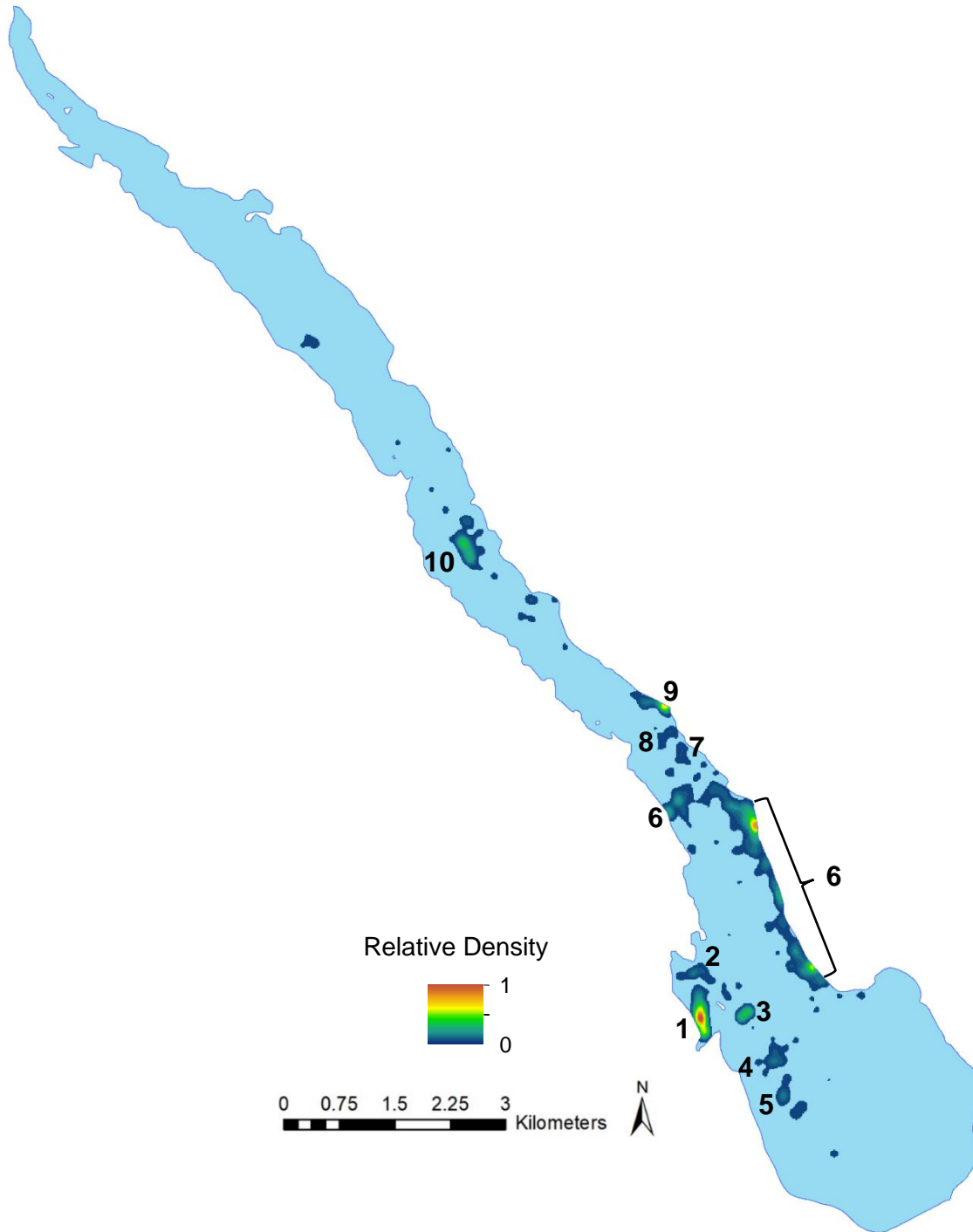


Figure 2. Kernel-density map of Lake Trout locations during September, October, and November of 2018 and 2019 in Swan Lake, Montana. Relative densities delineate Lake Trout aggregations. Unique spawning sites are numbered (1-10).

