EVALUATION OF SUPPRESSION METHODS TARGETING NON-NATIVE LAKE TROUT EMBRYOS IN YELLOWSTONE LAKE, YELLOWSTONE NATIONAL PARK, WYOMING, USA

by

Nathan Andrew Thomas

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2017

ACKNOWLEDGMENTS

This study would not have been possible without assistance from numerous biologists and technicians. I thank Yellowstone National Park Service biologists and technicians Phil Doepke, Ben Brogie, Drew Macdonald, and Andi Puchany, and U.S. Geological Survey technician Nick Heredia who provided essential help with field work. I thank my field technicians Riley Gallagher, Aaron McGuire, and Michelle Briggs who were excellent employees, always exceeding my expectations, oftentimes in inclement weather. I thank our dive safety officer Marc Blouin who provided necessary training, equipment, and valuable advice to safely and successfully complete diving operations.

I thank my graduate committee for allowing me to develop this project, but providing direction when needed. I am beyond grateful for the mentorship and guidance of my advisor Dr. Christopher Guy. His style of advising allowed me to develop not only as a scientist but also as a person. Dr. Todd Koel was instrumental in initiating this project and provided valuable advice throughout all stages of this study. Dr. Alexander Zale provided important suggestions regarding experimental design and critical insights during the writing process. I also thank my fellow graduate students who have provided assistance on this project. Finally, I thank my family who instilled a passion for the natural word in me at a young age and have encouraged me to develop that passion into a career.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

LIST OF FIGURES – CONTINUED

Figure Page

LIST OF FIGURES – CONTINUED

Figure Page

ABSTRACT

Non-native Lake Trout *Salvelinus namaycush* threaten to extirpate native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* in Yellowstone Lake, Yellowstone National Park. Suppression of Lake Trout in Yellowstone Lake has been ongoing since 1995, primarily by gillnetting. Unfortunately, bycatch of Yellowstone Cutthroat Trout is associated with this removal method, which targets adult and subadult Lake Trout. Alternative methods effective at causing mortality in Lake Trout early life stage(s) could be used simultaneously with gillnetting to improve suppression effectiveness. The vulnerability of salmonid embryos suggest increasing Lake Trout embryo mortality is feasible and because population growth rates are sensitive to age-0 survival an effective embryo suppression method could have population-level effects. Thus, the primary objective of this study was to evaluate the efficacy of methods to increase mortality of Lake Trout embryos. *In situ* experiments tested the effect of suction dredging, electroshocking, tarping, and Lake Trout carcass deposition on embryo mortality. The secondary objective of this study was to evaluate interstitial water flow using NaCl dry injection to better understand the feasibility of using chemicals for embryo suppression. Concurrent laboratory studies have shown that Lake Trout embryos experience high mortality after chemical exposure. Tarping and suction dredging were not effective at increasing embryo mortality. Electroshocking caused 0.92 mortality of embryos at the substrate surface but only 0.38 at 20 cm depth in the substrate. Lake Trout carcass deposition caused 0.99 mortality of embryos, both at the surface and at 20 cm in the substrate. The direction and rate of interstitial water flow was not consistent and future work on a larger scale is needed to inform the feasibility of chemical suppression. Hypoxic conditions within the carcass sites may have caused embryo mortality. In addition, carbon dioxide CO_2 and hydrogen sulfide H_2S are byproducts of organic matter decomposition that harm developing salmonid embryos. Embryo suppression methods are unlikely to replace traditional Lake Trout suppression methods. However, the success of Lake Trout carcass deposition shows potential for the development of an effective additional suppression method that could be implemented on a large scale.

EVALUATING THE EFFICACY OF METHODS TO INCREASE MORTALITY OF NON-NATIVE LAKE TROUT EMBRYOS IN YELLOWSTONE LAKE

Introduction

Non-native species have contributed to the decline of native species populations worldwide, consequently altering ecosystem function and increasing extinction risk (Simberloff 2001; Levine 2008). Because of these ecological effects, the spread of non-native species has long been recognized as a leading cause of global biodiversity loss (Vitousek et al. 1996). The rate of spread of non-native species is increasing because of globalization; thus, managing ecosystems invaded by non-native species is becoming increasingly common for natural resource managers (Simberloff et al. 2005).

Non-native species have not been limited to ecosystems heavily influenced by humans such as the Great Lakes (Leach 1995). Remote ecosystems, that have experienced less anthropogenic disturbances, commonly found in nature preserves and federally protected lands have also been altered by non-native species (Bratton 1982; Tempel et al. 2004). About 6,500 non-native species are present in National Parks within the United States and many threaten native species persistence and the associated ecosystem services provided (Beissinger et al. 2017). The United States National Park Service (NPS) was created to conserve naturally functioning ecosystems for the enjoyment of current and future generations (NPS Organic Act. 1916. 16 U.S.C. 1 2 3, and 4). This ecosystem conservation mission oftentimes involves non-native species suppression and eradication, if feasible (NPS 2006).

Yellowstone Lake, Yellowstone National Park, is the largest lake above 2,000 m elevation and supports the largest population of genetically pure Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* remaining (Endicott et al. 2016). Yellowstone Cutthroat Trout provide an important link between the aquatic and terrestrial communities in the Yellowstone Lake ecosystem because they are a desirable food source for grizzly bears and osprey (Felicetti et al. 2004; Koel et al. 2005; Baril et al. 2013). In addition, Yellowstone Cutthroat Trout are of high socioeconomic value to Yellowstone Park anglers (Varley and Schullery 1995).

The Yellowstone Cutthroat Trout population of Yellowstone Lake is threatened by non-native Lake Trout *Salvelinus namaycush*, introduced into the lake in the mid-1980s from nearby Lewis Lake (Munro et al. 2005) and first discovered in Yellowstone Lake in 1994 (Kaeding et al. 1995). Yellowstone Cutthroat Trout abundance has markedly declined since the discovery of Lake Trout (Koel et al. 2015). For example, the number of spawning Yellowstone Cutthroat Trout migrating upstream in Clear Creek, a tributary to Yellowstone Lake, declined from 55,000 fish in 1988 to 500 fish in 2007 (Koel et al. 2012). In addition, Lake Trout have indirectly affected the terrestrial communities; the number of grizzly bears observed near spawning tributaries and the number of nesting osprey near the lake have declined following the reduction in Yellowstone Cutthroat Trout (Koel et al. 2005; Baril et al. 2013; Koel et al. 2017).

Lake Trout suppression in Yellowstone Lake was considered necessary to conserve Yellowstone Cutthroat Trout and the Yellowstone Lake ecosystem (McIntyre 1995). Subsequently, Yellowstone National Park initiated a Lake Trout removal program

in 1995 (Ruzycki 2004). As of November 2016, about 2.3 million Lake Trout had been removed primarily through gillnetting (Bigelow et al. 2017). Annual gillnetting effort (1 unit = 100 m of net set for 1 night) from 2001–2011 averaged 20,500 units, from 2012–2015 averaged 65,200 units, and in 2016 was increased to 79,000 units (Bigelow et al. 2017). Lake Trout catch-per-unit-effort (CPUE) generally increased indicating gill nets were being fished more effectively, Lake Trout abundance was increasing, or both (Bigelow et al. 2017). Abundance of Yellowstone Cutthroat Trout remained low compared to pre-Lake Trout levels; however, annual lake wide monitoring and visual stream surveys of spawning tributaries indicated increasing abundance in recent years (Arnold et al. 2017).

Suppression of a non-native fish through mechanical removal, such as gillnetting, from a large water body requires high effort with potential risks to non-target species (Myers et al. 2000; Franssen et al. 2014). Annual gillnetting effort at or above 63,000 units for at least the next several years was recommended to suppress Lake Trout in Yellowstone Lake (Syslo 2015). As Yellowstone Cutthroat trout abundance expectantly continues to increase the bycatch of Yellowstone Cutthroat Trout will probably increase. Evaluating additional techniques to cause Lake Trout mortality is important because of the large amount of effort and resources required for gillnetting Lake Trout and the concern about Yellowstone Cutthroat Trout bycatch. Suppression methods with limited Yellowstone Cutthroat Trout bycatch could be used simultaneously with gillnetting to increase the effectiveness of Lake Trout suppression in Yellowstone Lake.

Multiple suppression methods targeting numerous life stages of a non-native species are usually more effective than a single suppression method (Simberloff 2014). For example, the Integrated Management of Sea Lamprey *Petromyzon marinus* in the Great Lakes, arguably the most effective control program of an aquatic non-native species in the world, incorporates chemical treatments of larvae (Christie and Goddard 2003), pheromone attractants to enhance mechanical removal of adults (Johnson et al. 2009), construction of barriers to block upstream migration, release of sterile-males to reduce recruitment, and the continued exploration of alternative methods for effective suppression of Sea Lampreys (Christie and Goddard 2003). Integrated Pest Management (IPM) is a non-native species management concept that focuses on a total system approach using a variety of suppression methods that target numerous life stages of a non-native species (Lewis et al. 1997; Ehler 2006). Incorporating an IPM approach through targeting additional life stages of Lake Trout could increase suppression effectiveness.

Lake Trout spawning behavior and the physiology of Lake Trout embryos provide an opportunity for embryo suppression with limited Yellowstone Cutthroat Trout bycatch. Spawning Lake Trout congregate on rocky shoals broadcasting gametes over angular clean cobble substrate (Binder et al. 2014), and demonstrate spawning site fidelity (Esteve et al. 2008). Lake Trout embryos are nonmotile and have undeveloped physiological systems with a limited ability to acclimate to environmental perturbations (Pörtner and Farrell 2008; Helvik et al. 2009). Increasing mortality beyond the gillnetting effort is probably feasible because of the vulnerability of Lake Trout embryos.

Effective embryo suppression could have population-level effects because Lake Trout population growth rates are highly sensitive to age-0 survival rates (Syslo et al. 2011; Cox et al. 2013).

The research presented here focused on suction dredging using a placer gold mining dredge, electroshocking, and tarping spawning substrate as a benthic barrier method. The effect of suction dredging on non-native species has not previously been studied. However, suction dredging is commonly used to collect gold from the substrate of streams and lakes (Walker et al. 2015) and gold is about 20 times more dense than a Lake Trout embryo (Bonham 1976; Okubo 1987); therefore, it could be an effective method to collect and increase mortality in Lake Trout embryos. Electroshocking and tarping were based on a foundation of studies conducted on non-native species in other ecosystems. For example, electricity can cause high mortality in fish embryos (Dwyer and Erdahl 1995; Muth and Ruppert 1997) and could potentially be used for suppression of non-native fishes (Gross et al. 2015). Lake Trout embryos are large in diameter (5 mm) and are more susceptible to electroshocking induced mortality than embryos of smaller diameter such as Walleye *Sander vitreus* (Bohl et al. 2010). A mobile electroshocking grid used to electroshock spawning substrate in Swan Lake, Montana, caused > 98% mortality of Lake Trout embryos near the substrate surface (Brown et al. 2017). Tarps are an effective benthic barrier method for suffocating non-native aquatic vegetation, mussels, and clams (Ussery et al. 1997; Laitala et al. 2012). For example, about 2,000 m^2 of Lake Tahoe substrate was covered with gas-impermeable tarps causing anoxic conditions under the tarps within 72 hours, resulting in 98% mortality of Asian

Clams *Corbicula fluminea* (Wittmann et al. 2012). Lake Trout embryos are probably susceptible to suffocation because embryos incubated in 10 °C water with dissolved oxygen (DO) concentrations < 2.5 mg/L had 0% hatch success (Garside 1959). The amount of available DO is dependent on biochemical oxygen demand (BOD), which is a measure of the DO consumed through oxidation, such as decomposition of organic matter (Penn et al. 2006). Thus, gas-impermeable tarps covering organic matter on the substrate surface can be more effective at reducing DO concentration than tarps not covering organic matter (Culver et al. 2013). Organic matter in the form of Lake Trout carcasses is already present within Yellowstone Lake and readily available because of the Lake Trout removal program.

