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MANAGEMENT BRIEF

Aerial Application of Organic Pellets Eliminates Lake Trout Recruitment from a Primary Spawning Reef in Yellowstone Lake

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Abstract

Invasive Lake Trout *Salvelinus namaycush* in the Yellowstone Lake ecosystem have been gillnetted since 1995 to suppress the population and allow for recovery of native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*. Although gillnetting is effective (Lake Trout population growth rate $\lambda \leq 0.6$ during 2012–2022), the effort only targets free-swimming, age-2 and older Lake Trout. We developed a complementary suppression method using organic (soy and wheat) pellets to cause Lake Trout embryo mortality and reduce recruitment from spawning areas. The entire Carrington Island spawning reef (0.5 ha) was aerially treated with 3.56 and 3.00 kg/m^2 of pellets in 2019 and 2020, respectively. Pellet decomposition caused dissolved oxygen concentrations to decline to lethal levels at 20 cm depth in the substrate, and pellets mostly dissipated from the reef within 12 d. Lake Trout fry trap CPUE was reduced to zero

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after ice-off each spring after the treatments. Prior to the treatments, 71 fry were captured during 58 trap-nights of effort in 2017–2019. After the treatments, no fry were captured during 273 trap-nights in 2020 and 2021. Lake Trout CPUE in large-mesh gill nets set near Carrington Island in September did not decline during 2017–2021 and fry were again trapped on the reef in spring 2022, suggesting that adults were not deterred from spawning there in the years after the pellet treatments. Complementary methods that increase mortality of prerecruits may allow for a reduction in gill-netting effort and the long-term costs of maintaining Lake Trout population suppression in Yellowstone Lake. Treatment of spawning areas may improve suppression efficiency for Lake Trout and invasive fish populations elsewhere because entire cohorts are targeted while immobile and temporarily concentrated in relatively small areas.

Invasive fish have caused ecological and economic damage worldwide by altering aquatic communities and disrupting natural ecosystem processes (Leprieur et al. 2008; Gallardo et al. 2016; Cuthbert et al. 2021). Invasive fish are particularly detrimental (O'Gorman et al. 2021) in the western United States, where fish species richness is naturally low, causing declines in native and popular wild sport fish populations through predation (Ruzycki 2004; Loppnow et al. 2013; Sepulveda et al. 2013), competition (Donald and Alger 1993; Roth et al. 2020; Wainright et al. 2021), and hybridization (Kovach et al. 2011; Mandeville et al. 2019; Heim et al. 2020). Invasive piscivores are especially harmful because they often add a novel predatory trophic level, resulting in trophic cascades that alter the structure of aquatic and terrestrial food webs (Ellis et al. 2011; Koel et al. 2019; Wainright et al. 2021). Managers have implemented invasive fish suppression programs to facilitate recovery of desirable fish populations and natural ecosystem function (Fredenberg et al. 2017; Hansen et al. 2019a; Healy et al. 2020).

Discovery of an invading fish species imparts a new unplanned burden on management agencies. In large aquatic ecosystems, invading fish cannot be eradicated (Britton et al. 2011; Rytwinski et al. 2018), thus requiring long-term commitments to maintain population suppression (Hansen et al. 2019b; Sorensen 2021). Cost-effective suppression is essential because resources are limited (Buhle et al. 2005). An integrated pest management (IPM) approach, which is most widely used in terrestrial systems (Flint and Van den Bosch 1981; Peshin et al. 2009), incorporates a variety of methods to target multiple life stages of an injurious species to increase suppression efficacy (FAO 1968; Dent 1995; Ehler 2006). For example, adult double-crested cormorants *Nannopterum auritum* are culled to reduce predation on fish populations in North America (Dorr et al. 2010; Schultz et al. 2013). Oiling of ground-nested cormorant eggs is used in an IPM approach to prevent hatching and consumption of fish by fledgling birds during a period of rapid individual growth (McGregor and Davis 2012; Ridgway et al. 2012; Dorr and Fielder 2017). Similarly, the Sea Lamprey *Petromyzon marinus* suppression program in the Laurentian Great Lakes uses pheromone attractants, migration barriers, chemical treatments, and other methods in combination to control this aquatic invasive species (Sawyer 1980; Christie and Goddard 2003; Johnson et al. 2009). Successful pest control programs in terrestrial ecosystems and the Laurentian Great Lakes serve as models for an IPM approach elsewhere.

Lake Trout *Salvelinus namaycush* were introduced into the western United States outside of their native range (Crossman 1995; Martinez et al. 2009) and have made invasive movements through river networks (Muhlfeld et al. 2012; Koel et al. 2020b), causing extensive declines in native and desirable sport fish populations (Vander Zanden et al. 2003; D'Angelo and Muhlfeld 2013; Hansen et al. 2016; Dux et al. 2019). Since 1995, an invasive Lake Trout population in Yellowstone Lake, Yellowstone National Park, has been suppressed with gill nets to conserve native Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri* and restore natural ecological processes (Koel et al. 2019, 2020a). Despite annual increases in gill-netting effort (Syslo et al. 2011), fishing mortality was not high enough to reduce adult biomass until 2012 (Koel et al. 2020a). Annual abundance of adult Lake Trout has declined each year since 2012 (Syslo et al. 2020), and age structure has shifted to fewer older fish, but the abundance of Lake Trout recruits (age 2) has varied, with no declining trend (Koel et al. 2022). Lake Trout embryos in Yellowstone Lake benefit from a lack of intraspecific competition and predators, thereby increasing survival rates (Bolnick et al. 2010; Syslo et al. 2020; Koel et al. 2020a). The high survival rates reduce the likelihood of recruitment overfishing and stock collapse (Zipkin et al. 2009; Ohlberger et al. 2011; Schröder et al. 2014).