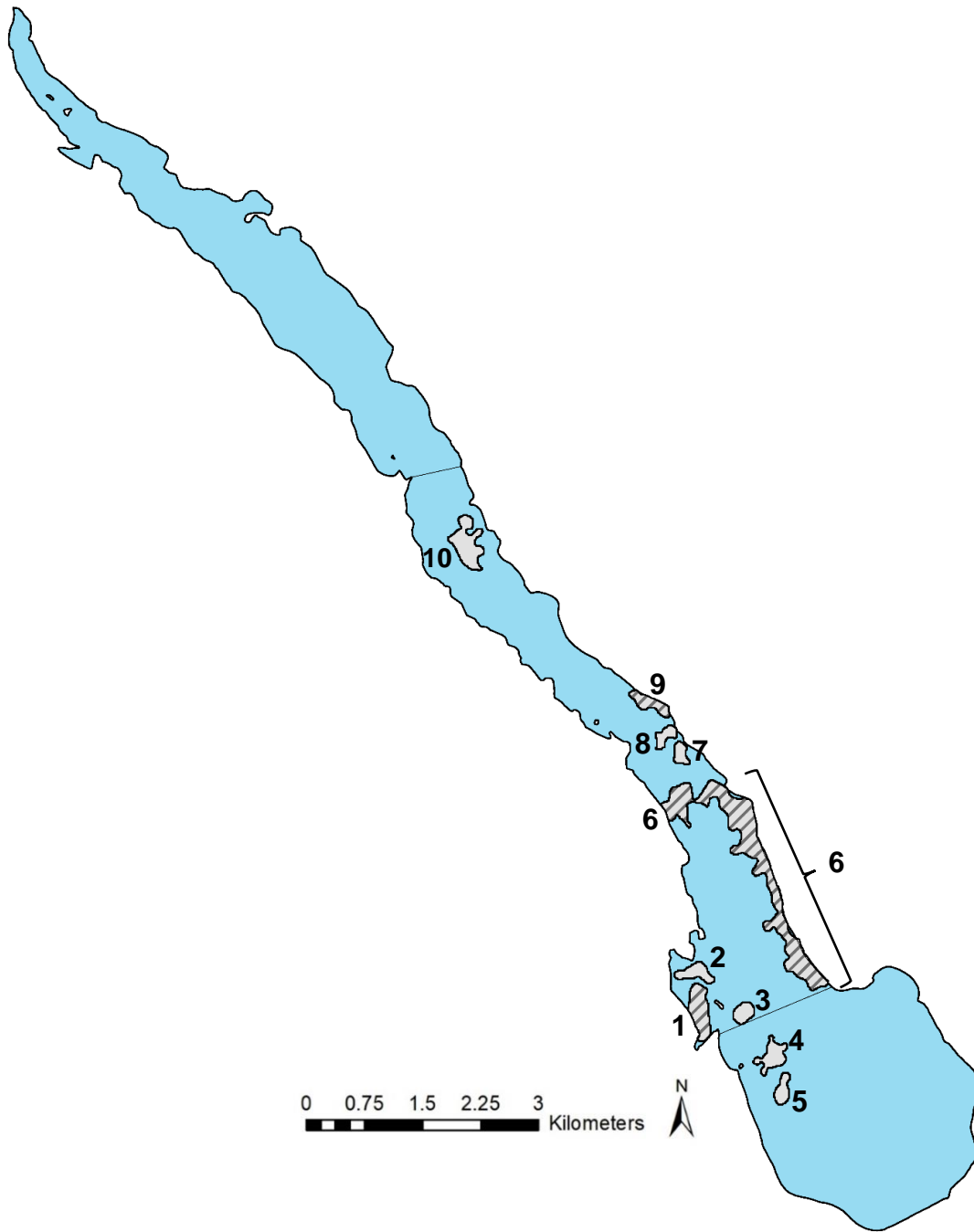


Figure 3. Map of three confirmed spawning sites (grey with crosshatch) and seven unconfirmed spawning sites (solid grey) in Swan Lake, Montana during September, October, and November of 2018 and 2019. Unique spawning sites are numbered (1-10).