In addition to reduced DO concentrations, Lake Trout embryos are susceptible to other changes in water chemistry (Sly 1988; Mohr et al. 1990). Concurrent laboratory studies have shown Lake Trout embryos had high mortality after chemical exposure (Alex Poole, Montana State University graduate student, personal communication). Thus, chemical treatment of spawning substrate could be an effective embryo suppression method. The effectiveness of using chemicals to increase embryo mortality *in situ* is dependent on interstitial water flow because water flow rates influence chemical persistence, which would influence the exposure duration to embryos (Brown and Zale 2012).

Lake Trout life-history traits, embryo physiology, and population dynamics suggest that embryo suppression methods, when used simultaneously with mechanical removal methods (e.g., gillnetting, trapnetting, and angling) as part of an IPM strategy,

could increase the effectiveness of suppressing a non-native Lake Trout population. Thus, the primary objective of my study was to experimentally evaluate the efficacy of methods to increase mortality of non-native Lake Trout embryos. *In situ* experiments were conducted in Yellowstone Lake to test the effect of suction dredging, electroshocking, tarping, and carcass deposition on embryo mortality. A secondary objective was to evaluate interstitial water flow within Lake Trout spawning substrate to better understand the feasibility of using chemicals for embryo suppression.

Lake Trout suppression is becoming an increasingly common management practice throughout the Intermountain West (Martinez et al. 2009; Syslo et al. 2011), with gillnetting being the primary suppression method (Martinez et al. 2009; Koel et al. 2012; Rosenthal et al. 2012). Results of this research provide information regarding the feasibility of increasing mortality of Lake Trout embryos and provide a foundation for investigating the full-scale effectiveness of incorporating embryo suppression techniques to an IPM approach for Lake Trout.

Study Area

Yellowstone Lake is located in east-central Yellowstone National Park, Wyoming, within the Yellowstone River basin. At an elevation of 2,357 m, it is the largest lake above 2,000 m with a surface area of 34,020 ha, mean depth of 48 m, and maximum depth of 133 m (Kaplinski 1991). Ice typically covers the lake from mid-December to late May or early June. Water temperatures fluctuate between 9°C and 18°C in the summer (Ruzycki et al. 2003) and a thermocline develops at about 15 m

during July and August (Koel et al. 2007). The native fish assemblage comprises Yellowstone Cutthroat Trout and Longnose Dace *Rhinichthys cataractae*. Non-native fish species now present include Longnose Sucker *Catastomous catostomus*, Red Side Shiner *Richardsonius balteatus*, Lake Chub *Couesius plumbeus*, and Lake Trout (Ruzycki et al. 2003). *In situ* Lake Trout embryo suppression experiments were conducted at two confirmed Lake Trout spawning locations, Thomas Bank in Flat Mountain Arm and Carrington Island in the West Thumb (Figure 1). Hydrology experiments evaluating interstitial water flow were conducted at the Elbow, another confirmed Lake Trout spawning location, in addition to Thomas Bank (Figure 1).

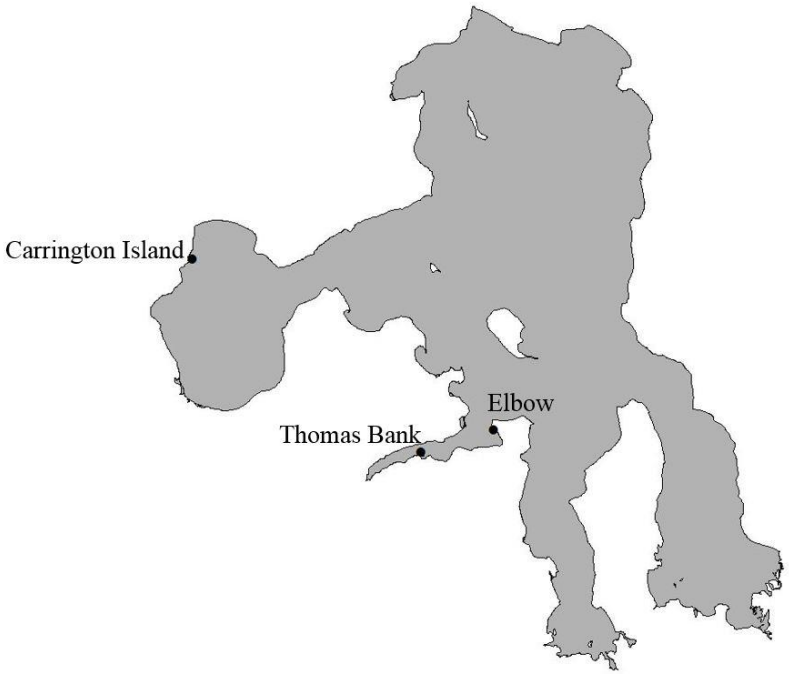

Figure 1. Locations of three confirmed Lake Trout spawning sites (delineated by black circles) in Yellowstone Lake, Yellowstone National Park. *In situ* Lake Trout embryo suppression experiments were conducted at Thomas Bank and Carrington Island. Hydrology experiments evaluating interstitial water flow were conducted at Thomas Bank and Elbow.

Methods

Suction Dredging

Cured Lake Trout eggs were used as a surrogate to Lake Trout embryos. This allowed suction dredging treatments to be conducted when Lake Trout were not spawning and no natural Lake Trout embryos were present to potentially confound results. Eggs were manually stripped by applying pressure along the abdomen in an anterior to posterior direction from sexually mature female Lake Trout in autumn 2015, cured using BorX O'Fire (Pautzke Bait Company), and frozen at -9°C until suction dredging treatments were conducted in summer 2016.

Four suction dredging treatments were conducted at Thomas Bank (Figure 1) in July 2016. Substrate from 5 to 50 cm in diameter with interstitial spaces resembling "ideal" Lake Trout spawning habitat (Wagner 1982) at water depths varying from 2.5 to 4.0 m was delineated into a sample frame (120-m long by 1-m wide). Because of limited resources, additional Lake Trout spawning sites within Yellowstone Lake were not included in the sample frame. Thus, the sample frame, as described by Hansen et al. (2007), was considered a subset of the Lake Trout spawning sites in Yellowstone Lake. Thirty 1-m by 1-m experiment sites were evenly distributed within the sample frame. Each site was outlined with yellow polypropylene rope anchored to the substrate surface.

Divers with self-contained underwater breathing apparatuses (SCUBA) placed the thawed cured Lake Trout eggs on the substrate within each site at three densities, 500 eggs/m^2 (n = 30), 1,000 eggs/m^2 (n = 30), or 2,000 eggs/m^2 (n = 18). To evaluate retention of eggs within experiment sites prior to suction dredging, eggs were placed on

the substrate within a mesh egg bag in addition to the experiment sites. Mesh egg bags consisted of a 29-cm diameter (surface area 0.067 m^2) polyvinyl chloride ring with a 50-cm-deep nylon-mesh netting (0.16 cm bar measure), similar to the mesh egg bags used to estimate Lake Trout deposition and survival (see Figure 1 in Perkins and Krueger 1994). Egg bags were deployed in the sample frame by excavating a 40- to 50-cm deep hole, placing the bag in the hole and back filling with the removed susbtrate. Three egg bags were deployed and eggs were placed within each bag at the same egg density that was in experiment sites for each treatment. Egg bags were collected from the sample frame immediately prior to conducting suction dredging treatments and the number of eggs remaining in each egg bag were counted. The proportion of eggs remaining was calculated by dividing the number of eggs remaining by the number of eggs placed.

Each site was suction dredged for 60 seconds the day following egg placement. An additional 30 sites with 500 eggs/m^2 were suction dredged for 120 seconds to evaluate a longer duration. Suction dredging was conducted from a boat directly above each site and consisted of moving the weighted nozzle end of a 10-cm diameter hose along the substrate surface within each site. A Keene model 6000 placer gold mining dredge powered by a 23-horsepower Vanguard engine pumped water through an intake hose and out an outflow hose creating suction at the nozzle end of a 10-cm diameter hose connected to the outflow hose. Maximum water velocity at the suction intake was 2.01 m/sec and maximum outflow discharge was 0.04 m^3/sec. Discharge from the outflow hose was directed over a mesh screen separating larger diameter substrate from the eggs.

The dependent variable was the proportion of eggs collected at each site and was calculated by dividing the number of eggs collected by the number of eggs placed at each site, which were the experimental units (replicates). The efficacy of suction dredging Lake Trout embryos from the substrate was estimated by calculating the mean proportion collected by treatment and the associated standard deviation.

Electroshocking

Lake Trout Gamete Collection, Fertilization, and Incubation. Eggs and milt were collected from sexually mature Lake Trout caught in NPS gill nets. Live fish were removed from gill nets and placed in tanks filled with lake water. Egg collection and fertilization methods followed Billard and Jensen (1996). Multiple female Lake Trout were blot dried and eggs were stripped into a dry container by applying pressure along the abdomen in an anterior to posterior direction. Milt was collected from multiple male Lake Trout using the same methods and gently mixed with the eggs using a turkey feather. Lake water was added to the gametes to activate the milt and promote fertilization. Embryos were incubated at 9°C in Living Stream (Frigid Units Inc.) recirculating tanks until initiation of electroshocking experiments.

Electroshocking experiments were conducted on September 21, September 29, and October 5, 2015, at Thomas Bank (Figure 1). Methods for sample frame delineation and site selection and delineation were the same as described in the suction dredging section (see above). Three 3.0-m by 6.1-m treatment sites and three 3.0-m by 6.1-m

control sites were evenly distributed within a 100-m long by 3-m wide sample frame at water depths varying from 0.33 to 1.00 m.

Live Lake Trout embryos were placed in rigid non-conductive 3-mm (bar measure) polyethylene mesh baskets that measured 5 x 5 x 1 cm. Baskets containing embryos were placed at the sites 24 h prior to experimental treatment (Brown et al. 2017). Embryo baskets were transported by boat to experiment sites at Thomas Bank in containers filled with 9°C water, similar to the water temperature in Yellowstone Lake. Lake Trout embryos are transparent orange when alive and turn opaque white when dead (Casselman 1995). Embryos were categorized as live or dead based on embryo color. Live embryos within each basket were counted, and 30 baskets were positioned in each site in the substrate at depths of 0 cm (surface), 20 cm, or 40 cm by SCUBA divers (10 baskets per depth).

The mobile electroshocking grid was similar to the one used by Brown et al. (2017) in Swan Lake, however, the grid used in this study did not have a hinge in the middle and was slightly smaller (3.0 m by 6.1 m) (see Figure 4 in Brown et al. 2017). The grid contained ten vinyl-coated 3.18-mm-diameter stainless steel cables running lengthwise inside of a fiberglass frame measuring 3.0 m by 6.1 m. Each lengthwise cable had a series of 15.2-cm long vinyl-coated 1.6-mm-diameter stainless steel cable droppers extending ventrally perpendicular from the lengthwise cables. Each dropper had a 2.54-cm long by 0.95-cm diameter stainless steel cylinder soldered at the cable end. The grid was electrified using a 7,500-W Smith-Root 7.5 Generator Powered Pulsator electrofishing shock box powered by a 10,000-W generator. The shock box output 1,000

V of pulsed direct current to a power switch box, which was used to set each of the ten lengthwise cables as an anode, cathode, or off, thus directing the current to selected cables within the grid.

Twenty-four hours after placing embryos in the substrate, the mobile electroshocking grid was positioned on the substrate surface within each site and electrified at treatment sites and not electrified at control sites (Brown et al. 2017). Electrodes on two adjacent cables (one anode and one cathode) were electrified with 1,000 V of pulsed direct current for 40 s while the other eight cables were switched to off and not electrified. Each cable was the anode for 20 s and the cathode for 20 s, allowing the electrical current to travel in both directions, potentially producing more complete electrical field coverage across the irregular substrate than would a unidirectional current. This process continued until all cables had been electrified. Embryo baskets were collected 24 h after the electroshocking treatment.