Lake Trout population growth rates are sensitive to changes in age-0 survival (Ferreri et al. 1995; Cox et al. 2013); therefore, we sought methods that increase prerecruit mortality (Doepke et al. 2017) to mimic the mortality that occurs in the native range of Lake Trout (Marsden et al. 1995; Fitzsimons et al. 2002; Claramunt et al. 2005; Riley and Marsden 2009). Specifically, we intentionally reduced the dissolved oxygen (DO) concentration within substrate interstices of Lake Trout spawning reefs in Yellowstone Lake because salmonid embryos are highly susceptible to degraded water quality (Gunn and Keller 1984; Haines and Baker 1986; Sly 1988). Rapid mortality of Lake Trout embryos occurs when DO concentrations are below 3.4 mg/L (Garside 1959; Carlson and Siefert 1974; Koel et al. 2020c). We began by placing Lake Trout carcasses from the gill-netting suppression program onto spawning reefs (Thomas et al. 2019; Poole et al. 2020). However, gill-netting operations end in mid-October with the onset of winter conditions. The short amount of work time (2–3 weeks) and the reduced availability of carcasses after the September spawning period forced us to pursue an alternative organic material.

Organic pellets were originally developed as carcass analogs to restore nutrients in areas where decomposition of anadromous salmonids had historically contributed to stream productivity (Wipfli et al. 2004; Pearsons et al. 2007; Benjamin et al. 2020). Experimental application of organic (soy and wheat gluten) pellets on Lake Trout spawning substrates was highly effective at causing in situ embryo mortality (Koel et al. 2020c). Biological oxygen demand of the decomposing pellets caused DO to decline to 0 mg/L soon after most treatments and was probably the primary cause of high embryo mortality (Garside 1959; Carlson and Siefert 1974). Decomposition probably also caused changes in other water quality parameters, such as increases in carbon dioxide (CO_2) and hydrogen sulfide (H_2S), which are known to harm early life stages of salmonids (Sly 1988). Regardless of the mechanisms, embryo mortality effects at various levels of organic pellet biomass justified further investigation into applications on a larger scale.

Our goal was to apply organic pellets to an entire Lake Trout spawning reef at a biomass sufficient to reduce fry production while not deterring adults from spawning at the reef during the following year, which could jeopardize future suppression efforts. Our specific questions were (1) “Could an adequate amount of pellets be transported and applied to a spawning reef and completely cover the interstices of the spawning substrate?”; (2) “Given wave action and lake currents, would pellet material remain in the substrate interstices long enough to create hypoxia or otherwise cause embryo mortality and curtail the recruitment of fry the following spring?”; and (3) “Would Lake Trout adults return undeterred to the treated reef to spawn in subsequent years?”

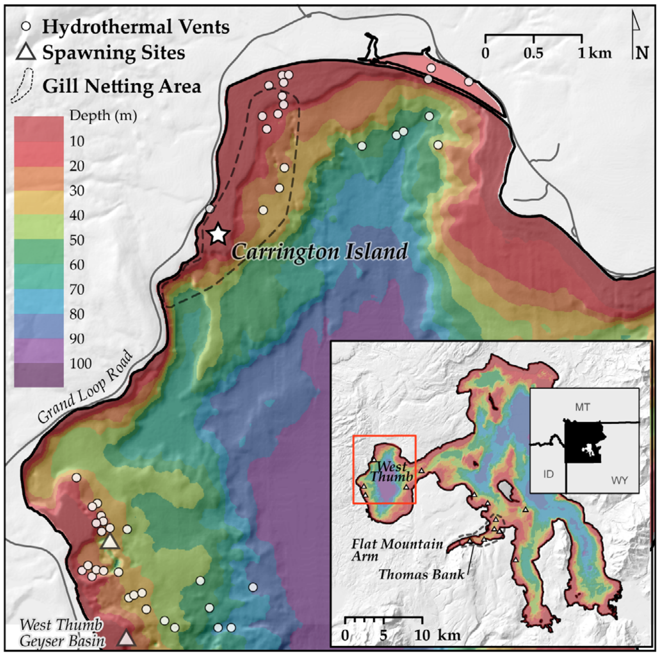

FIGURE 1. The Carrington Island Lake Trout spawning reef (0.5 ha) near the western (leeward) shoreline of the West Thumb basin of Yellowstone Lake, Wyoming. Volcanic forces shaped much of Yellowstone Lake, including the West Thumb. Now, numerous hydrothermal vents (white circles) on the lake floor input heat, influence water chemistry, and may enhance growth of Lake Trout fry emerging from the Carrington Island reef and other known spawning areas in this lake basin.