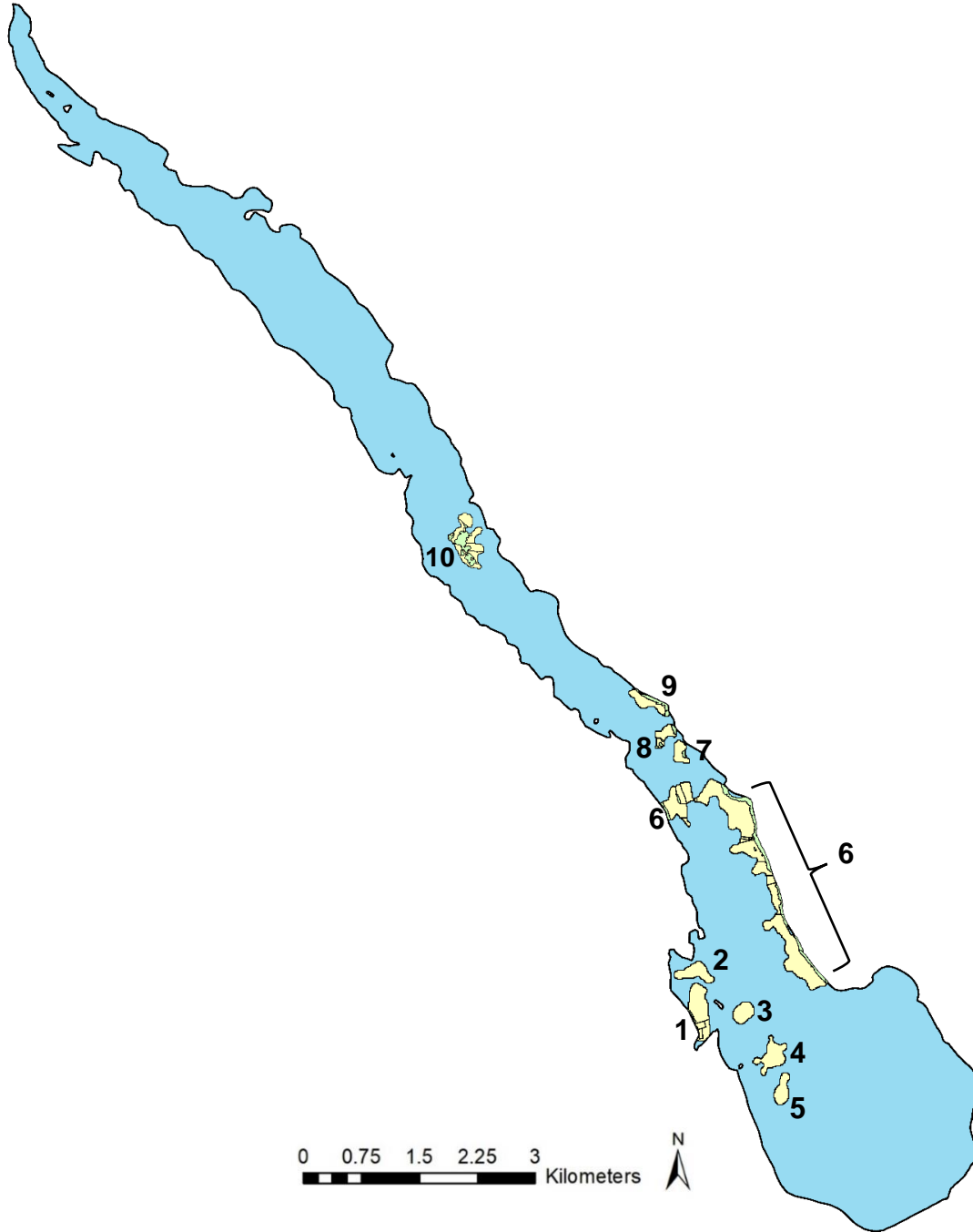


Figure 4. Substrate classification map for Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Green polygons delineate areas of unique sonar signature corresponding to cobble and rubble substrate categories. Unique spawning sites are numbered (1-10).