The number of live embryos was recorded post-treatment by depth in each site. The dependent variable was the proportional embryo mortality by depth for each control site (n=3) and treatment site (n=3), which were the experimental units (replicates). Proportional mortality was calculated by dividing the number of live embryos post-treatment by the number of live embryos pre-treatment and subtracting the proportional survival from one.

Three experiments were conducted at the same experiment sites using embryos two-days post fertilization (18 degree-days (1°C for 24 h = 1 degree-day)), eight-days post fertilization (72 degree-days), and twenty-two-days post fertilization (198 degree-

days). Two-way analysis of variance (ANOVA) was used to test for differences in proportional embryo mortality by treatment and depth ($\alpha = 0.05$) at each age. Ages were analyzed separately because they were treated on different days. A Tukey-Kramer test was used for multiple comparisons among depths and between treatments and controls.

Tarping

Tarping experiments were conducted at Carrington Island (Figure 1) from September 16, 2015 to October 14, 2015. Methods for sample frame delineation and site selection and delineation were the same as described in the suction dredging section (see above). Three 3-m by 3-m treatment sites and three 3-m by 3-m control sites were evenly distributed within a 30-m long by 3-m wide sample frame at water depths varying from 1 to 2 m. Methods for Lake Trout gamete collection, egg fertilization, and embryo incubation were the same as described in the Lake Trout gamete collection, fertilization, and incubation section (see above). Methods for categorizing live and dead embryos were the same as described in the electroshocking section (see above).

Plastic grid incubators (Dr. Ellen Marsden University of Vermont, personal communication) were used to hold Lake Trout embryos in the substrate within the experiments sites. Each incubator consisted of a 12-cm by 20-cm by 1.5-cm plastic grid panel containing 50 separate cells, each holding a single embryo. Cells were enclosed on both sides by fiberglass window screen mesh (1-mm bar mesh), which was secured in place by two thinner plastic grid panels (12 cm by 20 cm by 0.75 cm) each positioned on either side of the middle panel and bound together using cable ties.

Twenty-four hours before placing Lake Trout embryos at experiment sites, 50 live Lake Trout embryos two-days post fertilization (18 degree-days) were placed into each incubator. Incubators were transported by boat to experiment sites at Carrington Island in containers filled with 9°C water, similar to the water temperature in Yellowstone Lake. The number of pre-treatment live embryos was recorded for each incubator. Within each experiment site, eight incubators were positioned perpendicular to the substrate surface with the top of the incubator at the substrate surface and the bottom of the incubator 12 cm in the substrate. To account for a possible edge effect within treatment sites, four incubators were positioned at the center and four incubators were positioned at the edge. Dissolved oxygen (mg/L) and water temperature (°C) were recorded using a miniDOT logger (Precision Measurement Engineering) placed on the substrate surface in the center of one control site and one treatment site. Treatment sites were covered with a 1.143-mm thick ethylene propylene diene monomer (EPDM) gas-impermeable tarp anchored to the substrate, control sites were uncovered.

Incubators were collected on October 14, 2015. The number of live embryos in each incubator was recorded. Proportional embryo mortality in each incubator (subsample) was calculated by dividing the number of live embryos post-treatment by the number of live embryos pre-treatment and subtracting the proportional survival from one. The dependent variable was the mean proportional mortality of the eight incubators in each control site (n=3) and treatment site (n=3), which were the experimental units (replicates). Two sample t-test was used to test for a difference in mean proportional mortality between treatment and control ($\alpha = 0.05$).

Carcass Deposition

Carcass deposition experiments were conducted at Thomas Bank from September 21, 2016 to October 7, 2016 and at Carrington Island from September 22, 2016 to October 17, 2016 (Figure 1). Methods for sample frame delineation and site selection and delineation were the same as described in the suction dredging section (see above). Twelve 3-m by 3-m treatment sites and six 3-m by 3-m control sites were evenly distributed within a 120-m long by 3-m wide sample frame at Thomas Bank at water depths varying from 1.5 to 3.0 m. Three control sites and six treatment sites were evenly distributed within a 30-m long by 10-m wide sample frame at Carrington Island at water depths varying from 0.33 to 1.00 m. Methods for Lake Trout gamete collection, egg fertilization, and embryo incubation were the same as described in the Lake Trout gamete collection, fertilization, and incubation section (see above). Methods for categorizing live and dead embryos were the same as described in the electroshocking section (see above).

The same type of incubator described in the tarping section (see above) was used for the carcass experiments except the plastic grid panels were bolted together using stainless steel bolts and locking washers instead of cable ties. Twenty-four hours before placing Lake Trout embryos at experiment sites, 46 live and 4 dead Lake Trout embryos were placed into each incubator. Dead embryos were placed in the four corners of each incubator to determine if a dead embryo would completely decompose by the end of the experiments because during the tarping experiments embryos were missing from incubators and it was unknown if they died and decomposed completely or remained

alive but were not retained in the incubators. Embryos one-day post fertilization (9 degree-days) where loaded into incubators for Thomas Bank and three-days post fertilization (27 degree-days) for Carrington Island.

Incubators were transported by boat to experiment sites in containers filled with 9°C water, similar to the water temperature in Yellowstone Lake. The number of live embryos pre-treatment was recorded in each incubator, and eight incubators (four incubators per depth) were positioned in the substrate at 0 cm (surface) and 20 cm at each site. Lake Trout embryos were placed at Thomas Bank on September 15, 2016 and at Carrington Island on September 16, 2016. Dissolved oxygen concentration (mg/L) and water temperature (°C) were recorded using a miniDOT (Precision Measurement Engineering) logger placed on the substrate surface in the center of two control sites, two treatment sites to be covered with carcasses, and two treatment sites to be covered with carcasses and a gas-impermeable tarp at Thomas Bank, and one control site, one treatment site to be covered with carcasses, and one treatment site to be covered with carcasses and a gas-impermeable tarp at Carrington Island.

Lake Trout carcasses collected from NPS and contractor gill nets were deposited on the substrate from a boat positioned above each treatment site on September 19 and 20, 2016 at Thomas Bank and on September 21, 2016 at Carrington Island. Lake Trout carcasses were evenly distributed to achieve a biomass density of 28 kg/m^2 on the substrate surface within each treatment site on September 21, 2016 at Thomas Bank and on September 22, 2016 at Carrington Island. Half of the treatment sites (carcass-tarp)

were covered with a 1.143-mm thick gas-impermeable EPDM rubber tarp anchored to the substrate.

Incubators were collected from experiment sites on October 7, 2016 at Thomas Bank and on October 17, 2016 at Carrington Island. The number of live embryos in each incubator was recorded. Proportional embryo mortality in each incubator (subsample) was calculated by dividing the number of live embryos post-treatment by the number of live embryos pre-treatment and subtracting the proportional survival from one. The dependent variable was the mean proportional mortality calculated by depth for each control, carcass, and carcass-tarp site (Thomas Bank, n=6; Carrington Island, n=3), which were the experimental units (replicates). Two-way ANOVA was used to test for differences in embryo mortality by treatment and depth ($\alpha = 0.05$) at each location. A Tukey-Kramer test was used for multiple comparisons among depths and between treatments and controls.

Substrate-Biofilm Production. The short-term effect of carcass deposition on productivity was evaluated by comparing the change in area density of substrate biofilm dry biomass—before and after carcass treatments (Steinman et al. 2006). On September 8, 2016 one pre-treatment rock about 10-cm diameter was collected from each experiment site at Thomas Bank and Carrington Island. One post-treatment rock about 10-cm diameter was collected from each experiment site on October 11, 2016 at Thomas Bank and on October 17, 2016 at Carrington Island. For each rock, the biofilm was scraped from the rock surface, mixed with deionized water to form a homogenized slurry, and a sub-sample of the slurry was filtered through a pre-weighed Whatman GF/F (0.7

μm pore size) glass-fiber filter and dried for 24 hours at 105°C. Sub-sample biofilm dry biomass was obtained by weighing each filtered sample to the nearest 0.1 mg and subtracting the pre-filter weight. The sub-sample biofilm dry biomass was extrapolated to the original volume of the homogenized slurry to obtain a total biofilm dry biomass. Rock surface area (cm^2) was estimated using the foil method (Morin 1987) and area density of substrate biofilm dry biomass (g/cm^2) was obtained by dividing the total biofilm dry biomass by the rock surface area. The change in area density of substrate biofilm dry biomass at each experiment site was obtained by subtracting the post-treatment measurement from the pre-treatment measurement. The change in area density of substrate biofilm dry biomass was compared between the carcass and carcass-tarp treatments and the control using a paired *t*-test with an alternative hypothesis (change in biofilm biomass > 0) because it was assumed change would be greater in the treatments than the control.

Hydrology

Four littoral-zone hydrology experiments were conducted using NaCl dry injection (Hudson and Fraser 2005) in autumn 2016. One experiment was conducted at the Elbow and three experiments were conducted at Thomas Bank (Figure 1). Four conductivity loggers were positioned 0.67 m and four at 1.34 m from an injection point, one in each direction (i.e., north, south, east, west). During the first experiment only seven loggers were available so no logger was positioned 1.34 m south of the injection point towards shore. Conductivity loggers were buried at 20 cm in the substrate. Dry granular NaCl was injected at 20 cm in the substrate. Twenty-four hours after injecting

NaCl conductivity loggers were collected from the substrate. Loggers recorded conductivity in µS/cm in 60 s increments and average conductivity every five minutes. For the first experiment 500 grams of NaCl were injected and for the second, third, and fourth experiments 1,000 grams of NaCl were injected. The mass of NaCl was increased to increase conductivity measurements above the baseline conductivity, thus, providing a stronger signal to detect the direction and rate of water flow. Time at peak conductivity at 0.67 m from the injection point was subtracted from time at peak conductivity at 1.43 m from the injection point in each direction. The distance between the loggers (0.67 m) was divided by the time interval to estimate flow rate by direction.

Results

Suction Dredging

The proportions of eggs collected were low for all egg density and suction dredging duration treatments. Mean proportion collected was 0.05 (0.08 SD) when suction dredging occurred for 60 seconds/m^2 at an egg density of 500 eggs/m^2 (Figure 2). Proportion collected increased at the higher egg densities with a maximum mean proportion collected of 0.27 (0.22 SD) at an egg density of 1000 eggs/m^2 (Figure 2). Mean proportion of eggs collected increased to 0.16 (0.17 SD) when suction dredging occurred for 120 seconds/m^2 at 500 eggs/m^2 (Figure 3). Mean proportion of eggs remaining in egg bags when suction dredging treatments were initiated varied between 0.65 (0.10 SD) for 2,000 eggs/m^2 to 0.83 (0.15 SD) for 500 eggs/m^2.

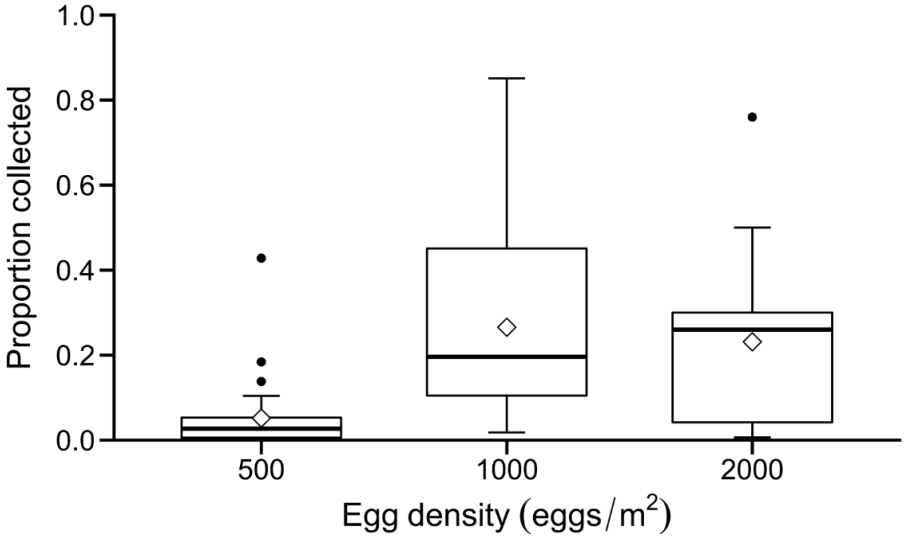

Figure 2. Proportion of cured Lake Trout eggs collected after suction dredging substrate for 60 seconds/m^2 at Thomas Bank, Yellowstone Lake, Yellowstone National Park during July 2016. Each site (1 m x 1 m) was seeded with 500 eggs/m^2 (left boxplot: n=30), 1,000 eggs/m^2 (middle boxplot: n=30), or 2,000 eggs/m^2 (right boxplot: n=18). The horizontal line delineates the median, the open diamond delineates the mean, the box represents the 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles, and dots represent outliers.