STUDY AREA

Yellowstone Lake is a large, temperate, meso-oligotrophic lake on the Yellowstone Plateau (2,357 m in elevation), with a highly protected watershed (>3,200 km^2) located within Yellowstone National Park and the Bridger-Teton Wilderness, Wyoming (Figure 1). Geologic processes contributed to the unusual shape of Yellowstone Lake, which straddles the southeastern margin of the Greater Yellowstone Volcanic Caldera (Morgan et al. 2003). Yellowstone Lake has a surface area of 34,000 ha, a mean depth of 48 m, a maximum depth of 137 m, a volume of 1.5×10^{10} m^3, and 239 km of shoreline (Kaplinski 1991), with an abundance of productive littoral areas. Ice covers the lake from late December through late May, and the lake's thermal structure is typically unstable, with a weak and variable thermocline during July, August, and September (Koel et al. 2019, 2020a). About one-third of Yellowstone Lake, including the West Thumb basin (also a volcanic caldera), is directly influenced by hydrothermal activity through hot-water vents and fumaroles (Knight 1975; Aguilar et al. 2002; Morgan et al. 2022). Fourteen Lake Trout spawning reefs were identified (11.4 ha, 0.03% of lake surface area; Figure 1) over the past two decades by gillnetting of spawning fish and by locating telemetered fish; spawning at these reefs was verified based on the presence of Lake Trout embryos (Koel et al. 2020c). Spawning habitat for Lake Trout is predicted to be abundant (Bigelow 2009); therefore, additional, yet-unverified Lake Trout spawning reefs probably exist (Williams et al. 2022). The reef surrounding Carrington Island in the West Thumb basin was confirmed as a spawning reef in 1996 (Ruzycki 2004), 2 years after the initial discovery of Lake Trout (Kaeding et al. 1996), and this reef continues to be one of the most highly used spawning reefs in Yellowstone Lake (Williams et al. 2022). The Carrington Island spawning reef consists of large rock, cobble, and embedded rock substrate, with a spatial extent of 0.5 ha and depths of 0–4 m on all sides of the island, which is located on the leeward side of West Thumb basin, with little fetch (Figures 1 and S1 [available in the Supplement in the online version of this article]).

METHODS

Organic pellet application.— Plant-based sinking pellets (~4.2 mm in diameter) were originally created at the Feed and Nutrition Laboratory of the U.S. Fish and Wildlife Service's Bozeman Fish Technology Center in Montana (see Supplementary Materials in Koel et al. 2020c for details of the ingredients used). Based on earlier in situ experiments, a pellet application density of 1.75 kg/m^2 was expected to achieve embryo mortality greater than 75% in treated areas at 20 cm depth within substrate interstices. A higher pellet density of 3.5 kg/m^2 was required to achieve near 100% mortality at 20 cm depth and at the substrate surface (Koel et al. 2020c). Therefore, treating the entire spawning reef at Carrington Island (0.5 ha) at a density of 3.5 kg/m^2 would require 17,500 kg of pellets. Rangen, Inc. (Buhl, Idaho), produced 17,800 kg (3.56 kg/m^2) and 15,000 kg (3.00 kg/m^2) of pellets during late September in 2019 and 2020, respectively. The cost of the pellets, including delivery to Yellowstone Lake, was US $22,500 each autumn. A feed truck-mounted auger was used to fill seeder/spreader hoppers (Isolair Helicopter Systems; 2,600-45G Dryslinger II; 1.27-m^3 capacity, 118-kg net weight, 10.1-kW [13.5-hp] gasoline motor), which are commonly used in terrestrial systems for broadcast seeding, herbicide and pesticide distribution, and reforestation (Figure S2). Huey helicopters (Bell UH-1H) with long lines were used to transport the Isolair spreaders and apply the pellets to the Carrington Island spawning reef, the outer margins of which had been marked with surface buoys (Figure S1). High-velocity downdraft from the helicopter rotors drove the pellets down into the water and onto the reef with little drift (Figures S3 and S4; Video S1). Pellet applications incurred total helicopter flight times of 6.6 h ($24,100) on October 3, 2019, and 6.0 h ($28,400) on October 5, 2020.

We photographed three 1-m^2 quadrats using a digital camera (GoPro HERO5; 2.3 megapixels) to monitor pellet dissipation from the spawning reef. ImageJ software (Rasband 2018) was used to estimate the percent area of each quadrat covered by pellets at 1 and 12 d posttreatment in 2019. Dissolved oxygen concentrations (mg/L) before and after treatment were recorded using miniDOT loggers (Precision Measurement Engineering; 60-min sampling interval) at eight locations on the substrate surface of the Carrington Island spawning reef in 2019 and on the substrate surface and at 20 cm depth within substrate interstices in 2020. No loggers were placed at 20 cm depth in 2019. One of the eight loggers at 20 cm depth was not recovered in 2020.