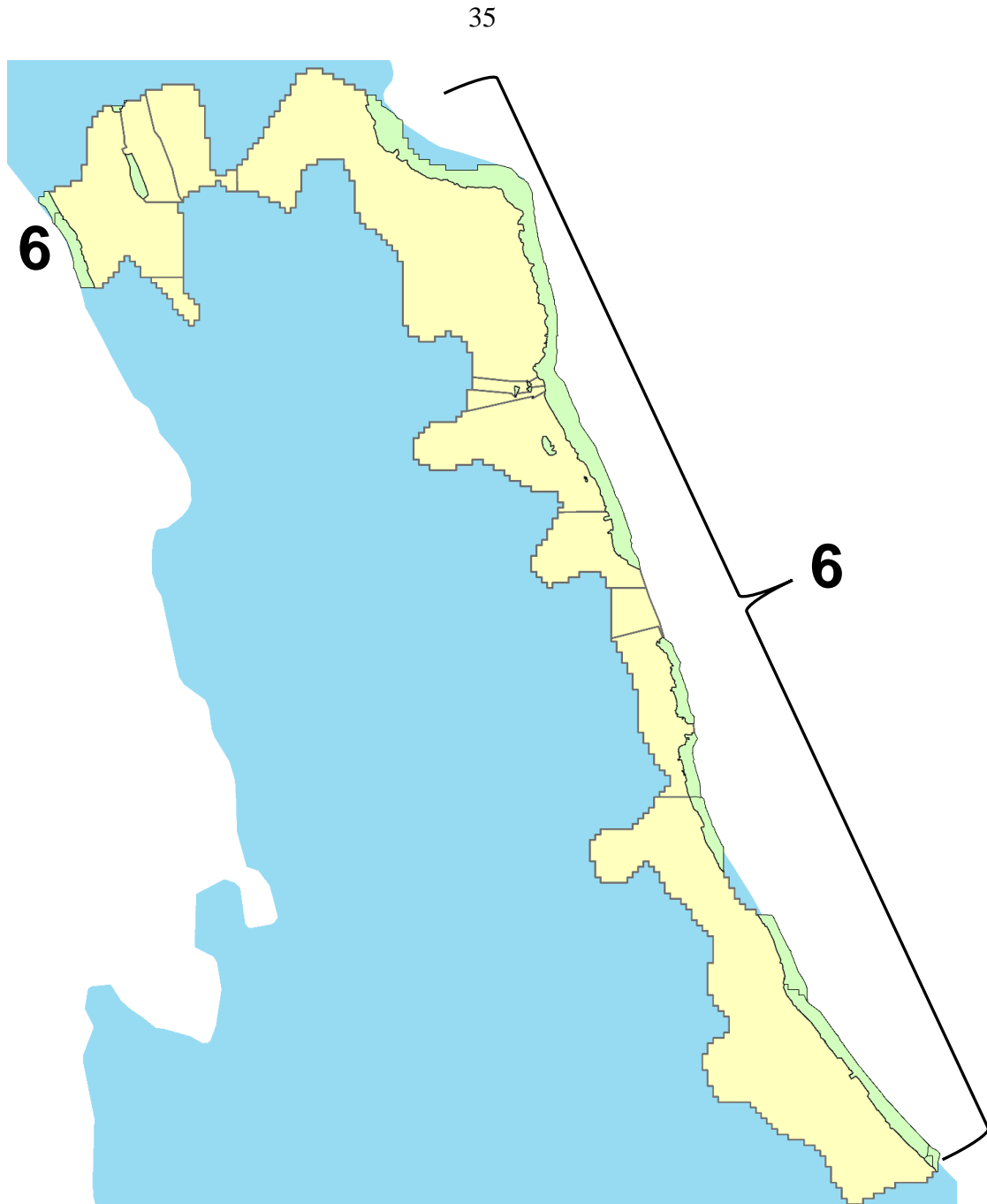


Figure 5. Substrate classification map for site 6 in the central region of Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Green polygons delineate areas of unique sonar signature corresponding to cobble and rubble substrate categories. Number indicates unique site identifier (see Figure 2).

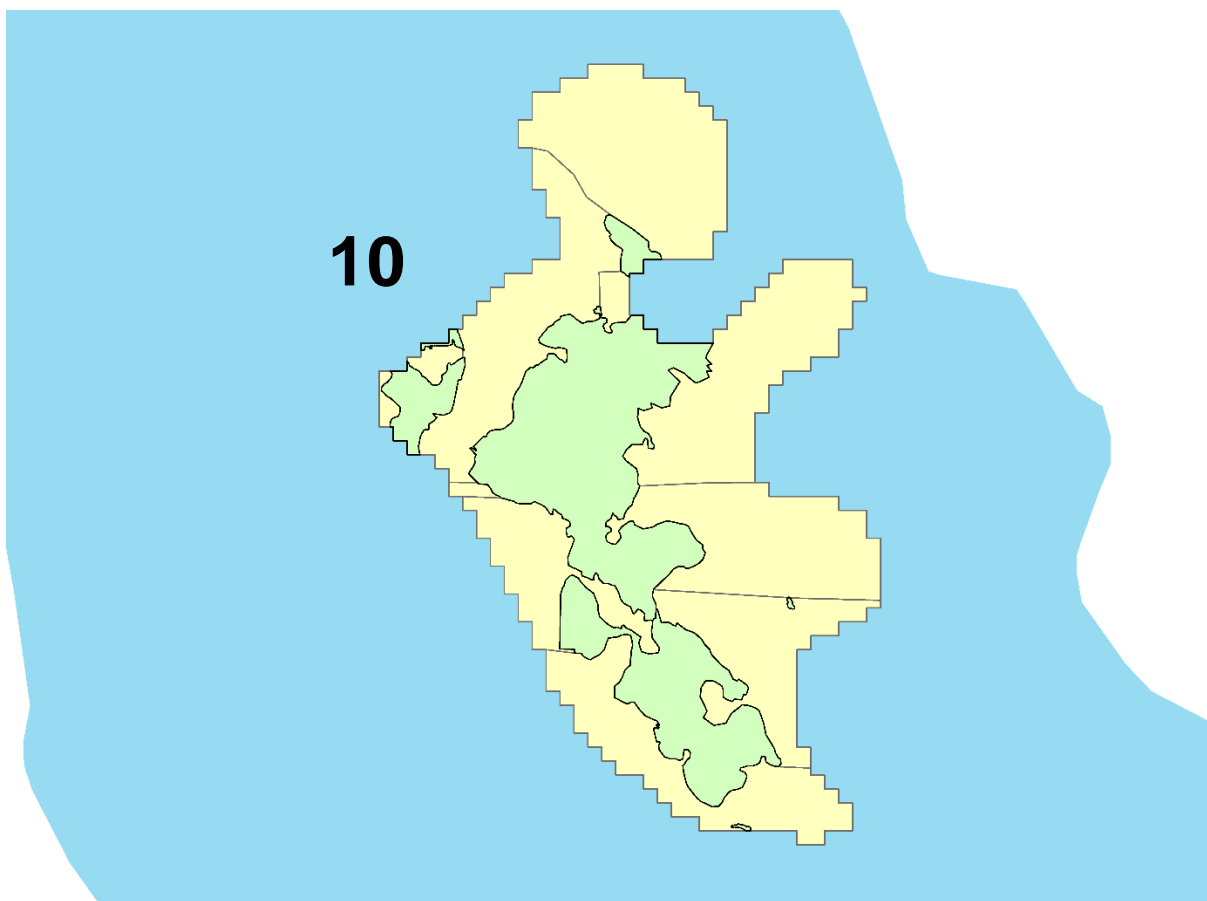


Figure 6. Substrate classification map for site 10 in the central region of Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Green polygons delineate areas of unique sonar signature corresponding to cobble and rubble substrate categories. Number indicates unique site identifier (see Figure 2).

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APPENDIX A

SWAN LAKE SIDE-SCAN SONAR

Table A.1. Error matrix of substrate assignments from side-scan sonar images (rows) and verified substrate assignments from SCUBA (columns). Substrate assignment values are the number of locations where substrate type was assigned and verified. Accuracy describes the percentage of correct substrate assignments from sonar images for each substrate type.