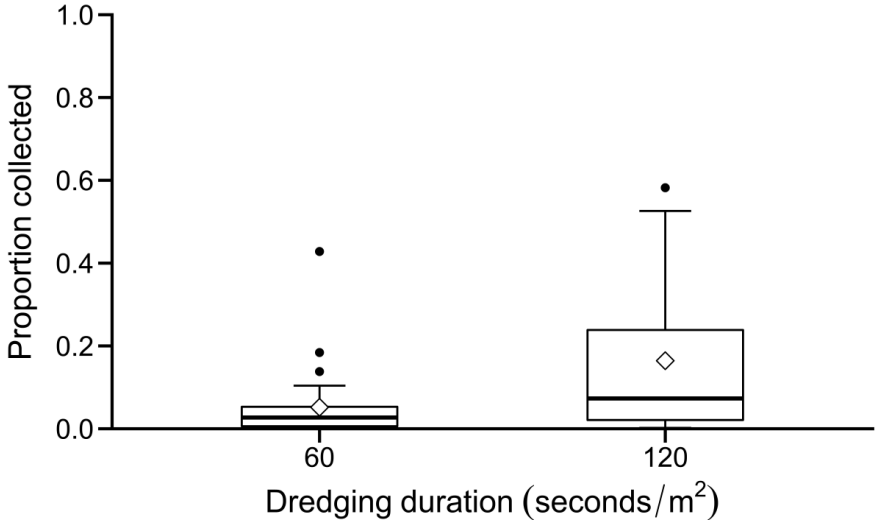

Figure 3. Proportion of cured Lake Trout eggs collected after suction dredging substrate seeded with 500 eggs/m^2 at Thomas Bank, Yellowstone Lake, Yellowstone National Park during July 2016. Each site (1 m x 1 m) was dredged for 60 seconds/m^2 (left boxplot: n=30) or 120 seconds/m^2 (right boxplot: n=30). The horizontal line delineates the median, the open diamond delineates the mean, the box represents the 25th and 75th percentiles, whiskers represent the 10th and 90th percentiles, and dots represent outliers.

Electroshocking

Mortality of embryos of all ages increased as substrate depth increased; mortalities in the 40-cm treatments were similar to those of controls (Figure 4). Mean proportional mortality was higher than 0.83 at the 0-cm treatment and decreased to less than 0.08 at the 40-cm treatment (Figure 4). Mean proportional mortalities in the controls were similar among all depths varying from 0.01 to 0.25 (Figure 4). Strong evidence supported a treatment by depth interaction for two-day post-fertilization embryos (18 degree-days) (ANOVA: $F_{2, 18} = 8.13$, $P = 0.006$), eight-day post-fertilization embryos (72 degree-days) (ANOVA: $F_{2, 18} = 12.84$, $P = 0.001$), and twenty-two-day post-fertilization embryos (198 degree-days) (ANOVA: $F_{2, 18} = 38.94$, $P < 0.001$), indicating the treatment effect of electroshocking was influenced by depth (Figure 4).

The effect of depth was consistent for two-day (18 degree-days) and eight-day (72 degree-days) post-fertilization embryos (Figure 4, panels A and B). Embryos in the 0-cm treatment had higher mortality than the 20-cm and 40-cm treatments and controls (Figure 4, panels A and B). Embryos in the 20-cm treatment had higher mortality than the 40-cm treatment and control (Figure 4, panels A and B). Embryo mortality for the 40-cm treatment did not differ from the control (Figure 4, panels A and B). Embryo mortality for the 0-cm control did not differ from the 20-cm and 40-cm control (Figure 4, panels A and B).

Twenty-two-day post-fertilization embryos (198 degree-days) had higher mortality in the 0-cm treatment than the 20-cm and 40-cm treatments and control (Figure 4, panel C). Embryos in the 20-cm and 40-cm treatments and the controls had similar

mortality (Figure 4, panel C). Similar to the two-day (18 degree-days) and eight-day (72 degree-days) post-fertilization embryos, embryo mortality for the controls at all depths did not differ for the twenty-two-day post-fertilization embryos (198 degree-days) (Figure 4, panel C).

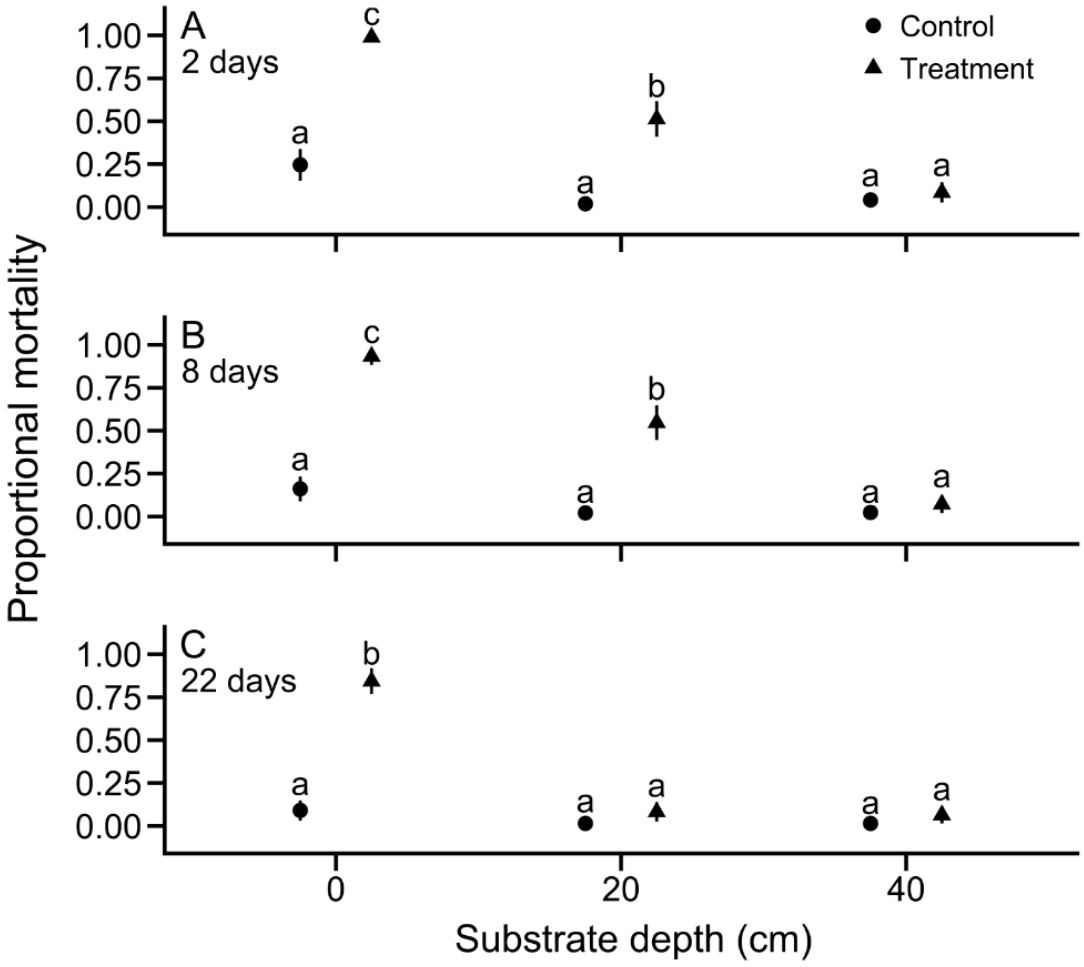

Figure 4. Proportional Lake Trout embryo mortality (mean ± 95% CI) in control (circles, *n*=3) and treatment (triangles, *n*=3) sites for two-day post fertilization embryos (18 degree-days, panel A), eight-day post fertilization embryos (72 degree-days, panel B), and twenty-two-day post fertilization embryos (198 degree-days, panel C) after electroshocking experiments conducted at Thomas Bank, Yellowstone Lake, Yellowstone National Park in autumn 2015. Embryos were positioned at three depths in the substrate, 0 cm (substrate surface), 20 cm, or 40 cm. Same letters indicate no statistical difference.

Tarping

Tarping did not increase mortality of embryos (Figure 5). Mean proportional mortality of embryos in the control was 0.20 (0.05 SE) and 0.18 (0.08 SE) in the treatment; thus, no evidence suggested embryo mortality differed between treatment and control (t = 0.38, df = 4, P = 0.73; Figure 5). One treatment incubator was not recovered during experiments and nine treatment incubators and five control incubators had embryos missing from individual compartments. Data from these incubators were not included in the analysis because it was unknown if the missing embryos died during experiments and decomposed or remained alive but were not retained within incubators because of the incubator panels shifting. During the tarping experiments mean DO concentration at the substrate surface in treatment sites was similar to the control sites (Table 1). Mean water temperature (°C) at the substrate surface in control sites was 0.1°C lower than in treatment sites (Table 1).

Table 1. Mean water temperature (°C) and dissolved oxygen (mg/L) with ±1 SD in parentheses at the substrate surface in control sites and treatment sites (treatment sites were covered with a gas impermeable tarp [see Methods]) during tarping experiments conducted at Carrington Island, Yellowstone Lake, Yellowstone National Park for 28 days in autumn 2015.

	Water temperature (°C)	Dissolved oxygen (mg/L)
Control	11.2 (0.62)	7.5 (0.12)
Treatment	11.3 (0.61)	6.7 (0.53)

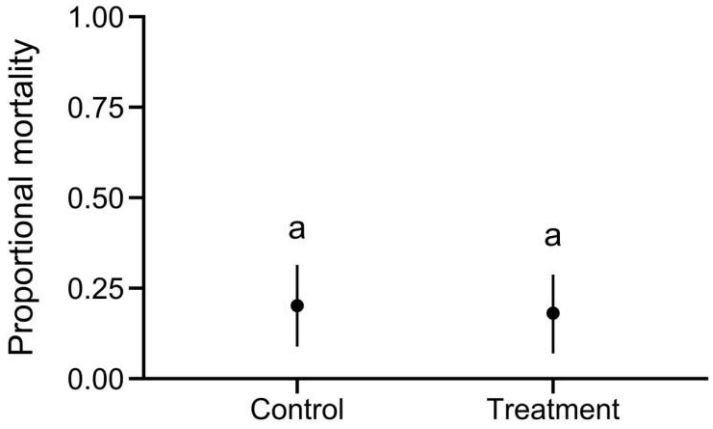

Figure 5. Proportional Lake Trout embryo mortality (mean ± 95% CI) in control (n=3) and treatment (n=3) sites after tarping experiments conducted at Carrington Island, Yellowstone Lake, Yellowstone National Park for 28 days in autumn 2015. Same letters indicate no statistical difference.

Carcass Deposition

At Thomas Bank, mean proportional mortalities for embryos in the carcass and carcass-tarp treatment varied from 0.98 to 1.00 and were higher than the mean of the control at each depth (Figure 6, panel A). Embryos in the 0-cm control had higher mortality than the 20-cm control (Figure 6, panel A). Strong evidence supported a treatment by depth interaction for embryo mortality (ANOVA: $F_{2, 36} = 71.49$, $P < 0.001$), caused by the difference in embryo mortality in the control by depth (Figure 6, panel A).