Assessing fry production and adult deterrence.— To assess the effectiveness of pellet treatments for causing age-0 Lake Trout mortality, we placed emergent fry traps (like those described by Marsden et al. 1988) on the Carrington Island spawning reef during a 14-d period each spring immediately after ice-off (typically late May) in 2017–2022. The traps were steel-mesh cones with 73-cm-diameter bases; 1-L bottles containing inverted funnels on top of the traps captured fry rising from underneath (Figure S5). The traps were marked with surface buoys and were inspected for the presence of fry by lifting them to the surface about twice per week. Trapping effort was relatively low prior to the pellet treatments; effort was 24, 24, and 10 trap-nights in 2017, 2018, and 2019, respectively. After the pellet treatments, we increased our effort to 126 and 147 trap-nights during 2020 and 2021, respectively. Moreover, we continued fry trapping through June to further assess fry production during both springs after the pellet treatments; the additional effort was 135 and 330 trap-nights during 2020 and 2021, respectively. Control fry traps were placed on an untreated spawning reef, Thomas Bank in the Flat Mountain Arm (Figure 1 inset), with an effort of 75, 157, and 140 trap-nights in 2020, 2021, and 2022, respectively.

To assess adult Lake Trout deterrence from spawning at the Carrington Island reef in the years after the pellet treatments, we (1) used the CPUE of large-mesh (44–76-mm bar measure) gill nets that were set to suppress aggregations near the reef during autumn, (2) used the CPUE of large-mesh gill nets that were set near Thomas Bank and four other spawning reefs in the Flat Mountain Arm, and (3) continued fry trapping on the Carrington Island reef, with an effort of 140 trap-nights in spring 2022. During 2017–2021, gill nets were set with start depths of 2–21 m (mean = 9 m) and end depths of 2–53 m (mean = 29 m) near the Carrington Island reef and within the Flat Mountain Arm in September (Figure 1), the month when Lake Trout spawning peaked in Yellowstone Lake (Williams et al. 2022). A total of 10,282 gill-net effort units (1 effort unit = 100 m of gill net set for one night) was expended over the five spawning periods, with a low of 1,915 effort units in 2019 and a high of 2,184 effort units in 2020 (mean = 2,056 effort units). Gill-netted Lake Trout were killed by piercing their air bladders with a knife and were deposited in deep (>60-m) lake regions in accordance with normal suppression procedures in Yellowstone Lake (Koel et al. 2020a).

Data collection and analysis.— The effect of pellets on the distribution of fry trap CPUE (number of fry per trap-night during spring) among 6 years (2017–2022) was determined using a Kruskal–Wallis test because the data did not meet the assumption of normality. Dunn's post hoc nonparametric pairwise multiple comparison procedure

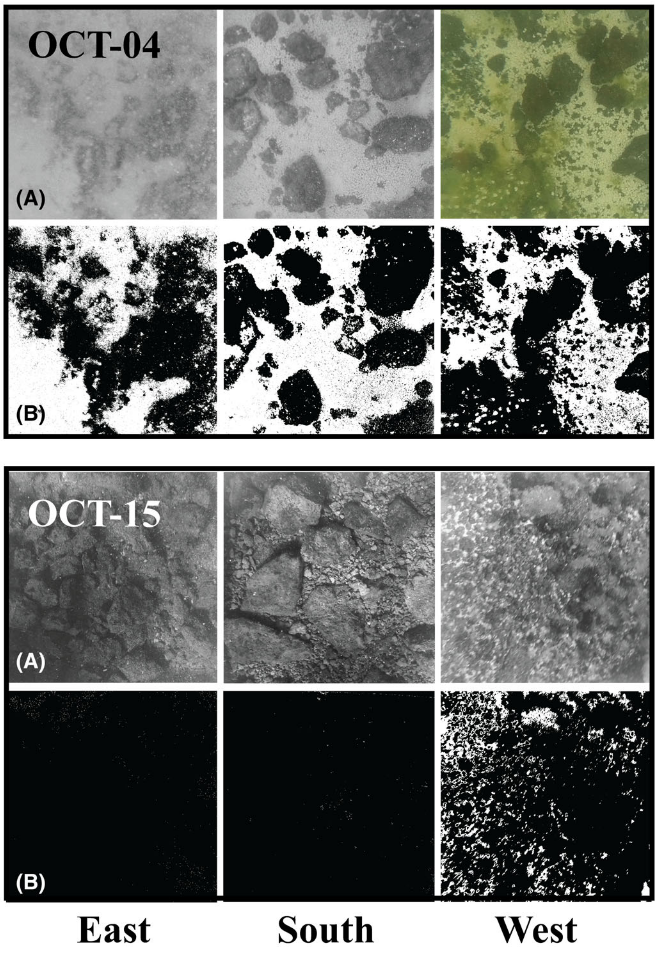

FIGURE 2. **(A)** Photographs on three sides of the Carrington Island spawning reef in 2019 after organic pellet treatment and **(B)** the same photographs enhanced with ImageJ software (Rasband 2018) to further highlight pellets (in white) and estimate dissipation. Pellet coverage across all of the substrate (including exposed rock surfaces) was 40.3–51.3% 1 d after the treatment (October 4; upper panels) and was reduced to 0.3–17.4% 12 d after the treatment (October 15; lower panels).