Substrate assignment (sonar)	Substrate assignment (verified)			Row total	Accuracy (%)
	Organic, sand, gravel	Rubble and cobble	Boulder		
Organic, sand, gravel	7	0	0	7	100
Rubble and cobble	0	14	0	14	100
Boulder	0	0	1	1	100
Column total	7	14	1	22	100

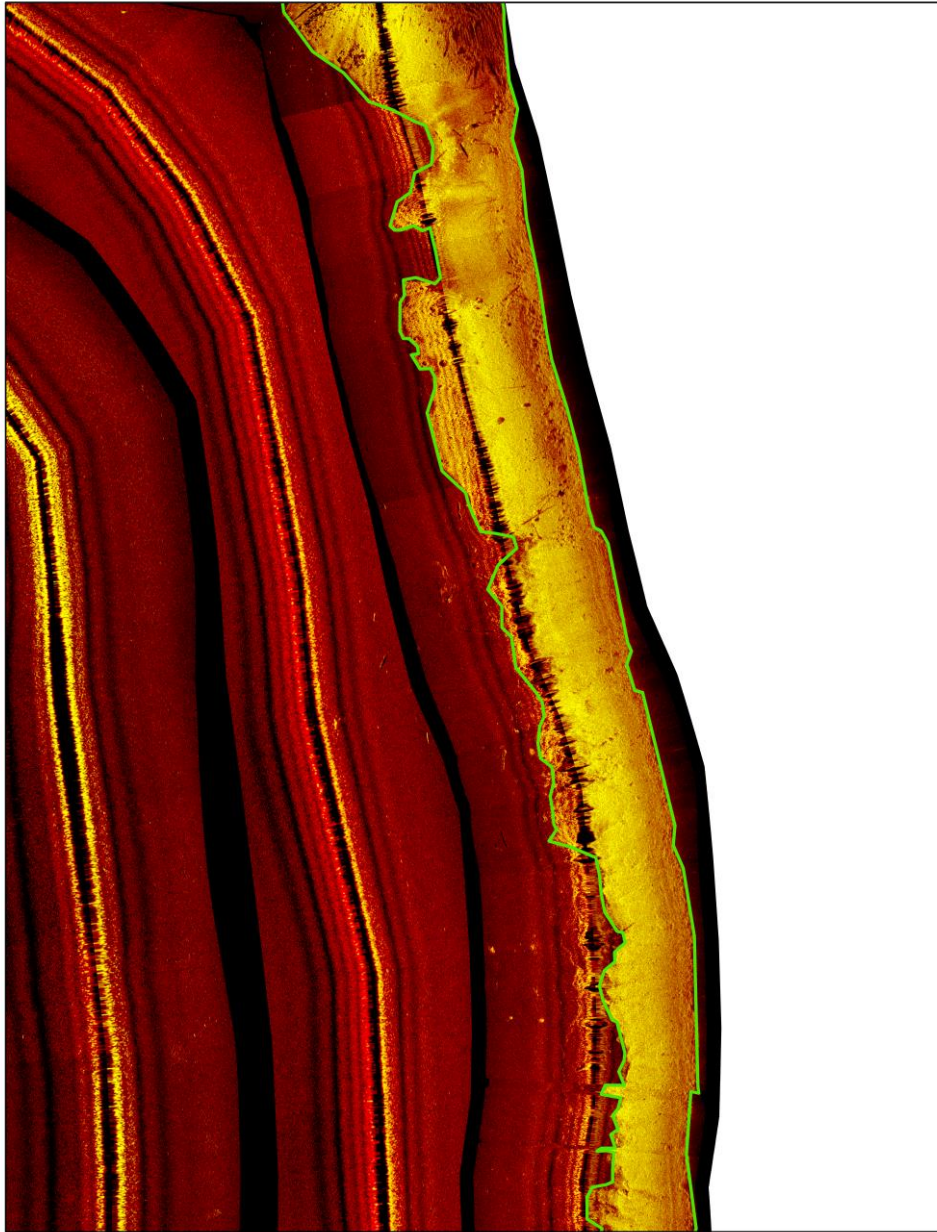


Figure A.1. Side-scan sonar imagery used to delineate suitable spawning substrate in area informed by kernel density estimation of Lake Trout relocations during September, October, and November of 2018 and 2019. Green line delineates area considered to be suitable spawning substrate.



Figure A.2. Substrate classification map for site 1 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, and grey polygons correspond to the boulder substrate category. Number indicates unique site identifier (see Figure 2).