At Carrington Island, mean proportional mortalities for embryos in the carcass and carcass-tarp treatment varied from 0.59 to 0.88 (Figure 6, panel B). Control embryos had the lowest mean proportional mortality and carcass-tarp treatment embryos had the highest mean proportional mortality at each depth (Figure 6, panel B). Embryo mortality in the carcass and carcass-tarp treatment were similar and higher than the control at the 20-cm depth (Figure 6, panel B). Embryo mortality in the carcass and carcass-tarp

treatment were similar and the carcass treatment and the control were similar at the 0-cm depth (Figure 6, panel B). Embryo mortality in the carcass-tarp treatment was higher than the control at the 0-cm depth (Figure 6, panel B). Embryo mortality in the control did not differ by depth (Figure 6, panel B). No evidence suggested a treatment by depth interaction for embryo mortality (ANOVA: $F_{2, 18} = 2.15$, $P = 0.16$) and no evidence suggested depth affected embryo mortality (ANOVA: $F_{1, 18} = 0.58$, $P = 0.46$; Figure 6, panel B). Strong evidence indicated embryo mortality was different among the carcass treatment, carcass-tarp treatment, and control (ANOVA: $F_{2, 18} = 25.57$, $P < 0.001$).

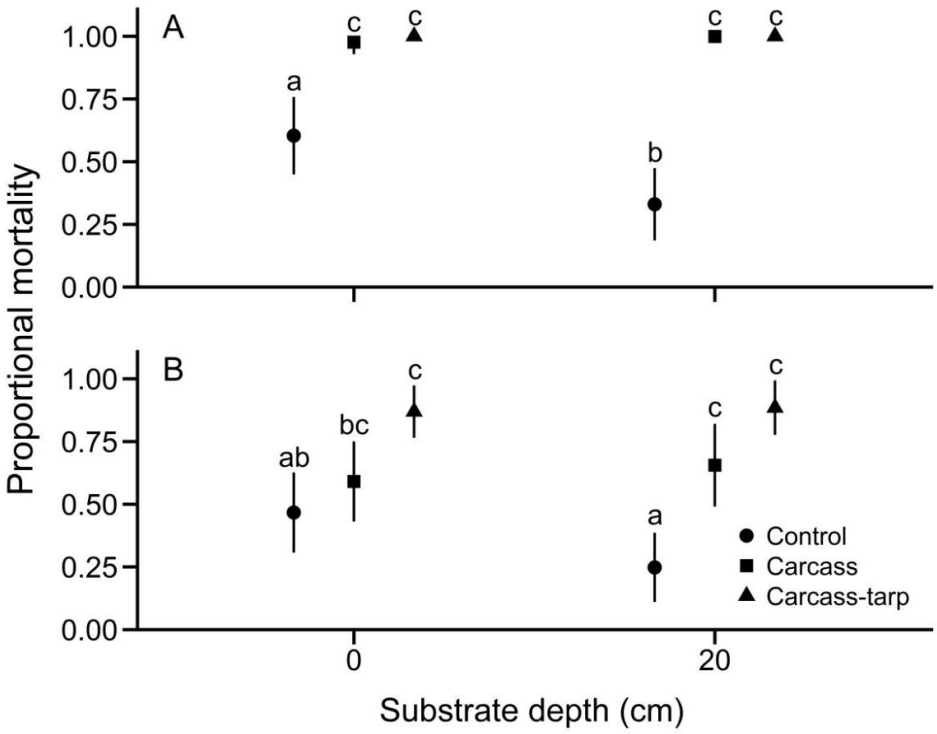

Figure 6. Proportional Lake Trout embryo mortality (mean ± 95% CI) at 0 cm (substrate surface) or 20 cm in the substrate in control sites (circles), carcass treatment sites (squares), or carcass-tarp treatment sites (triangles). Experiments were conducted in autumn 2016 for 16 days at Thomas Bank (panel A, n=6) and for 26 days at Carrington Island (panel B, n=3), Yellowstone Lake, Yellowstone National Park. Same letters indicated no statistical difference.

At Thomas Bank, carcass deposition reduced DO concentrations at the substrate surface (Figure 7, panel A). In control sites, DO concentrations were about 8 mg/L during the experiment and in the carcass and carcass-tarp treatment sites DO concentrations declined immediately after carcasses were placed on the substrate on September 21, 2016 (Figure 7, panel A). The minimum DO concentration in carcass treatment sites was 0.06 mg/L and in carcass-tarp treatment sites was 0.05 mg/L, both occurring on September 26, 2016 (Figure 7, panel A). In treatment sites, DO concentrations increased at the beginning of October and reached 6.7 mg/L in carcass treatment sites and 3.3 mg/L in carcass-tarp treatment sites on October 3, 2016 and decreased again until October 5, 2016. From October 5 to October 7, 2016 DO concentrations in carcass treatment sites were about 4 mg/L and in carcass-tarp treatment sites DO concentrations varied from 0.7 to 2.1 mg/L (Figure 7, panel A).

Carcass deposition at Carrington Island did not have the same effect on DO concentrations as at Thomas Bank because carcasses drifted from the treatment sites. In control sites, DO concentrations were about 8 mg/L during the experiment and in carcass treatment sites DO concentrations were slightly lower than the control sites, varying from 5.9 to 8.3 mg/L (Figure 7, panel B). In carcass-tarp treatment sites, DO concentrations declined immediately after carcasses were placed on the substrate on September 22, 2016 and reached a minimum of 0.02 mg/L on September 29, 2016 (Figure 7, panel B). Dissolved oxygen concentrations increased steadily in the carcass-tarp treatments from September 30 to October 17, 2016 and were similar to the control sites when the experiments ended (Figure 7, panel B).

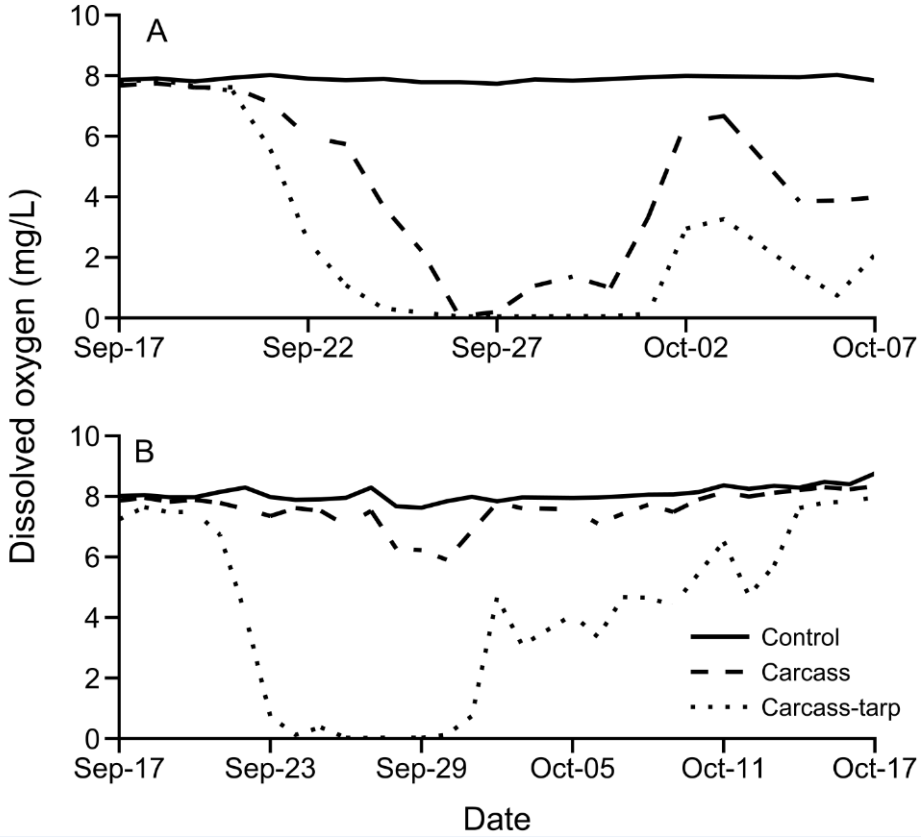

Figure 7. Dissolved oxygen concentration (mg/L) at the substrate surface within control sites, carcass treatment sites, and carcass-tarp treatment sites during carcass experiments conducted at Thomas Bank (panel A, *n*=2) and Carrington Island (panel B, *n*=1), Yellowstone Lake, Yellowstone National Park in autumn 2016. Carcasses were placed on the substrate at treatment sites on September 21 at Thomas Bank and September 22 at Carrington Island.

At Thomas Bank, mean water temperatures were similar among the carcass treatment sites, carcass-tarp treatment sites, and the control sites, varying from 10.9°C (control and carcass treatment) to 11.0°C (carcass-tarp treatment) (Table 2). At Carrington Island, mean water temperatures were 0.9°C lower than at Thomas Bank (Table 2). Mean water temperature in the control and carcass treatment were both 10.0°C and in the carcass-tarp treatment mean water temperature was 10.1°C (Table 2).

Table 2. Mean water temperature (°C) with ±1 SD in parentheses at the substrate surface in control sites, carcass treatment sites (carcass treatment sites were covered with Lake Trout carcasses [see Methods]), and carcass-tarp treatment sites (carcass-tarp treatment sites were covered with Lake Trout carcasses and a gas impermeable tarp [see Methods]) during carcass deposition experiments at Thomas Bank from September 21 to October 7, 2016 and Carrington Island from September 22 to October 17, 2016, Yellowstone Lake, Yellowstone National Park.

Location	Water temperature (°C)
Thomas Bank (*n*=2)	
Control	10.9 (1.12)
Carcass	10.9 (1.11)
Carcass-tarp	11.0 (1.12)
Carrington Island (*n*=1)	
Control	10.0 (1.62)
Carcass	10.0 (1.57)
Carcass-tarp	10.1 (1.65)

Substrate-Biofilm Production. The change in biofilm dry biomass after carcass deposition experiments were similar between treatments and controls at Thomas Bank and Carrington Island (Table 3). Among the four comparisons between the treatments and the control, the maximum difference in the mean change in biofilm dry biomass was -0.000630 g/m^2 between the carcass treatment sites and the control sites at Carrington Island, with no evidence suggesting this difference was > 0 (paired *t*-test, df = 2, *t*-stat = -1.533, *P* = 0.867; Table 3).

Table 3. Difference in mean change in biofilm dry biomass (g/m^2) before and after carcass deposition experiments between carcass treatment sites (carcass treatment sites were covered with Lake Trout carcasses [see Methods above] and control sites and carcass-tarp treatment sites (carcass-tarp treatment sites were covered with Lake Trout carcasses and a gas impermeable tarp [see Methods above]) and control sites at Carrington Island and Thomas Bank, Yellowstone Lake, Yellowstone National Park in autumn 2016. A one-tailed paired *t*-test (alternative > 0) was used for statistical analysis.

Location	Comparison	Biofilm (g/m^2) difference	df	*t*-stat	*P*-value
Carrington Island	carcass-tarp–control	-0.000294	2	-0.443	0.649
Carrington Island	carcass–control	-0.000630	2	-1.533	0.867
Thomas Bank	carcass-tarp–control	-0.000313	5	-0.995	0.817
Thomas Bank	carcass–control	-0.000499	5	-1.765	0.931

Hydrology

Interstitial flow rates and direction of flow varied among hydrology experiments. At Thomas Bank, conductivity measurements remained near baseline south of the injection point for all three experiments (Figures 8, 9, and 10). During the first experiment when 500 g of NaCl were injected, conductivity measurements were recorded above the baseline north and west of the injection point, with interstitial water flowing faster to the west (0.23 m/h) than the north (0.14 m/h) (Figure 8). Conductivity measurements were recorded above the baseline north, east, and west of the injection point when 1,000 g of NaCl were injected for the second and third experiments (Figure 9 and 10). During the second experiment, peak conductivity measurements were recorded at the exact same time at 0.67 m and 1.34 m from the injection point in the north, west and east directions, indicating interstitial water was flowing at a rate > 2,412 m/h in each direction (Figure 9). Interstitial water flow rates were not consistent among directions during the third trial varying from > 2,412 m/h (east) to 1.34 m/h (north) (Figure 10).