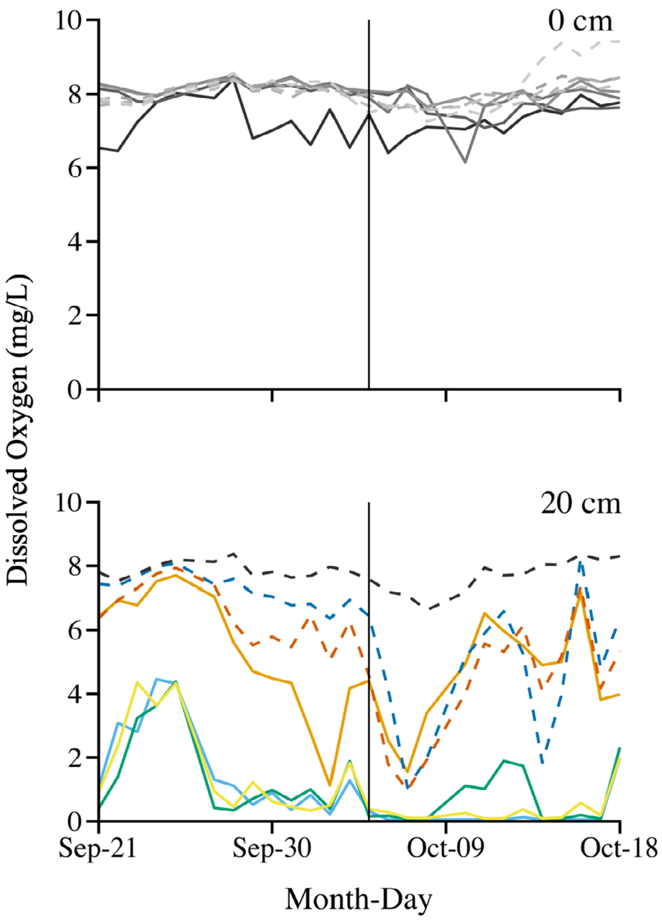

FIGURE 3. Mean daily dissolved oxygen (DO) concentrations (mg/L) at 0 cm (substrate surface) and at 20 cm below the substrate surface, measured before and after organic pellet treatment on October 5, 2020 (vertical solid line), at the Carrington Island spawning reef. Colored lines are from loggers that indicated a decline in DO to lethal concentrations (<3.4 mg/L). Dashed lines represent DO levels from loggers on the south end of the spawning reef, where prevailing currents supplied oxygenated water. Solid lines represent DO levels from loggers on the north end of the spawning reef, which received less oxygenated water and more pellet material (Figure S4).

was used to test for differences between years based on rank sums (α = 0.05; Dinno 2015). One-way ANOVA was used to evaluate for differences in mean large-mesh gill-net CPUE (number of adults/100 m of gill net nightly during autumn) among 5 years (2017–2021), and the Tukey–Kramer post hoc multiple comparison procedure was used to test for differences among years (α = 0.05) because the data were normally distributed. Data were analyzed using the dplyr (Wickham et al. 2022), FSA (Ogle et al. 2022), and car (Fox and Weisberg 2019) packages in R version 4.2.0 (R Core Team 2022).

RESULTS

Visual inspections confirmed that the Carrington Island spawning reef interstices were covered with pellets immediately after the applications (Figure S4). However, pellet persistence was minimal within 2 weeks posttreatment. Pellet coverage across all of the substrate (including exposed rock surfaces) was 40.3–51.3% on October 4, 2019 (1 d after the treatment) and was reduced to 0.3–17.4% by October 15, 2019 (12 d after the treatment; Figure 2). The DO concentration at the substrate surface in 2019 varied but did not decline to lethal levels for Lake Trout embryos (<3.4 mg/L) at most logger locations. In 2020, DO levels did not decline at any of the eight loggers deployed at the substrate surface; however, DO rapidly declined to lethal levels at six of the seven loggers recovered at 20 cm depth within the substrate (Figure 3). The one 20-cm-deep logger that did not record lethal DO was