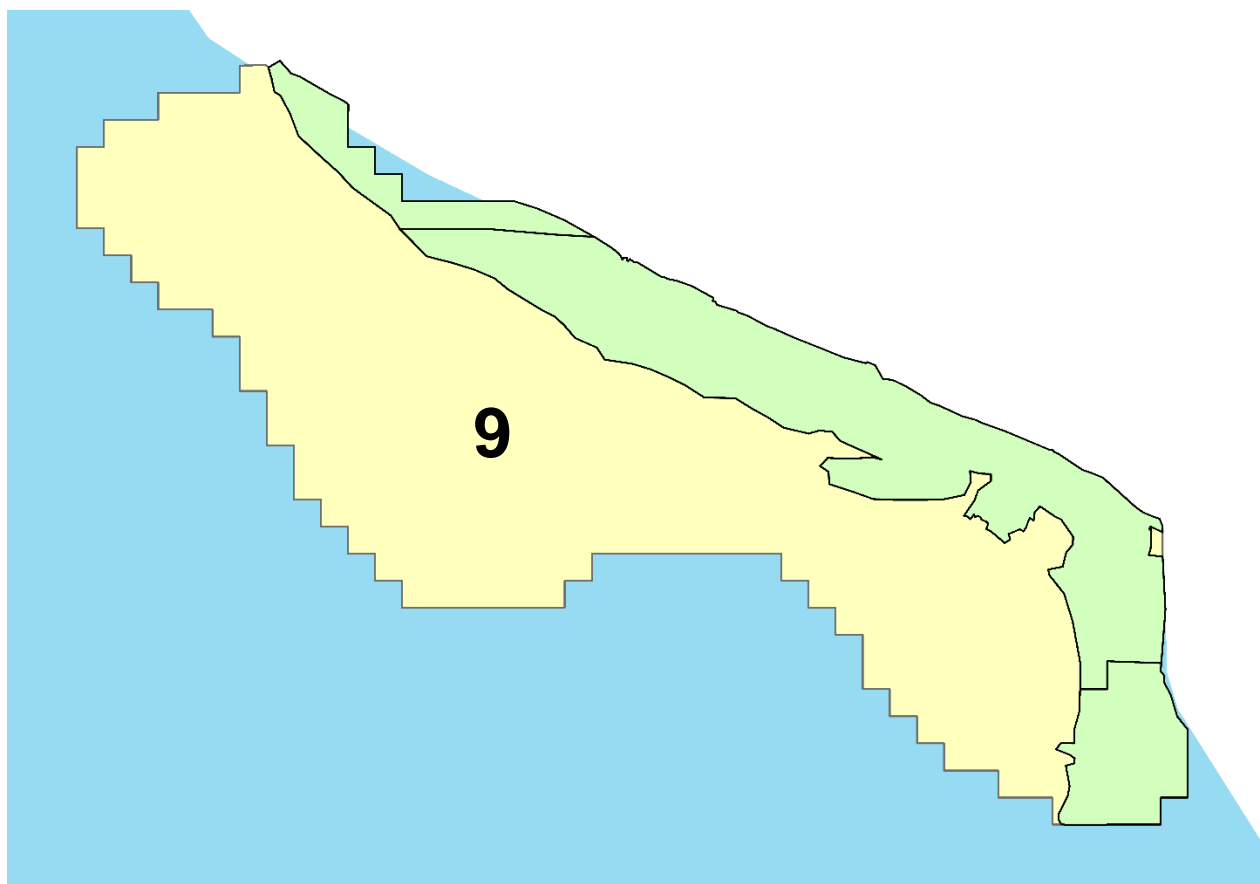


Figure A.3. Substrate classification map for site 9 in the central region of Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Green polygons delineate areas of unique sonar signature corresponding to cobble and rubble substrate categories. Number indicates unique site identifier (see Figure 2).