Data from the hydrology experiment conducted at the Elbow were not analyzed because conductivity measurements for two of the loggers were suspect.

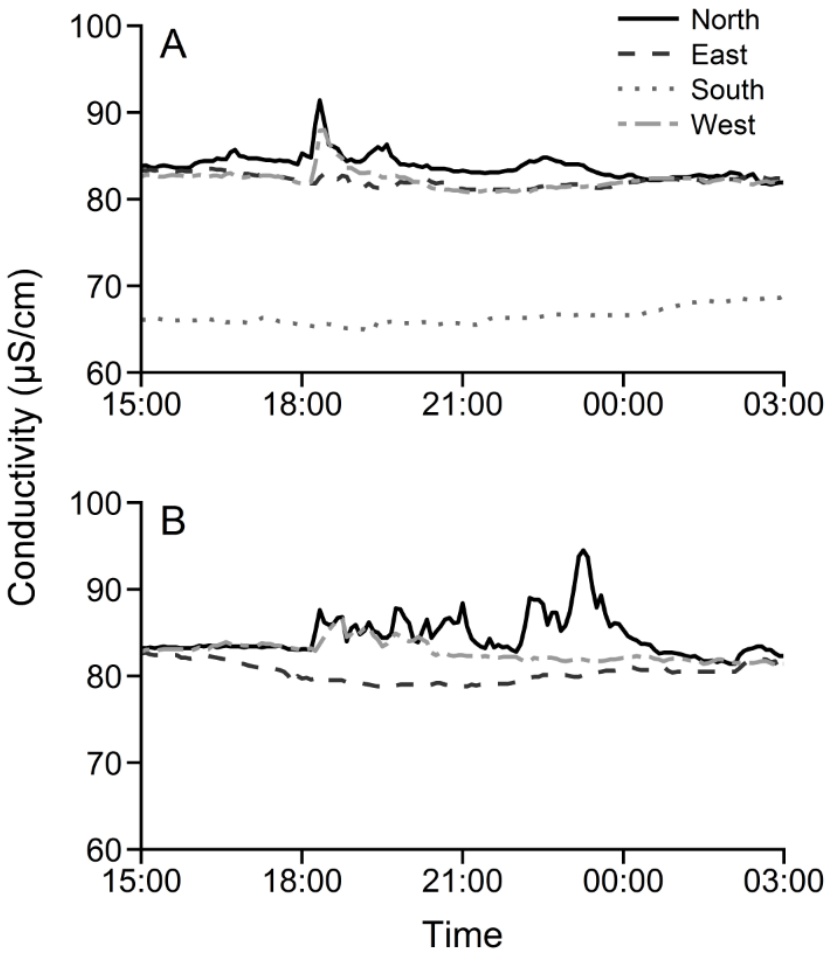

Figure 8. Water conductivity (µS/cm) measured at 20 cm in the substrate in four directions from a source of 500 grams of dry granular Sodium Chloride (NaCl) injected at 15:00 20 cm in the substrate at Thomas Bank, Yellowstone Lake, Yellowstone National Park. Four conductivity loggers were positioned 0.67 m from the injection point (panel A) and three conductivity loggers were positioned 1.34 m from the injection point (panel B). Baseline conductivity varied from 75 to 85 µS/cm.

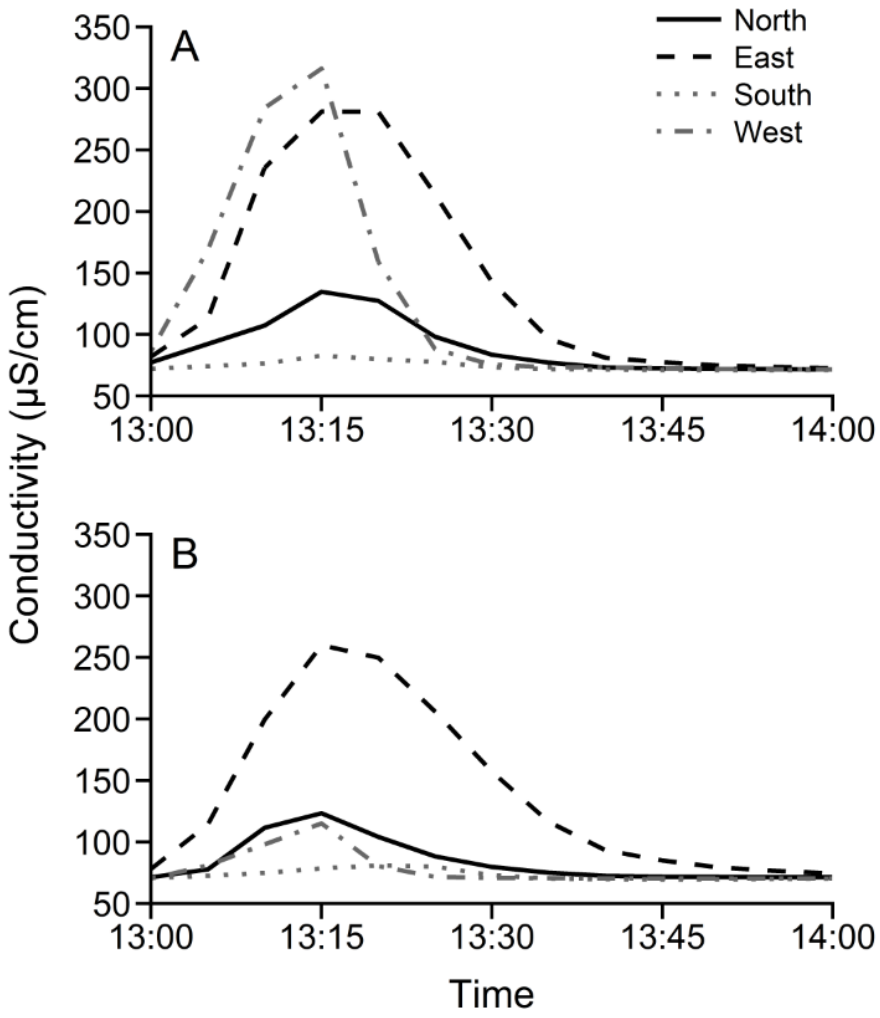

Figure 9. Water conductivity (µS/cm) measured at 20 cm in the substrate in four directions from a source of 1,000 grams of dry granular Sodium Chloride (NaCl) injected at 13:00 20 cm in the substrate at Thomas Bank, Yellowstone Lake, Yellowstone National Park. Four conductivity loggers were positioned 0.67 m from the injection point (panel A) and four conductivity loggers were positioned 1.34 m from the injection point (panel B). Baseline conductivity varied from 65 to 75 µS/cm.

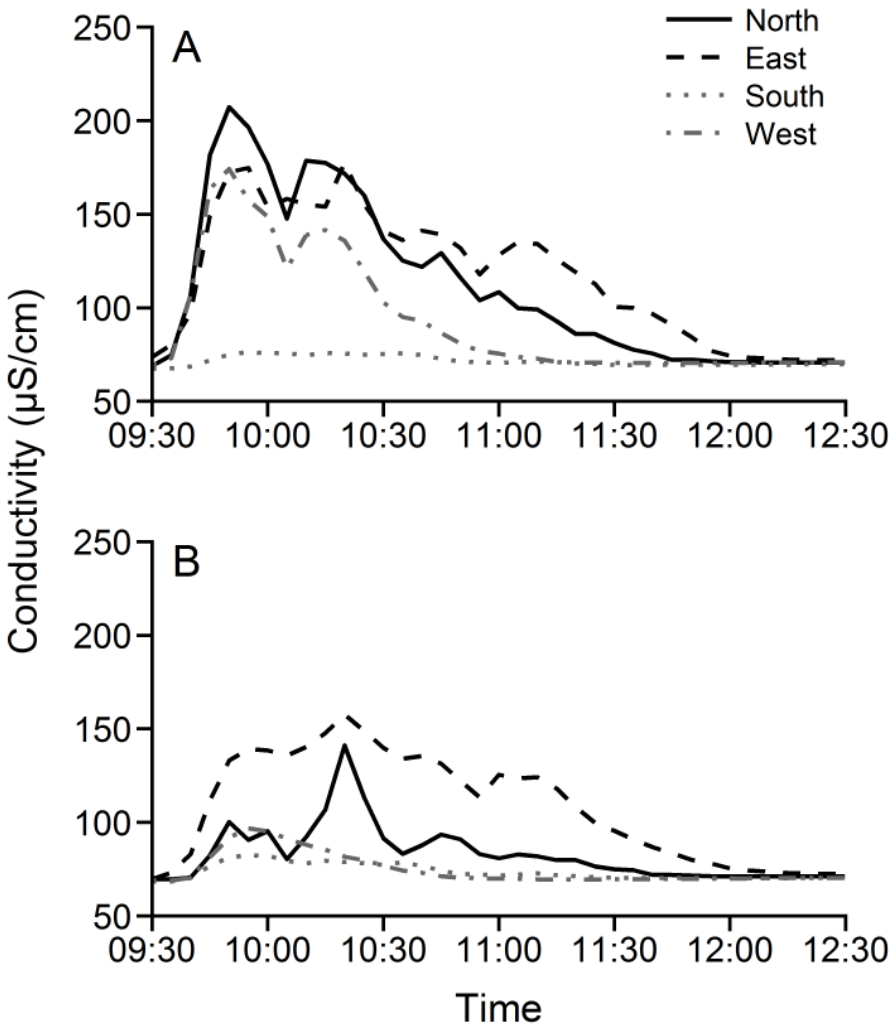

Figure 10. Water conductivity (µS/cm) measured at 20 cm in the substrate in four directions from a source of 1,000 grams of dry granular Sodium Chloride (NaCl) injected at 09:30 20 cm in the substrate at Thomas Bank, Yellowstone Lake, Yellowstone National Park. Four conductivity loggers were positioned 0.67 m from the injection point (panel A) and four conductivity loggers were positioned 1.34 m from the injection point (panel B). Baseline conductivity varied from 65 to 75 µS/cm.

Discussion

The efficacy of the suppression methods tested in this study was variable. Carcass deposition treatments with and without tarps were highly effective and mortality was > 92% when carcasses remained on the treatment site. Electroshocking was effective at causing high mortality at the substrate surface, but was less effective on embryos at depths of 20 cm, and ineffective at 40 cm. Incorporating carcass deposition into a Lake Trout suppression program using an IPM strategy is recommended because mortality would be increased beyond traditional mechanical removal techniques. Integrating electroshocking as a suppression tool would increase suppression effectiveness but only if implemented where embryos are near the substrate surface. Suction dredging and tarping were not effective at causing embryo mortality and are not recommended for full-scale implementation in an IPM approach.

The efficacy of electroshocking was influenced by substrate interstitial depth. Embryos were positioned at known depths in the substrate because Lake Trout embryos are negatively buoyant and will settle into the substrate interstices (Marsden and Tobi 2014). As predicted and observed by Brown et al. (2017), embryo mortality declined with distance from the electrical grid. In this study the electrical grid was most effective at the surface and had little effect at 20 cm. In Swan Lake, the efficacy of a similar electrical grid was high at 20 cm (Brown et al. 2017). The difference between this study and the Swan Lake study was a result of water conductivity differences. The capacity of an electrical current to flow through water depends on the specific conductance of the water (Beaumont et al. 2002). The specific conductance at Swan Lake varies from 185 to

210 µS/cm (Brown et al. 2017) and at Yellowstone Lake varies from 90 to 95 µS/cm (Jeff Arnold, NPS fisheries biologist, personal communication). When electrified with the same type and model shock box and same size generator used in this study the specific conductance of Yellowstone Lake limits the size of the electrical field. Increasing the power output would increase the size and strength of the electrical field; however, the shock box used in this study was at maximum capacity. Electroshocking could probably cause high embryo mortality at ≤ 40 cm in the substrate given a more powerful electrofishing design.