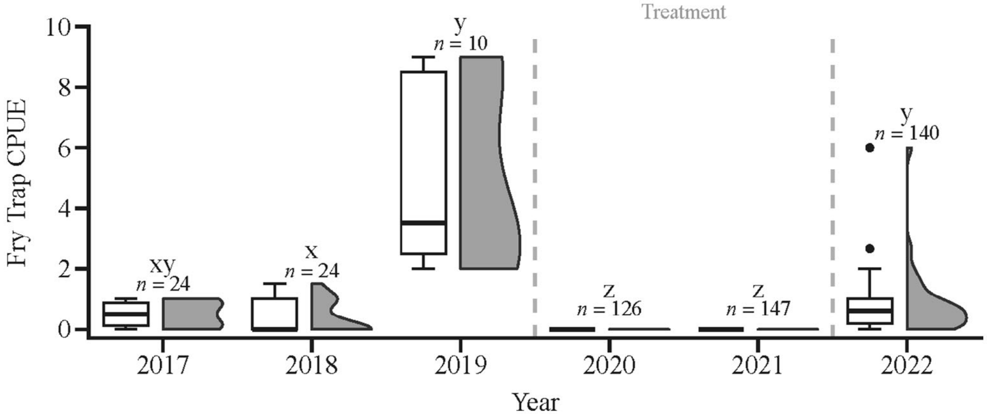

FIGURE 4. Lake Trout fry trap CPUE (number of fry/trap-night) at the Carrington Island spawning reef during 14-d periods immediately after ice-off (typically late May) in 2017–2022. Fry trap sampling in 2020 and 2021 followed treatments with organic pellets during the previous October; for all other years, no treatments occurred during the previous year. Boxes represent the interquartile range (IQR), the black horizontal line in each box is the median, and the bars above and below each box are the maximum (Q3 + 1.5*IQR) and minimum (Q1 − 1.5*IQR) values, respectively. The black circles are data outliers, the gray cloud is the shape of the data distribution, and n is the number of trap-nights. The same letters (x–z) above each year indicate no difference in the distribution of CPUE ($\alpha = 0.05$).

located on the south end of the spawning reef, where prevailing currents (south to north; Figure S4) supplied oxygenated water during the treatments in both years.

Distributions of Lake Trout fry trap CPUE at the Carrington Island spawning reef differed among the 6 years (Kruskal–Wallis $H = 105.09$, df = 5, $P = 2.2 \times 10^{-16}$). Post hoc pairwise comparisons suggested that the pellet treatments reduced Lake Trout fry trap CPUE. In years with no pellet treatment occurring the previous autumn (2017–2019, 2022), a total of 189 Lake Trout fry was captured with 198 trap-nights of effort and the median fry trap CPUE was 0.50 (interquartile range [IQR] = 0.75), 0.00 (IQR = 0.75), 3.50 (IQR = 6.00), and 0.60 (IQR = 0.80) fry/trap-night in 2017, 2018, 2019, and 2022, respectively (Figures 4 and S6). In the years after pellet treatments, no fry were captured during a total of 273 trap-nights of effort; median fry trap CPUE declined to 0.00 fry/trap-night (IQR = 0.00) in both 2020 and 2021. Additional effort of 135 and 330 (465 total additional) trap-nights through June in 2020 and 2021, respectively, resulted in the capture of one fry during 2020. The untreated Thomas Bank (control) spawning reef continued to produce fry, but distributions of Lake Trout fry trap CPUE differed among years (Kruskal–Wallis $H = 17.13$, df = 2, $P = 1.9 \times 10^{-4}$). A total of 130 fry was captured with 372 trap-nights of effort, and the median fry trap CPUE was 0.25 (IQR = 1.12), 0.00 (IQR = 0.00), and 0.00 (IQR = 0.30) fry/trap-night in 2020, 2021, and 2022, respectively (Figure S7).

Pellet treatments did not deter Lake Trout adults from spawning on the Carrington Island reef in subsequent years, as indexed by large-mesh gill-net CPUE from 2017 to 2021 (Figures 1 and 5; ANOVA: $F_{4,\ 25} = 1.954$, $P = 0.133$). Prior to the pellet treatments, mean gill-net CPUE was 1.3 (95% CI = 0.8–1.8), 1.0 (95% CI = 0.2–1.8), and 0.8 (95% CI = 0.5–1.2) adults/100 m of net nightly in 2017, 2018, and 2019, respectively (Figure 5). After the pellet treatments, gill-net CPUE remained unchanged, with a mean of 0.6 (95% CI = 0.2–0.9) and 0.8 (95% CI = 0.1–1.6) adults/100 m of net nightly in 2020 and 2021, respectively. Pellet treatments of Carrington Island did not increase adult CPUE elsewhere. Large-mesh gill-net CPUE within the Flat Mountain Arm declined (ANOVA: $F_{4,\ 84} = 15.687$, $P = 1.263 \times 10^{-9}$). Mean gill-net CPUE was 1.5 adults/100 m of net nightly (95% CI = 1.1–2.0) in 2017 and declined to 0.6 (95% CI = 0.4–0.7), 0.6 (95% CI = 0.4–0.7), 0.5 (95% CI = 0.4–0.7), and 0.6 (95% CI = 0.5–0.7) adults/100 m of net nightly in 2018, 2019, 2020, and 2021, respectively (Figure S8).

DISCUSSION

The realization that high survival of prerecruit Lake Trout may offset increased gill-net mortality of older age-classes heightened our interest in an IPM approach with complementary suppression methods targeting prerecruit life stages in Yellowstone Lake (Koel et al. 2020a). Size- or age-selective mortality (i.e., uneven mortality across life stages; sensu Karatayev et al. 2015) of suppressed (gill-netted) Lake Trout may be increasing juvenile recruitment and total population abundance through an overcompensatory response (Schröder et al. 2014; Grosholz et al. 2021). Although predation on Yellowstone Cutthroat Trout is reduced, density-dependent processes may be confounding removal efforts (Zipkin et al. 2008, 2009; Evangelista et al. 2015; Weber et al. 2016; Walsworth