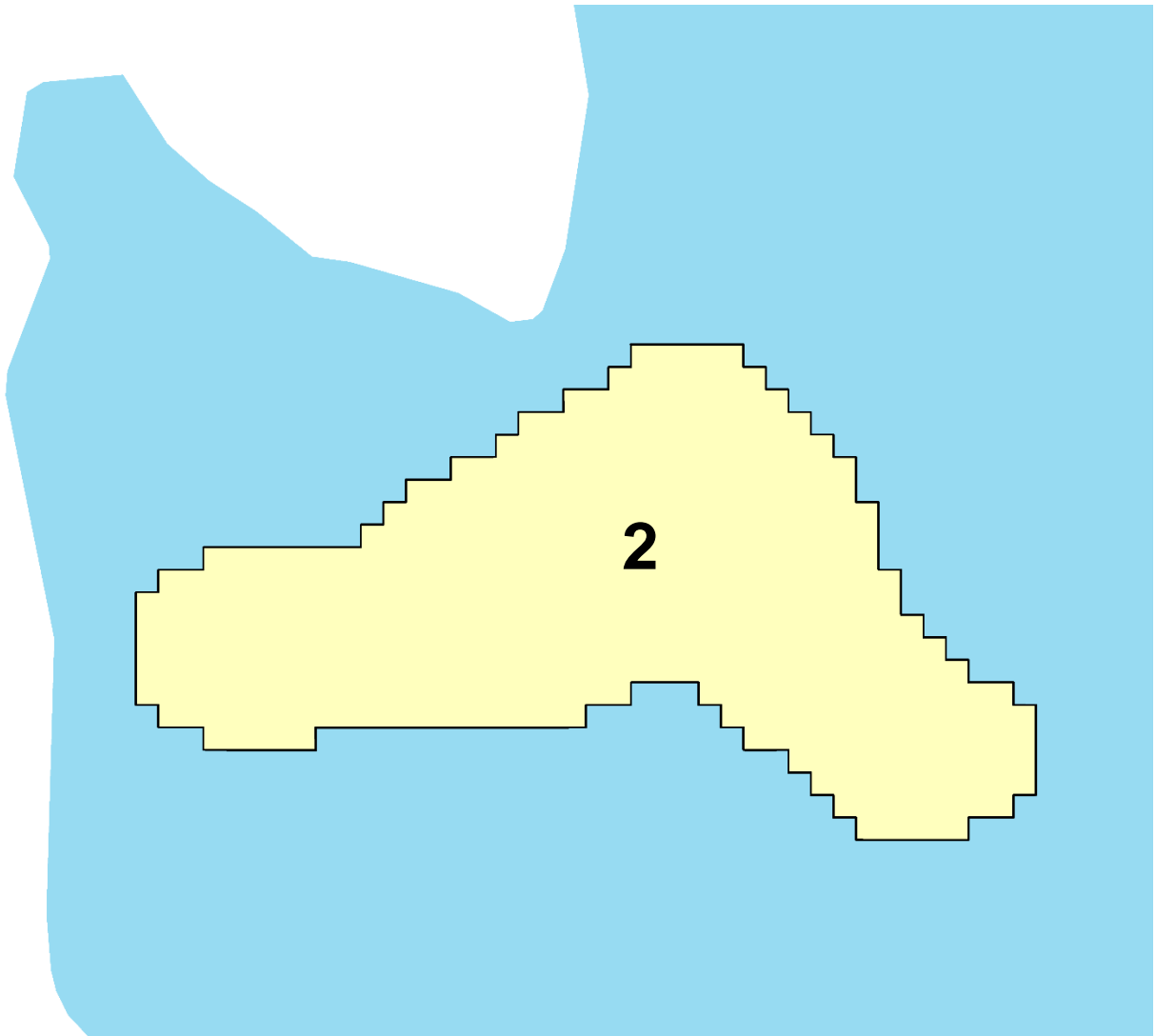


Figure A.4. Substrate classification map for site 2 in the central region of Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Number indicates unique site identifier (see Figure 2).

