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ORIGINAL ARTICLE

Fish carcass deposition to suppress invasive lake trout through hypoxia causes limited, non-target effects on benthic invertebrates in Yellowstone Lake

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Abstract

Invasive species can have negative effects on native biodiversity and ecosystem function, and suppression is often required to minimize the effects. However, management actions to suppress invasive species may cause negative, unintended effects on non-target taxa. Across the United States, lake trout (*Salvelinus namaycush*) are invasive in many freshwater ecosystems, reducing native fish abundance and diversity through predation and competition. In an integrated pest management approach, lake trout embryos in Yellowstone Lake, Wyoming, are suppressed by depositing lake trout carcasses onto spawning sites; the carcasses reduce dissolved oxygen concentrations as they decay, causing embryo mortality. We conducted a field experiment during one ice-free season at four sites in Yellowstone Lake to investigate the non-target effects of carcass treatment on benthic invertebrates, which could have consequences for native fish diets. While overall invertebrate density and biomass did not respond to carcass treatment, Chironomidae midges and Sphaeriidae fingernail clams decreased in abundance. Carcass treatment altered invertebrate community structure based on density, but not biomass. Carcass treatment to suppress invasive fish embryos has spatially localized, non-target effects on some benthic invertebrate taxa. Given the small spatial extent of carcass treatment within the lake, we conclude it is unlikely that carcass treatment will alter food availability for native fishes.

KEYWORDS

applied limnology, dissolved oxygen, integrated pest management, invasive species suppression, Salvelinus namaycush

1 | INTRODUCTION

Invasive species are among the greatest threats to native biodiversity, and as they continue to spread globally, the negative effects of invasions are becoming increasingly severe and widespread (Clavero & García-Berthou, 2005; McNeely et al., 2001). In addition to altering native biodiversity, invasive species jeopardize ecosystem processes, with significant economic and cultural ramifications (Paini et al., 2016; Pimentel et al., 2005; Pejchar & Mooney, 2009). To mitigate the negative effects of invasive species, managers implement suppression actions, but some management actions may have unintended, negative effects on non-target species and ecosystem function (Simberloff et al., 2013; Zavaleta et al., 2001). Possible non-target effects include mortality of native species in response to the suppression method (Mangum & Madrigal, 1999), trophic cascades caused by the removal of an invasive predator in systems with multiple invaders (Bergstrom et al., 2009), the opportunity for secondary invasions (Peterson et al., 2020), and the loss of habitat for native species when established invasive species are removed (Sogge et al., 2008). Thus, considering non-target effects is vital for maintaining biodiversity and ecosystem services through invasive species management.

One species that has prompted the implementation of large-scale, multifaceted invasive species management programmes is the lake trout (*Salvelinus namaycush*), an apex predatory invasive fish that has been introduced to over 200 waterbodies throughout the western United States (Martinez et al., 2009). Lake trout alter ecosystems by preying on and competing with native fishes, resulting in cascading consequences for both aquatic and terrestrial food webs (Ellis et al., 2011; Vander Zanden et al., 2003). In Yellowstone Lake, Wyoming, invasive lake trout consume native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*), reducing the availability of this key prey item for native predators such as bear and osprey (Koel et al., 2019). To restore native Yellowstone cutthroat trout in this iconic ecosystem, the National Park Service (NPS) removes lake trout (age 2+) by gill netting and is investigating additional, novel suppression methods to target earlier life stages (Doepke et al., 2017; Koel, Arnold, et al., 2020). The NPS deposits carcasses from gill netting operations onto lake trout spawning sites in the littoral zone beginning in late summer to discourage egg deposition on preferred spawning sites. Carcass treatment continues through the autumn spawning period (late September to early October) to smother lake trout embryos that have been deposited by female fish (Poole et al., 2020; Thomas et al., 2019). When applied at densities of $\geq$7 kg wet mass/m^2, the carcasses cause short-term (<2 weeks) reductions in dissolved oxygen (DO) concentrations as they decay, causing up to 100% mortality in lake trout embryos (Poole et al., 2020; Thomas et al., 2019).