In addition to interstitial depth, embryo age influenced embryo mortality in the electroshocking treatments. Lake Trout embryos twenty-two-days (198 degree-days) post fertilization had lower treatment mortality than embryos two-days (18 degree-days) and eight-days (72 degree-days) post fertilization. Our results corroborate previous studies indicating salmonid embryos become less susceptible to shock induced mortality in later developmental stages (Dwyer et al. 1993; Gross et al. 2015). Therefore, electroshocking will be more effective if implemented when embryos have recently been fertilized and are in early developmental stages. Conducting electroshocking treatments throughout the entire spawning season would be necessary to maximize embryo mortality because the Lake Trout spawning season lasts for several weeks.

The efficacy of tarping (i.e., without the addition of carcasses) was probably influenced by substrate size. The same gas-impermeable tarps used in this study caused anoxic conditions in sand substrate in Lake Tahoe (Wittmann et al. 2012). A tight seal is difficult to create at the tarp edge on suitable Lake Trout spawning substrate because the

substrate is often large diameter cobble. Thus, water exchange occurs between the outside of the tarped area and the inside resulting in no effect on DO concentrations and subsequently similar embryo mortality rates between control and treatment sites. Given the preferred habitat for spawning Lake Trout, tarping without any added organic material is not an effective method for embryo suppression.

Tarping with Lake Trout carcasses underneath the tarps caused high mortality in Lake Trout embryos; for example, all embryos died at the surface and 20 cm in the substrate in all of the carcass-tarp treatment sites at Thomas Bank and two of the three carcass-tarp treatment sites at Carrington Island. At both experiment locations, tarping with carcasses caused hypoxic conditions. Interestingly, DO concentrations started to decline from ambient conditions immediately after the introduction of carcasses.

Similar to embryo mortalities in carcass-tarp treatments, embryo mortalities in carcass only treatments were high, but more variable among experiment sites than the carcass-tarp experiment. Embryo mortality at Thomas Bank was about twice the mortality at Carrington Island. The difference in treatment effect between Carrington Island and Thomas Bank was probably a result of carcass drift. Carrington Island is more exposed to waves than Thomas Bank and carcasses were observed drifting away from the Carrington Island experiment site shortly after the experiment was initiated. Furthermore, carcasses drifted from under the tarps at Carrington Island—also a function of wave action. The carcass drift was corroborated by the DO concentration data where for the entire treatment duration at Carrington Island DO concentrations were near control site levels. Furthermore, embryo mortality at the substrate surface in the carcass

treatment was similar to the control. However, at the 20-cm carcass treatment embryo mortality differed from the 20-cm control, indicating low DO concentrations might not have been the only cause of embryo mortality.

The cause of embryo mortality within carcass treatments may have been a result of hypoxic conditions. Dissolved oxygen levels < 2.5 mg/L caused 0% hatching success of Lake Trout embryos when incubated at 10°C (Garside 1959); however, in this study mortality was observed well before hatch at 24-days post fertilization at Thomas Bank. In addition to hypoxic conditions, carbon dioxide (CO_2) and hydrogen sulfide (H_2S) were probably produced through carcass decomposition (Sly 1988). These chemical compounds can harm early life stages of salmonids, potentially causing mortality (Sly 1988). For example, Brown Trout *Salmo trutta* alevins exposed to concentrations of 13 µg H_2S/L for 144 h experienced 100% mortality (Reynolds and Haines 1980) and exposure to dissolved CO_2 levels from 10–35 mg/L can cause sublethal effects on Atlantic Salmon smolts *Salmo salar* (Gil-Martens et al. 2006). The effects of CO_2 are influenced by DO concentrations; as DO concentrations decrease CO_2 becomes more toxic (Wedemeyer 1996). Thus, the combination of these chemical compounds present in hypoxic conditions probably interacted to increase mortality of Lake Trout embryos.

In addition to hypoxic conditions and exposure to CO_2 and H_2S, embryo mortality could have been a result of fungal infection. Salmonid embryos are susceptible to fungi of the genus *Saprolegnia* (Pottinger and Day 1999) and because *Saprolegnia* spp. colonize fish carcasses (Garman 1992) the Lake Trout carcasses could have facilitated its growth. However, the carcasses were at the surface and embryos 20 cm in the substrate

died, indicating the *Saprolegnia* spp. would have had to spread 20 cm from the carcasses if it were the only mechanism that caused embryo mortality.

For an embryo suppression method to be fully integrated into an IPM design, the method should be feasible at a scale beyond *in situ* experiments. Several methods were shown to cause embryo mortality, but large-scale implementation may be difficult. For example, the mobile electrical grid was effective at causing embryo mortality at the substrate surface, but multiple deployments would be required to treat an entire spawning site (grid was 3.0 m by 6.1 m)—and would thus be labor intensive. Furthermore, the electrofishing grid can be used at depths up to 18 m, but the ability to control where the gird is placed on the substrate is limited, potentially allowing for gaps in coverage of spawning areas. Tarping with Lake Trout carcasses underneath the tarps was effective, but is labor intensive because it requires SCUBA divers to anchor the tarps. Given this requirement, tarping has limited use especially in high elevation lakes. Lake Trout carcass deposition without tarps was as effective as the carcass-tarp experiments, but was less labor intensive because it did not require SCUBA. Therefore, of the methods tested in this study, Lake Trout carcass deposition has the most promise for large-scale implementation.

Some factors are limiting the use of Lake Trout carcass deposition as a full-scale suppression method. Treating the estimated 28.2 acres of confirmed Lake Trout spawning sites within Yellowstone Lake (Phil Doepke, NPS fisheries biologist, personal communication) at a carcass biomass density of 28 kg/m^2 would require more carcasses than what is available during the spawning season. Also, bears were attracted to the near

shore carcass sites at Thomas Bank, which could limit the use of this method in shallow water littoral areas frequented by humans. Treating spawning sites with strong wave action may be unsuccessful because carcasses will drift off the spawning sites. Carcasses can be deposited at any water depth; however, to ensure complete coverage of spawning sites at depths where the substrate is not visible from the surface a camera will need to be deployed or SCUBA divers would need to inspect the treatment area to guide the procedure.

Future work is needed to determine if Lake Trout carcass deposition can successfully complement gillnetting and improve a Lake Trout suppression program. The minimum amount of Lake Trout carcasses needed to effectively treat all spawning sites could be determined through evaluating the minimum amount of carcass biomass density (kg/m^2) required to cause 100% mortality of Lake Trout embryos. Placing ground carcasses on the spawning sites could increase the effectiveness of this method, but would require more pre-treatment work. Ground carcasses would settle in the interstitial spaces and be less susceptible to drifting caused by waves. Also, because of the increased surface area of the ground up carcass material, decomposition would probably occur more rapidly, potentially increasing embryo mortality over a shorter time. Ground carcasses could effectively treat more spawning area than using whole carcasses because of the increased rate of decomposition. In addition, bears attracted to shallow water spawning sites treated with ground carcasses would receive less of a food reward than if whole carcasses were present. Evaluating the mechanism(s) that caused embryo

mortality could inform the development of a carcass analog, which could be used when the availability of carcasses is limited.

Treating spawning sites with carcasses could affect the local abiotic and biotic communities. No short-term increase in substrate biofilm was detected at the carcass sites in this study, however, the use of carcass deposition at a large-scale could result in a long-term increase and a change in the littoral community. Evaluating the concentrations of chemical compounds produced during carcass decomposition and monitoring the biotic community where carcasses are placed will be important to understand potential undesired effects (e.g., algal blooms) associated with implementing carcass deposition.

Embryo suppression methods are unlikely to completely replace mechanical suppression methods for Lake Trout. However, the success of Lake Trout carcass deposition shows potential for the development of an embryo suppression method that could be effectively implemented on a larger scale. Through implementing an IPM approach by targeting multiple life stages of a Lake Trout population an effective embryo suppression method used simultaneously with gillnetting could improve Lake Trout suppression. In addition, when Lake Trout abundance declines, the ratio of Lake Trout captured to Yellowstone Cutthroat Trout will decline, which may result in undesirable bycatch of Yellowstone Cutthroat Trout. I surmise that embryo suppression will be more effective when Lake Trout abundance declines because fewer spawning areas will need to be targeted. Thus, embryo suppression could be particularly valuable for controlling a Lake Trout population at low abundance.

REFERENCES CITED

Arnold, J. L., P. D. Doepke, B. D. Ertel, and T. M. Koel. 2017. Fish population responses to the suppression of non-native Lake Trout. Yellowstone Science 25(1):60-64.

Baril, L. M., D. W. Smith, T. Drummer, and T. M. Koel. 2013. Implications of Cutthroat Trout declines for breeding ospreys and bald eagles at Yellowstone Lake. Journal of Raptor Research 47:234-245.

Beaumont, W. R. C., A. A. L. Taylor, M. J. Lee, and J. S. Welton. 2002. Guidelines for electricfishing best practice. Report to environmental agency. Bristol: Environmental Agency Technical Report W2-054.

Beissinger, S. R., D. D. Ackerly, H. Doremus, and G. E. Machlis, editors. 2017. Science, conservation, and national parks. University of Chicago Press, Chicago.

Bigelow, P. E., P. D. Doepke, B. D. Ertel, C. S. Guy, J. M. Syslo, and T. M. Koel. 2017. Suppressing non-native Lake Trout to restore native Cutthroat Trout in Yellowstone Lake. Yellowstone Science 25(1):53-59.

Billard, R., and J. O. Jensen. 1996. Gamete removal, fertilization, and incubation. Pages 291-364 *in* W. Pennell and B. A. Barton, editors. 1996. Principles of salmonid culture. Elsevier Science, Amsterdam.

Binder, T. R., H. T. Thompson, A. M. Muir, S. C. Riley, J. E. Marsden, C. R. Bronte, and C. C. Krueger. 2014. New insight into the spawning behavior of Lake Trout, *Salvelinus namaycush*, from a recovering population in the Laurentian Great Lakes. Environmental Biology of Fishes 98:173-181.

Bohl, R. J., T. B. Henry, and R. J. Strange. 2010. Electroshock-induced mortality in freshwater fish embryos increases with embryo diameter: a model based on results from 10 species. Journal of Fish Biology 76:975-986.

Bonham, K. 1976. Specific gravity of salmonid eggs. Transactions of the American Fisheries Society 105:351-352.

Bratton, S. P. 1982. The effects of exotic plant and animal species on nature preserves. Natural Areas Journal 2:3-13.

Brown, P. J., and A. V. Zale. 2012. Rotenone persistence model for montane streams. Transactions of the American Fisheries Society 141:560-569.

Brown, P. J., C. S. Guy, and M. H. Meeuwig. 2017. A comparison of two mobile electrode arrays for increasing mortality of Lake Trout embryos. North American Journal of Fisheries Management 37:363-369.

Casselman, J. M. 1995. Survival and development of Lake Trout eggs and fry in eastern Lake Ontario-in situ incubation, Yorkshire Bar, 1989–1993. Journal of Great Lakes Research 21:384-399.

Christie, G. C., and C. I. Goddard. 2003. Sea Lamprey international symposium (SLISII): advances in the integrated management of Sea Lampreys in the Great Lakes. Journal of Great Lakes Research 29:1-14.

Cox, B. S., C. S. Guy, W. A. Fredenberg, and L. R. Rosenthal. 2013. Baseline demographics of a non-native Lake Trout population and inferences for suppression from sensitivity elasticity analyses. Fisheries Management and Ecology 20:390-400.

Culver, C., H. Lahr, L. Johnson, and J. Cassell. 2013. Quagga and zebra mussel eradication and control tactics. UC San Diego: California Sea Grant College Program. Available: https://escholarship.org/uc/item/4sx8s02v. (March 2015).

Dwyer, W. P., and D. A. Erdahl. 1995. Effects of electroshock voltage, wave form, and pulse rate on survival of Cutthroat Trout eggs. North American Journal of Fisheries Management 15:647-650.