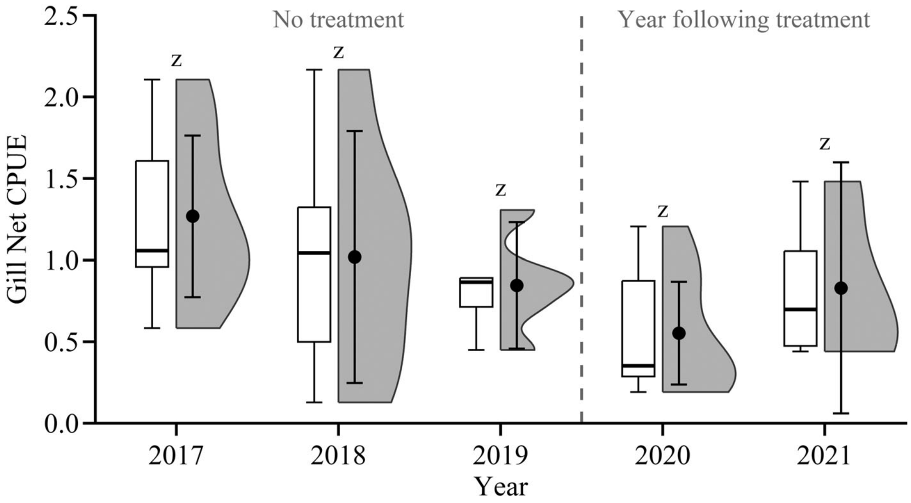

FIGURE 5. Lake Trout CPUE (number of adults/100 m of gill net nightly) in large-mesh gill nets set near Carrington Island during the Lake Trout spawning period in September of 2017–2019 (years with no pellet treatment occurring in the previous year) and 2020–2021 (years with a pellet treatment occurring in the previous year). Boxes represent the interquartile range (IQR), the black horizontal line in each box is the median, and the bars above and below each box are the maximum (Q3 + 1.5*IQR) and minimum (Q1 − 1.5*IQR) values, respectively. The black circle is the mean with 95% CI (black error bar), and the gray cloud represents the shape of the data distribution. The same letter (z) above each year indicates no difference in CPUE (α = 0.05).

et al. 2020). We sought methods to reduce prerecruit survival and offset these effects (Hilborn and Walters 2021). We demonstrated that organic pellets can be transported and applied across an entire spawning reef in a large subalpine lake to induce decomposition and localized reduction of DO through increased biological oxygen demand, thereby increasing the mortality of invasive prerecruit fish (Koel et al. 2020c). The method did not cause deterrence of spawning adults, which would further complicate population suppression in future years.

Treatment of spawning areas to suppress invasive prerecruits is appealing because an entire cohort is immobile and temporarily concentrated in small areas of Yellowstone Lake. Free-swimming juvenile and adult life stages are far more widespread and challenging to remove, especially when occurring in sympatry with desired species (Britton et al. 2011; Hansen et al. 2019b). The strategy requires locating spawning areas and documenting their relative use, which for Lake Trout can be accomplished by acoustic telemetry of adults during autumn (Flavelle et al. 2002; Dux et al. 2011; Siemiantkowski et al. 2022; Williams et al. 2022). In addition, microhabitats consisting of the most suitable (and productive) substrate are typically located within large spawning areas (Marsden et al. 1995; Muir et al. 2012). These microhabitats can be located by fine-scale telemetry of spawning adults (Binder et al. 2018) or visually by scuba divers or remotely operated vehicles (Farha et al. 2020). The spatial extent of these microhabitats can be delineated using side-scan sonar (Richter et al. 2016; Dow 2018; Siemiantkowski et al. 2022) and then can be specifically targeted to increase prerecruit suppression efficiency.

Assumptions of our study were that the timing of Lake Trout fry dispersal from the Carrington Island spawning reef did not vary greatly among years and that the absence of fry production on the Carrington Island reef in 2020 and 2021 was not caused by confounding factors other than the pellet treatments. Lake Trout in Yellowstone Lake spawn earlier than other invasive (Dux et al. 2011; Siemiantkowski et al. 2022) and native (Marsden et al. 2005) populations at similar latitudes, and water temperatures at most known Yellowstone Lake spawning areas could facilitate hatching (Koel et al. 2020a), emergence, and potentially dispersal months earlier than these events would occur within the native range of the species (Krueger and Ihssen 1995; Ladago et al. 2016). Yellowstone Lake fry contained more food, dispersed later, and achieved a greater maximum length before dispersal than did fry in Lake Champlain, Vermont, within the Lake Trout's native range (Simard et al. 2020). Dispersal from the Carrington Island spawning reef before mid-summer in any year was therefore unlikely. Moreover, fry were captured in fry traps placed at Thomas Bank and other spawning reefs during the spring in 2020 and 2021, indicating that the complete absence of fry at Carrington Island in those years was probably caused by the pellet treatments.