Carcass addition alters water chemistry and increases otherwise limiting nutrients (Lujan et al., 2022; Theriot et al., 1997); however, it is unknown how this action affects organisms such as benthic invertebrates in the littoral zone of a lake. In lotic ecosystems, fish carcass additions are commonly used to stimulate stream productivity in response to reduced runs of anadromous fish. This management strategy has been successful in increasing periphyton and benthic invertebrate biomass, consumption of invertebrates by fish, and fish production (Collins et al., 2016; Wipfli et al., 2004). Salmon carcasses provide direct and indirect food sources for benthic invertebrates, which can increase growth rates, biomass, and abundance of some taxa (Chaloner & Wipfli, 2002; Wipfli et al., 1998). However, environmental factors, such as light limitation, background nutrient levels, and discharge, can reduce the effect of carcass additions on basal resource production in some ecosystems (Ambrose et al., 2004; Bellmore et al., 2014; Chaloner et al., 2007). Most research to date on carcass additions has been performed in rivers, and their non-target effects in lakes are unknown; however, natural salmon spawning runs in lakes suggest that nutrients from carcass material are readily incorporated into the food web (Denton et al., 2010; Schmidt et al., 1998). Additionally, invertebrates have been documented consuming and colonizing carcass material in lentic systems (Lyabzina 2013; Premke et al., 2010). Non-target influences on aquatic benthic invertebrates could have major consequences because invertebrates are important components of food webs and contribute to nutrient cycling, energy transfer, and decomposition (Covich et al., 1999).

Carcass treatments may differentially affect the abundance and biomass of benthic invertebrate taxa depending on their physiological characteristics (Dolédec et al., 2011). Hypoxic or anoxic conditions may result in mortality, or reduction in growth or reproduction, in sensitive invertebrate taxa (Briggs et al., 2021; Connolly et al., 2004; Nebeker 1972). Sessile taxa may be particularly susceptible to mortality in response to carcass treatment due to an inability to move away from unfavourable conditions caused by carcass decay, such as reduced DO and increased fungal and bacterial growth (Fenoglio et al., 2010; Poole et al., 2020). Mobile taxa may emigrate from the area, resulting in declines in density. Factors such as algal blooms that influence oxygen concentrations are a global concern, and reductions in oxygen availability are increasing in economically important lake and marine shoreline environments (Jenny et al., 2016; Tellier et al., 2022); thus, understanding invertebrate responses to hypoxic environments has implications beyond Yellowstone Lake. Some invertebrate taxa, particularly those tolerant of low DO and likely to consume carcass material, may benefit from the addition of carcasses into the littoral zone (Chaloner & Wipfli, 2002; Collins et al., 2016). In Yellowstone Lake, benthic invertebrates, and particularly amphipods, are an important food source for fish. Amphipods comprise up to 99% and 81% of Yellowstone cutthroat trout and lake trout diets, respectively (Syslo et al., 2016), so changes to invertebrate populations, either positive or negative, could alter food availability for fish.

We conducted an in situ experiment at four sites in Yellowstone Lake during one ice-free season to determine how carcass treatment to suppress lake trout embryos affects invertebrate communities. Our objectives were (1) to determine how effectively carcass treatment was implemented by quantifying the amount of carcass material present at treatment sites and measuring changes in DO; and (2) to determine if carcass treatment altered invertebrate density, biomass, and community structure by characterizing general trends in invertebrate communities as well as specifically documenting patterns of relatively abundant taxa, hypoxia-sensitive taxa, or immobile taxa. We