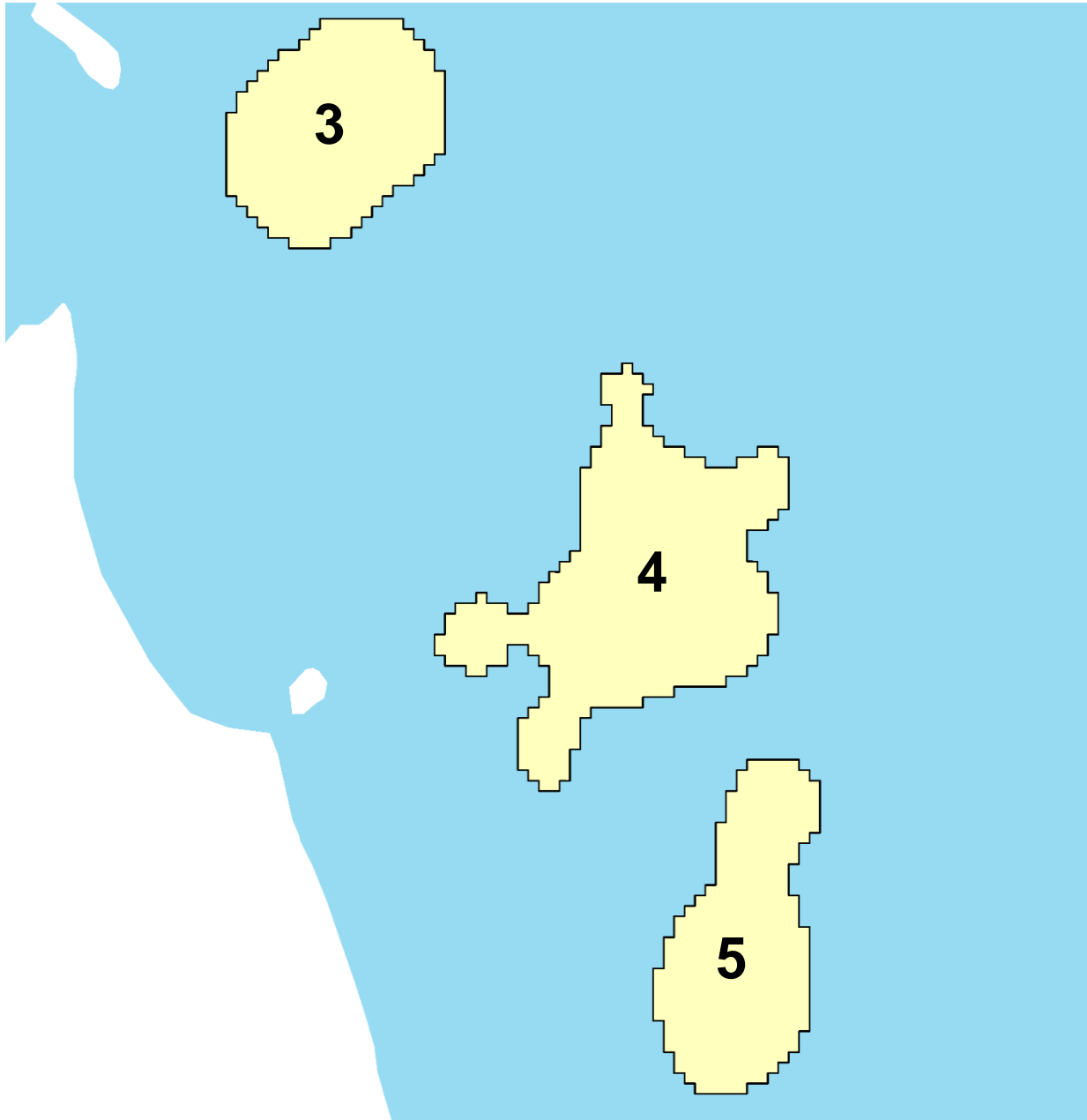


Figure A.5. Substrate classification map for site 3 in the central region, and site 4 and 5 in the south region of Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Number indicates unique site identifier (see Figure 2).

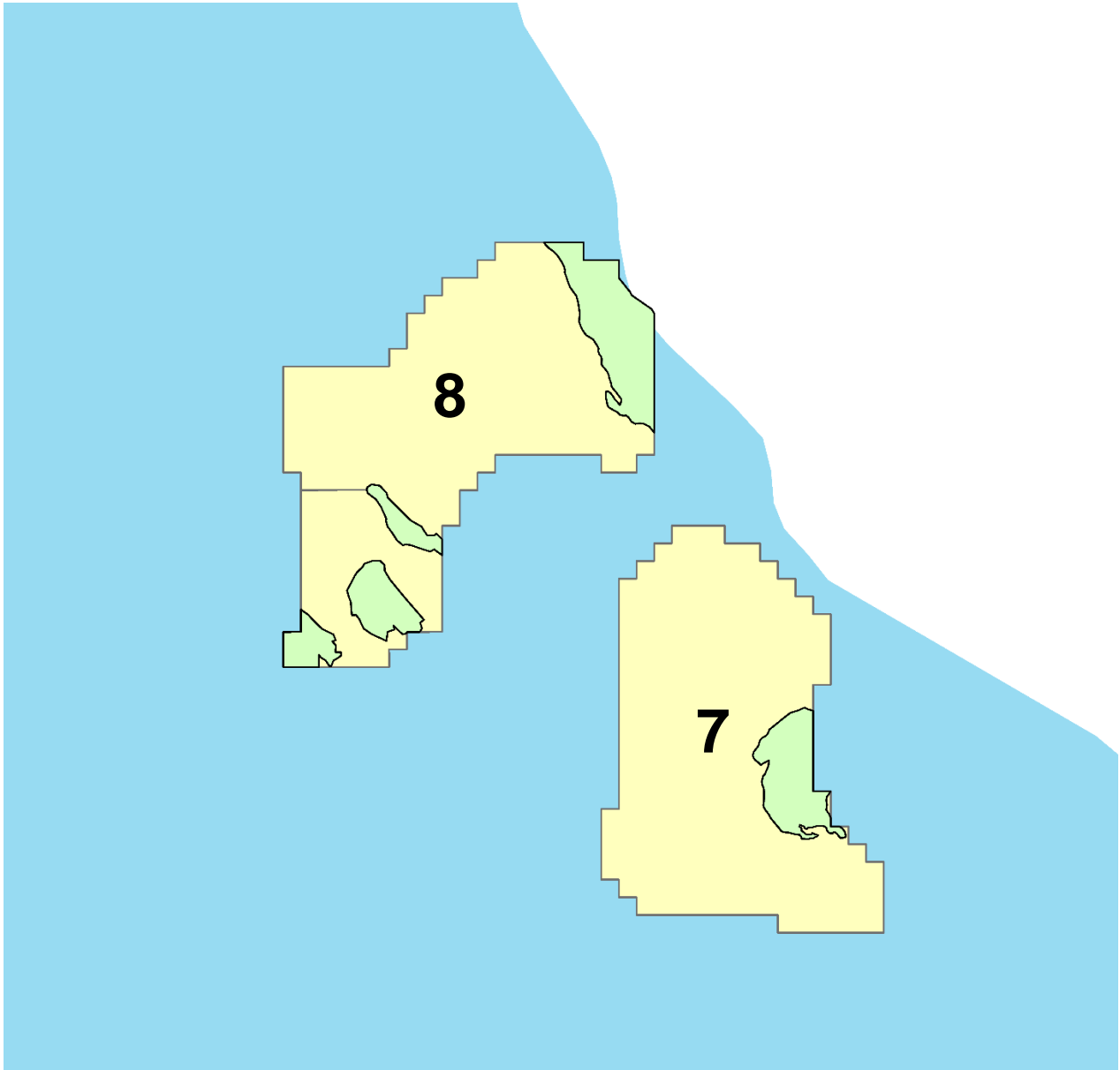


Figure A.6. Substrate classification map for site 7 and 8 in the central region of Swan Lake, Montana. Yellow polygons delineate areas of unique sonar signature corresponding to organic matter, sand, and gravel substrate categories. Green polygons delineate areas of unique sonar signature corresponding to cobble and rubble substrate categories. Number indicates unique site identifier (see Figure 2).