Treatment of spawning reefs with organic material may unintentionally increase primary production through nutrient addition or may reduce abundances of nontarget benthic macroinvertebrates through DO limitation. Nitrogen and phosphorus co-limited periphyton before the spawning reef treatments but not after (Lujan et al. 2022). However, the ingredients in the pellets (vitamin E, phytoestrogen, and soybean oil) reduced the growth of primary producers, possibly offsetting the increased growth caused by nutrients (Lujan et al. 2022). The probability of mortality of limnephilid caddisflies was more than three times higher in organic (carcass) treated spawning reefs than in control reefs, whereas mortality of the amphipods *Gammarus lacustris* and *Hyalella azteca* did not differ (Briggs et al. 2021). Amphipods are abundant and make up a large proportion of fish diets in Yellowstone Lake (Glassic et al. 2021; Glassic 2022). Nevertheless, adverse ecosystem-scale effects are unlikely (Siemiantkowski et al. 2022) because the total surface area of all 14 known spawning reefs (11.4 ha) represents only 0.03% of the surface area of Yellowstone Lake (Koel et al. 2020c) and pellets are applied in autumn, thus providing sufficient time for decomposition and dispersal before the growing season. Accordingly, only limited short-term ecological effects were detected after treatments with organic material (Lujan 2020; Briggs et al. 2022). However, if pellet treatments are implemented at a larger scale in the future, monitoring will assess nutrient dynamics and whole-lake metabolism to guide management practices if unintended effects are detected. If needed, the trophic effects of pellet additions (3.6% N) could be countered by the removal of gill-netted Lake Trout carcasses (about 11% N).

Suppression of Lake Trout prerecruits may be inconsequential if the mortality caused by pellet treatments is not additive; survival of prerecruits is naturally low (Healey 1978). Although the relative contribution to recruitment from each of the 14 spawning reefs in Yellowstone Lake is unknown, we contend that Carrington Island is among the most productive because it was the first spawning reef discovered during the early stages of the Lake Trout invasion (Ruzycki 2004), it has higher-quality spawning substrate than most other known spawning areas (angular rock with abundant interstices; Koel et al. 2020c), and it continues to rank highest based upon individual days of use (product of mean individuals per survey and mean length of stay) by telemetered spawning adults (Williams et al. 2022). Telemetry studies have demonstrated that Lake Trout in Yellowstone Lake exhibit low spawning reef fidelity (Williams et al. 2022). The high amount of suppression gillnetting on spawning reefs could be altering behavioral traits (Uusi-Heikkilä et al. 2008; Diaz Pauli and Sih 2017), selecting for fish that move more among reefs and that use a broader range of spawning substrate types, some of which are less suitable (e.g., cobble embedded in sand). Although adults probably dispersed to or from other nearby spawning reefs during our study period (Binder et al. 2016), telemetered spawning adults continued to use the Carrington Island spawning reef (Williams et al. 2022). Prerecruit survival in Yellowstone Lake is estimated to be four to six times greater than survival rates within the native range (Syslo et al. 2020) because of ecological release from predators (Keane and Crawley 2002; Bolnick et al. 2010). However, if the Carrington Island spawning reef has been disproportionately productive due to being pioneered early in the invasion, high days of individual use by adults, growth and size-based advantages (Miller et al. 1988; Houde 1997; Sogard 1997; Stige et al. 2019), behavioral advantages (Crowder et al. 1997), or other factors enhancing prerecruit survival (Anderson 1988), the pellet-induced mortalities may be additive (Allen et al. 1998; Allen and Hightower 2010) and contribute to the lakewide Lake Trout population decline.

CONCLUSIONS

Population models indicate that focusing suppression effort on adults is the best strategy for controlling invasive Lake Trout in the western USA (Hansen et al. 2016, 2019a; Syslo et al. 2020); however, incorporating methods that suppress early life stages may also benefit these programs (Syslo et al. 2013; Glassic 2022). Yellowstone Lake is naturally low in species richness, and Lake Trout solely occupy the top (fourth piscivorous) trophic level (Tronstad et al. 2010). Because no native predator fills this niche, suppression gill netting is currently the only large-scale regulatory factor preventing a Lake Trout population rebound. The degree to which gill-netting effort could be reduced after population goals are achieved while also maintaining suppression is uncertain (Syslo et al. 2020; Koel et al. 2020a). Complementary methods that target prerecruits in an IPM approach may increase efficiency and reduce the uncertainty and costs of maintaining gill-netting suppression over the long term. The cost of eliminating Lake Trout recruitment from the Carrington Island spawning reef was about $50,000 over a period of 1–2 d annually. Pellet treatments while cohorts are concentrated on all known spawning reefs (11.4 ha) would require 199,500 kg of pellets at a cost of $250,000 and may ultimately reduce the more than $2 million spent annually on gill-netting suppression of free-swimming life stages in Yellowstone Lake (Koel et al. 2020c). Moreover, treatment of spawning reefs with pellets does not elicit deterrence by Lake Trout adults and avoids the Yellowstone Cutthroat Trout bycatch mortality incurred by suppression gill nets. The effect of eliminating recruitment from the Carrington Island spawning reef on the lakewide Lake Trout population remains unknown. However, additional spawning reefs in Yellowstone Lake are also suitable for aerial application of pellets due to their shallow depths and relative proximity to roads and helicopter landing zones (Koel et al. 2020a, 2020c), and these areas could be treated to cause additional mortality of prerecruits. Research and development of new, additional complementary suppression methods in the future should focus on deeper, more remote spawning reefs that may be less suitable for aerial application of pellets.

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SUPPORTING INFORMATION

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