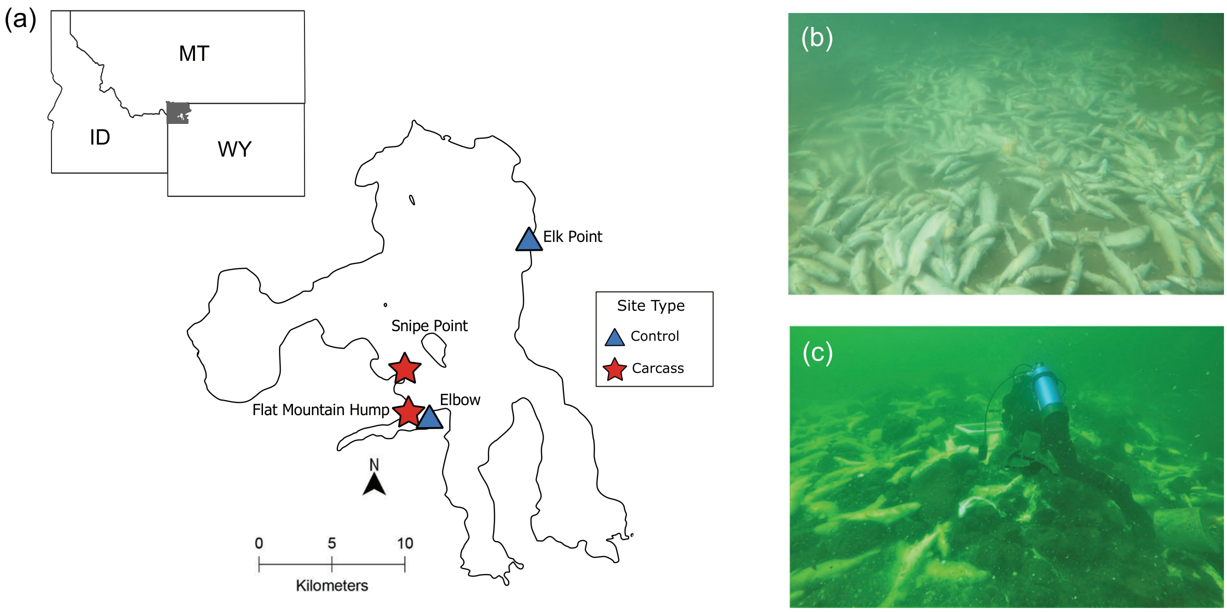

FIGURE 1 (a) Sampling locations within Yellowstone Lake in Yellowstone National Park (grey inset) in the northwestern states of Montana, Idaho, and Wyoming, USA. (b) Lake trout carcasses covering the substrate at Snipe Point on September 16, 2019. (c) M. Briggs dives to collect samples during the carcass treatment period at Flat Mountain Hump on September 18, 2019. Photo credit: S. Poratti

predicted that carcass treatment would reduce DO concentrations at treatment sites and would differentially affect benthic invertebrate taxa, with tolerant taxa such as amphipods increasing in abundance due to the availability of carcass material as a food source, and sensitive taxa decreasing in abundance due to reduced DO concentrations. Our findings provide some of the first description of potential non-target effects of invasive fish suppression using carcass material in lake ecosystems and can be used to inform future invasive fish suppression efforts using carcass treatment.

2 | METHODS

2.1 | Study area

Yellowstone Lake is located in Yellowstone National Park in northwestern Wyoming at an elevation of 2357 m (Figure 1). With a surface area of 340 km^2, it is the largest high-elevation lake in North America and is generally ice-covered from late December to mid-May. Yellowstone Lake is a mesotrophic, dimictic lake that thermally stratifies in the summer (Kilham et al., 1996). It has complex bathymetry, with a mean depth of 43 m, a maximum depth of 148 m, and hydrothermal vents distributed throughout the northern and western regions of the lake (Kaplinski, 1991). Benthic invertebrate assemblages are dominated by two amphipod genera, *Hyallela* and *Gammarus*, which together comprise approximately 55% of invertebrate biomass (Wilmot et al., 2016).

Lake trout are a large, piscivorous species that is native throughout Canada and parts of the northern United States. Lake trout were first discovered in Yellowstone Lake in 1994 and reached peak abundance in 2012, with an estimated adult population of nearly 1 million individuals (Koel, Arnold, et al., 2020). The lake trout suppression programme in Yellowstone Lake began in 1995 and currently removes about 300,000 adult lake trout each year (Koel, Arnold, et al., 2020). More than 4 million were killed between 1995 and 2021 with a majority of the carcasses deposited into deep areas (>70 m) of the lake (Koel et al., 2022). This extensive suppression effort has reduced adult lake trout abundance by >80% since 2012; however, recruitment of young lake trout remains high (Koel, Arnold, et al., 2020). The lake trout spawn from late September to early October (Heredia et al., 2021) at sites characterized primarily by cobble and bedrock substrate; confirmed lake trout spawning sites range in size from 0.3 to 2.0 ha and comprise 0.03% of the total area of Yellowstone Lake (Koel, Thomas, et al., 2020). To curtail lake trout recruitment and improve suppression efficiency, the NPS has developed a novel method that deposits carcasses directly on spawning areas in the littoral zone of the lake to induce decomposition and cause mortality in lake trout embryos via oxygen depletion (Poole et al., 2020; Thomas et al., 2019).