Dwyer, W. P., W. A. Fredenburg, and D. A. Erdahl. 1993. Influence of electroshock and mechanical shock on survival of trout eggs. North American Journal of Fisheries Management 13:839-843.

Ehler, L. E. 2006. Integrated pest management (IPM): definition, historical development and implementation, and the other IPM. Pest Management Science 62:787-789.

Endicott, C., L. Nelson, S. Opitz, A. Peterson, J. Burckhardt, S. Yekel, D. Garren, T. M. Koel, and B. B. Shepard. 2016. Range-wide status assessment for Yellowstone Cutthroat Trout (*Oncorhynchus clarkii bouvieri*): 2012. Yellowstone Cutthroat Trout Interagency Coordination Group, Helena, MT.

Esteve, M., D. A. McLennan, and J. Gunn. 2008. Lake Trout (*Salvelinus namaycush*) spawning behaviour: the evolution of a new female strategy. Environmental Biology of Fishes 83:69-76.

Felicetti, L. A., C. C. Schwartz, R. O. Rye, K. A. Gunther, M. A. Haroldson, L. P. Waits, and C. T. Robbins. 2004. Use of naturally-occurring mercury to determine the importance of Cutthroat Trout to Yellowstone grizzly bears. Canadian Journal of Zoology 82:493-501.

Franssen, N. R., J. E. Davis, D. W. Ryden, and K. B. Gido. 2014. Fish community responses to mechanical removal of nonnative fishes in a large southwestern river. Fisheries 39:352-363.

Garman, G. C. 1992. Fate and potential significance of postspawning anadromous fish carcasses in an Atlantic coastal river. Transactions of the American Fisheries Society 121:390-394.

Garside, E. T. 1959. Some effects of oxygen in relation to temperature on the development of Lake Trout embryos. Canadian Journal of Zoology 37:689-698.

Gil-Martens, L., P. E. Witten, S. Fivelstad, A. Huysseune, B. Sævareid, V. Vikeså, and A. Obach. 2006. Impact of high water carbon dioxide levels on Atlantic Salmon smolts (*Salmo salar L.*): effects on fish performance, vertebrae composition and structure. Aquaculture 261:80-88.

Gross, J., B. Farokhkish, M. Cornacione, S. Shaw, P. L. Nguyen, and T. B. Henry. 2015. Potential use of direct current electric fields to eradicate Rainbow Trout embryos from freshwater ecosystems. North American Journal of Fisheries Management 35:871-879.

Hansen, M. J., T. D. Beard, Jr., and D. B. Hayes. 2007. Sampling and experimental design. Pages 51-120 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Helvik, J. V., K. Hamre, I. Hordvik, T. van der Meeren, H. Ressem, M. Schartl, H. Tveiten, and G. Øie. 2009. The fish larva: a transitional life form, the foundation for aquaculture and fisheries. Report from a working group on research on early life stages of fish. The Research Council of Norway, Oslo, Norway.

Hudson, R., and J. Fraser. 2005. Introduction to salt dilution gauging for streamflow measurement, part IV: the mass balance (or dry injection) method. Streamline Watershed Management Bulletin 9:6-12.

Johnson, N. S., S. S. Yun, H. T. Thompson, C. O. Brant, and W. Li. 2009. A synthesized pheromone induces upstream movement in female sea lamprey and summons them into traps. Proceedings of the National Academy of Sciences 106:1021-1026.

Kaeding, L. R., G. D. Boltz, and D. G. Carty. 1995. Lake Trout discovered in Yellowstone Lake. Pages 4-11 *in* J. D. Varley and P. Schullery, editors. The Yellowstone Lake crisis: confronting a Lake Trout invasion. Report to the Director of the National Park Service. Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

Kaplinski, M. 1991. Geomorphology and geology of Yellowstone Lake, Yellowstone National Park, Wyoming. Master's thesis, Northern Arizona University, Flagstaff.

Koel, T. M., J. L. Arnold, L. A. Baril, K. A. Gunther, D. W. Smith, J. M. Syslo, and L. M. Tronstand. 2017. Non-native Lake Trout induce cascading changes in the Yellowstone Lake ecosystem. Yellowstone Science 25(1):42-50.

Koel, T. M., J. L. Arnold, P. E. Bigelow, C. R. Detjens, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2015. Native fish conservation program, Yellowstone fisheries & aquatic sciences 2012–2014 Yellowstone National Park. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA, YCR-2015-01.

Koel, T. M., J. L. Arnold, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2007. Yellowstone fisheries & aquatic sciences: annual report, 2006. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2007-04.

Koel, T. M., J. L. Arnold, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and M. E. Ruhl. 2012. Yellowstone fisheries & aquatic sciences: annual report, 2011. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2012-03.

Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and D. L. Mahony. 2005. Nonnative Lake Trout result in Yellowstone Cutthroat Trout decline and impacts to bears and anglers. Fisheries 30:10-19.

Laitala, K. L., T. S. Prather, D. C. Thill, B. Kennedy, and C. Caudill. 2012. Efficacy of benthicbarriers as a control measure for eurasian watermilfoil (*Myriophyllum spicatum*). Invasive Plant Science and Management 5:170-177.

Leach, J. H. 1995. Non-indigenous species in the Great Lakes: were colonization and damage to ecosystem health predictable? Journal of Aquatic Ecosystem Health 4:117-128.

Levine, J. M. 2008. Biological invasions. Current Biology 18:57-60.

Lewis, W. J., J. C. van Lenteren, S. C. Phatak, and J. H. Tumlinson. 1997. A total system approach to sustainable pest management. Proceedings of the National Academy of Science 94:1243-1248.

Marsden, J. E., and H. Tobi. 2014. Sculpin predation on Lake Trout eggs in interstices: skull compression as a novel foraging mechanism. Copeia 2014:654-658.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W. A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino, and A. E. Viola. 2009. Western Lake Trout woes. Fisheries 34:424-442.

McIntyre, J. D. 1995. Review and assessment of possibilities for protecting the Cutthroat Trout of Yellowstone Lake from introduced Lake Trout. Pages 28-35 *in* J. D. Varley and P. Schullery, editors. The Yellowstone Lake crisis: confronting a Lake Trout invasion. Report to the director of the National Park Service. Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

Mohr, L. C., K. H. Mills, and J. F. Klaverkamp. 1990. Survival and development of Lake Trout (*Salvelinus namaycush*) embryos in an acidified lake in northwestern Ontario. Canadian Journal of Fisheries and Aquatic Sciences 47:236-243.

Morin, A. 1987. Unsuitability of introduced tiles for sampling blackfly larvae (Diptera: Simuliidae). Freshwater Biology 17:143-150.

Munro, A. R., T. E. McMahon, and J. R. Ruzycki. 2005. Natural chemical markers identify source and date of introduction of an exotic species: Lake Trout (*Salvelinus namaycush*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Science 62:79-87.

Muth, R. T., and J. B. Ruppert. 1997. Effects of electrofishing fields on captive embryos and larvae of Razorback Sucker. North American Journal of Fisheries Management 17:160-166.

Myers, J. H., D. Simberloff, A. M. Kuris, and J. R. Carey. 2000. Eradication revisited: dealing with exotic species. Trends in Ecology and Evolution 15:316-320.

National Park Service. 2006. Management policies 2006: the guide to managing the national park system. U.S. Department of the Interior, Washington, DC.

Okubo, T. 1987. Microscopic observation of ordered colloids in sedimentation equilibrium and the important role of debye screening length. 4. Gold particles (specific gravity=19.3) in aqueous suspension. Colloid and Polymer Science 265:522-527.

Penn, M. R., J. J. Pauer, and J. R. Mihelcic. 2006. Biochemical oxygen demand. Pages 278 - 297 *in* A. Sabljic, editor. Environmental and ecological chemistry. Encyclopedia of Life Support Systems (EOLSS), Eolss Publishers, Oxford.

Perkins, D. L., and C. C. Krueger. 1994. Design and use of mesh bags to estimate deposition and survival of fish eggs in cobble substrate. North American Journal of Fisheries Management 14:866-869.

Pörtner, H. O., and A. P. Farrell. 2008. Ecology: physiology and climate change. Science 322:690-692.

Pottinger, T. G., and J. G. Day. 1999. A *Saprolegnia parasitica* challenge system, for Rainbow Trout: assessment of Pyceze as an anti-fungal agent for both fish and ova. Diseases of Aquatic Organisms 36:129-141.

Reynolds, F. A., and T. A. Haines. 1980. Effects of chronic exposure to H_2S on newly hatched Brown Trout, *Salmo trutta L*. Environmental Pollution 22:11-17.

Rosenthal, L. R., W. Fredenberg, J. Syslo, and C. Guy. 2012. Experimental removal of Lake Trout in Swan Lake, MT: 3-year summary report. Prepared for the Swan Valley Bull Trout Working Group. Kalispell, Montana.

Ruzycki, J. R. 2004. Impact of Lake Trout introductions on Cutthroat Trout of selected western lakes of the continental United States. Doctoral dissertation. Utah State University, Logan.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced Lake Trout on native Cutthroat Trout in Yellowstone Lake. Ecological Applications 13:23 37.

Simberloff, D. 2014. Biological invasions: what's worth fighting and what can be won? Ecological Engineering 65:112-121.

Simberloff, D. 2001. Biological invasions—how are they affecting us, and what can we do about them? Western North American Naturalist 63:308-315.

Simberloff, D., I. M. Parker, and P. N. Windle. 2005. Introduced species policy, management, and future research needs. Frontiers in Ecology and the Environment 3:12-20.

Sly, P. G. 1988. Interstitial water quality of Lake Trout spawning habitat. Journal of Great Lakes Research 14:301-315.

Steinman, A. D., G. A. Lamberti, and P. R. Leavitt. 2006. Biomass and pigments of benthic algae. Pages 357-379 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology, 2nd edition. Academic Press, Cambridge, MA.

Syslo, J. M., 2015. Dynamics of Yellowstone Cutthroat Trout and Lake Trout in the Yellowstone Lake ecosystem: a case study for the ecology and management on non-native fishes. Doctoral dissertation, Montana State University, Bozeman.

Syslo, J. M., C. S. Guy, P. E. Bigelow, P. D. Doepke, B. D. Ertel, and T. M. Koel. 2011. Response of non-native Lake Trout (*Salvelinus namaycush*) to 15 years of harvest in Yellowstone Lake, Yellowstone National Park. Canadian Journal of Fisheries and Aquatic Sciences 68:2132-2145.

Tempel, D. J., A. B. Cilimburg, and V. Wright. 2004. The status and management of exotic invasive species in national wildlife refuge wilderness areas. Natural Areas Journal 24:300-306.

Ussery, T. A., H. L. Eakin, B. S. Payne, A. C. Miller, and J. W. Barko. 1997. Effects of benthicbarriers on aquatic habitat conditions and macroinvertebrate communities. Journal of Aquatic Plant Management 35:69-73.

Varley, J. D., and P. Schullery. 1995. Socioeconomic values associated with the Yellowstone Lake Cutthroat Trout. Pages 22-27 *in* J. D. Varley and P. Schullery, editors. The Yellowstone Lake crisis: confronting an invasion. A report to the director of the National Park Service. National Park Service, Yellowstone Park, Wyoming.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westerbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468-478.

Wagner, W. C. 1982. Lake Trout spawning habitat in the Great Lakes. Fisheries research report 1904. Michigan Department of Natural Resources, Fisheries Division.

Walker, B., C. Hladick, and B. Cioni-Haywood. 2015. Nome suction dredge study. Available: http://commerce.state.ak.us/dnn/Portals/6/pub/NomeSuctionDredgeStdy.pdf. (April 2015).

Wedemeyer, G. A. 1996. Physiology of fish in intensive culture systems. Chapman & Hall, New York.

Wittmann, M. E., S. Candra, J. E. Reuter, G. S. Schladow, B. C. Allen, and J. Webb. 2012. The control of an invasive bivalve, *Corbicula fluminea*, using gas impermeable benthic barriers in a large natural lake. Environmental Management 49:1163-1173.