2.2 | Carcass treatment

Carcass treatment occurred at two lake trout spawning sites, Flat Mountain Hump and Snipe Point, from 12 August to 2 October 2019 (Figure 1). Of the 14 confirmed lake trout spawning sites on Yellowstone Lake (Koel, Thomas, et al., 2020), these two sites were selected because they were deep enough and far enough from shore to avoid attracting terrestrial wildlife (Thomas et al., 2019) and were adjacent to frequently targeted suppression netting locations to facilitate the transportation of lake trout carcasses. Carcass treatment only occurred at two spawning sites due to limited availability of lake trout carcasses during the autumn and logistical difficulties of transporting carcasses across a large lake. Two control sites, Flat Mountain Elbow and Elk Point, were selected based on similar depths, substrate type, and logistical considerations, including avoiding sites frequently targeted by suppression netting. Substrate at carcass treatment and control sites was dominated by bedrock or cobble (<250 mm), and the sites varied from 2.5 to 9.5 m deep. Limited carcass treatment occurred at both treatment sites in 2018 as part of a pilot study, but carcass coverage was extremely low (<3% coverage in October 2018). When sampling began in June 2019, no carcass material was observed at Snipe Point, and small amounts were observed at Flat Mountain Hump (<1% coverage). Carcass treatment sites were marked with buoys anchored to the substrate with concrete blocks. Gill netting crews dumped whole and shredded lake trout carcass material from boats within 5 m of marker buoys. Carcass dumps occurred opportunistically when gill netting crews had been fishing near the carcass treatment sites. Approximately 6000 kg of fish carcass material were deposited at each carcass treatment site.

To measure DO, scuba divers secured one miniDOT logger (Precision Measurement Engineering) to the substrate surface at each carcass treatment and control site. The loggers recorded DO (mg/L) at 60-min increments throughout the entire sampling period (17 June–1 October 2019). See Supporting Information for details on methods and data analysis.

To monitor carcass cover at the carcass treatment sites, we photographed a 1 m^2 quadrat placed on the substrate surface using a GoPro underwater camera. We took five adjacent photographs of the quadrat along a 0° heading, starting directly north of the concrete anchor marking the site, and we took five additional photographs along a 180° heading, directly south of the concrete anchor. We used ImageJ (Rashband, 2018) to calculate the percent area of each quadrat covered by carcass material and averaged across all 10 quadrats to estimate mean carcass cover every 2 weeks during the carcass treatment period, resulting in four measurements per site.

2.3 | Invertebrate collection

At each site, triplicate benthic invertebrate samples were collected monthly for 3 months before carcass treatment started (17 June–11 August 2019) and every 2 weeks (4 sampling intervals) after carcass treatment started (12 August–1 October 2019). To quantitatively sample benthic invertebrates, we used a Scuba diver-operated suction sampler constructed from an electric bilge pump mounted on a plastic cutting board with a 500-μm mesh collection net (Cross et al., 2011). We randomly placed a 0.25 m^2 quadrat on the substrate surface and used the suction sampler to collect invertebrates within the quadrat. While we did not use a quantitative method to randomly select quadrat placement locations, we placed the quadrat where the substrate was undisturbed by divers, and the same diver placed the quadrat for each sample to reduce sampling variability. After surfacing, we rinsed all contents of the collection nets into a 500-μm sieve and preserved all material retained by the sieve in 75% ethanol.

In the laboratory, we subsampled invertebrate samples to the smallest fraction that included ≥100 individuals using a plankton splitter. Subsample fractions ranged from 1/2 to 1/16. We sorted invertebrates from debris and organic material, and identified individuals to the lowest practical taxonomic level, which was often genus or family and occasionally order (Merritt et al., 2008; Rabeni & Wang, 2001). We measured 25 randomly selected individuals of each taxon and used published length-mass regressions to calculate biomass (AFDM) of each taxon (Benke et al., 1999; Bottrell et al., 1976; Méthot et al., 2012).

2.4 | Data analysis

To determine if invertebrate density and biomass changed in response to carcass treatment, we assessed the interaction between time (a categorical variable with two levels: before and during treatment) and treatment using linear mixed effects or zero-inflated negative binomial (ZINB) models. Our models included treatment, time, and their interaction as fixed effects, and sampling date nested within site as random effects to account for temporal and spatial autocorrelation. We used linear mixed effects models for most metrics, and we natural log-transformed response variables when necessary to meet model assumptions. Because we expected the control and treatment sites to change over time due to seasonal variation, we used the interaction between time and treatment as evidence of a treatment effect. We focused on the three most abundant taxa (*Gammarus* sp. and *Hyallela* sp. amphipods and non-Tanypodinae Chironomidae; Table S1), hypoxia-sensitive taxa (Ephemeroptera and Trichoptera), and sessile taxa (Sphaeriidae). We chose Ephemeroptera and Trichoptera to represent hypoxia-sensitive taxa instead of a metric including Ephemeroptera, Trichoptera, and Plecoptera (EPT, Karr 1991) because Plecoptera are not present in Yellowstone Lake. Because some taxa were present at control sites but not carcass sites, our analyses of Ephemeroptera and Trichoptera density and biomass combined taxa within these two orders and only included taxa observed at control and carcass sites. We used ZINB models for Ephemeroptera and Trichoptera density and Sphaeriidae density, because these data were overdispersed and had many zeros (Brooks et al., 2017). We used Akaike information criterion corrected for small sample sizes to select ZINB models over other possible models (Table S2). We did not perform statistical analysis on hypoxia-sensitive taxa (i.e., Ephemeroptera and Trichoptera) biomass or Sphaeriidae biomass because ZINB models are only appropriate for count data (such as abundance), and these overdispersed data did not meet model assumptions for other types of analytical tools. Statistical significance was tested with an alpha value of 0.1 because of variation expected from such a large-scale experiment with low replication, to improve our detection of invertebrate responses, and to reduce the possibility of Type II error. Model assumptions were examined and met. All statistical analyses were conducted in R version 3.6.2 (R Core Team, 2019) using the lme4 package for linear mixed effects models

(Bates et al., 2015) and the glmmTMB package for zero-inflated negative binomial models (Brooks et al., 2017).

We used non-metric multidimensional scaling based on Bray–Curtis dissimilarities to visualize how invertebrate community structure based on untransformed density and biomass responded to carcass treatment (Kruskal, 1964; Minchin, 1987). To test if invertebrate community structure changed in response to carcass treatment, we used a two-way mixed effects permutational multivariate analysis of variance including time, treatment, and their interaction as fixed effects and site as a random effect (Anderson, 2014). We used similarity percentages (SIMPER) analysis to identify the taxa that contributed most to differences in multivariate position by group, which allowed us to interpret changes in community structure (Clarke, 1993). Community analysis was conducted using the vegan package (Oksanen et al., 2019).

3 | RESULTS

3.1 | Dissolved oxygen and carcass cover

Carcass treatment at the scale of whole spawning sites led to a decline in DO concentrations, likely associated with carcass decomposition (Figure 2a,b; Supporting Information). At Flat Mountain Hump, mean daily DO concentrations declined below 3.4 mg/L (a threshold known to cause lake trout embryo mortality, Koel, Thomas, et al., 2020) after 4 weeks of carcass treatment and remained low for the remainder of the carcass treatment period. At Snipe Point, mean daily DO concentrations declined below 3.4 mg/L after 5 weeks of carcass treatment and then fluctuated from 2.0 to 6.6 mg/L until the 8th week of treatment, when DO concentrations were consistently hypoxic at <1.0 mg/L. Mean percent carcass cover at Flat Mountain Hump was 21.6% and 20.1% on the second and eighth weeks of carcass treatment, respectively (Figure 2c). At Snipe Point, carcass material did not accumulate as quickly, and carcass cover was more variable (Figure 2d), ranging from a mean of <1.0% on the second week of treatment to 30.0% on the eighth week of treatment.

3.2 | Invertebrate response to carcass treatment

Carcass treatment was not associated with detectable changes in the density or biomass of most taxa of benthic invertebrates. Total invertebrate density, densities of *Gammarus* sp. and *Hyallela* sp. amphipods, and density of Ephemeroptera and Trichoptera did not change due to carcass treatment (Figure 3a–c,f; Figure S1; Table S3). The density of non-Tanypodinae Chironomidae decreased in response to carcass treatment ($df = 22$, $t = -3.51$, $p = 0.002$, Figure 3d), with predicted densities decreasing from 567.7 individuals (ind)/m^2 (90% confidence interval [CI] 382.4–2286.1) to 320.5 ind/m^2 (90% CI 227.7–4816.5) at carcass treatment sites and increasing from 557.2 ind/m^2 (90% CI 375.4–832.5) to 1,520.7 ind/m^2 (90% CI 1080.1–3920.0) at control sites during the same time period. Density of Sphaeriidae also decreased in response to carcass treatment ($z = -1.76$, $p = 0.078$,

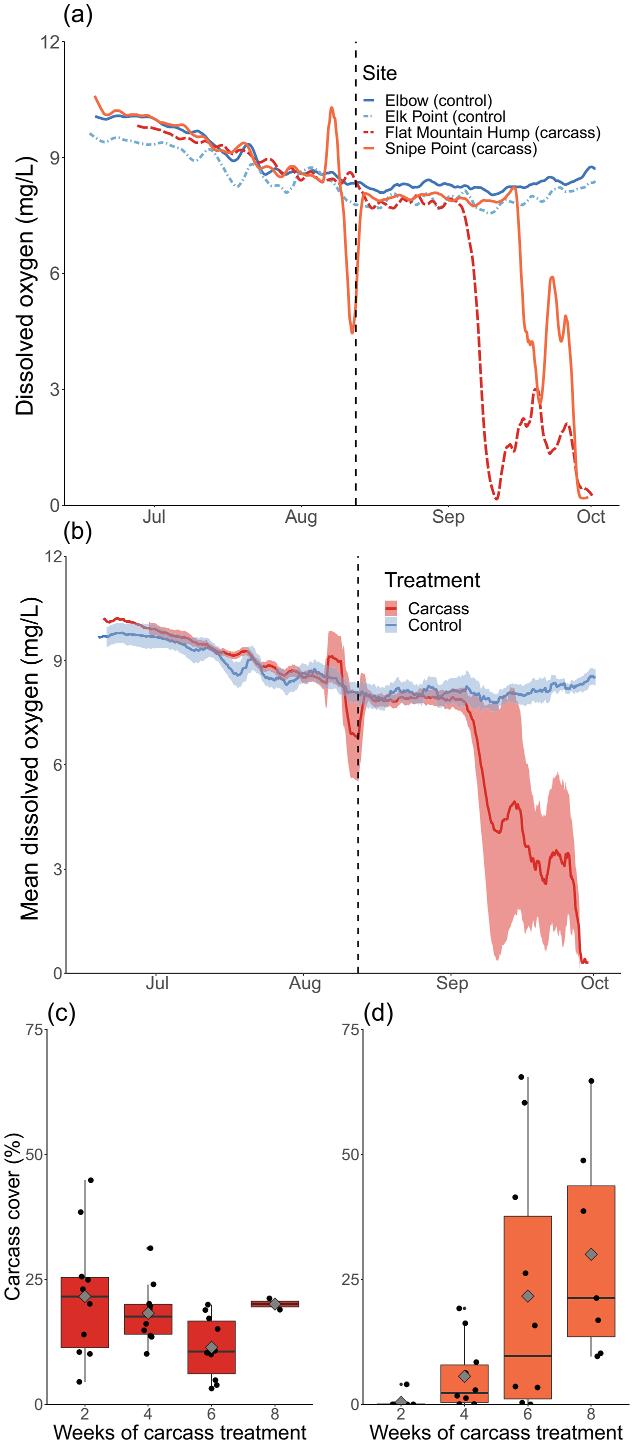

FIGURE 2 (a) Dissolved oxygen at control and carcass sites during the sampling period. The vertical line indicates the beginning of the carcass treatment period. (b) Mean and standard error of dissolved oxygen concentrations at control and carcass sites during the sampling period. The vertical line indicates the beginning of the carcass treatment period. (c) Percent area of the substrate covered with carcass at Flat Mountain Hump and (d) Snipe Point, measured every 2 weeks during the carcass treatment period. Gray diamonds indicate mean carcass cover. We obtained fewer measurements of carcass cover at 8 weeks of carcass treatment because highly decomposed carcass material obscured visibility and prevented accurate analysis of photographs.

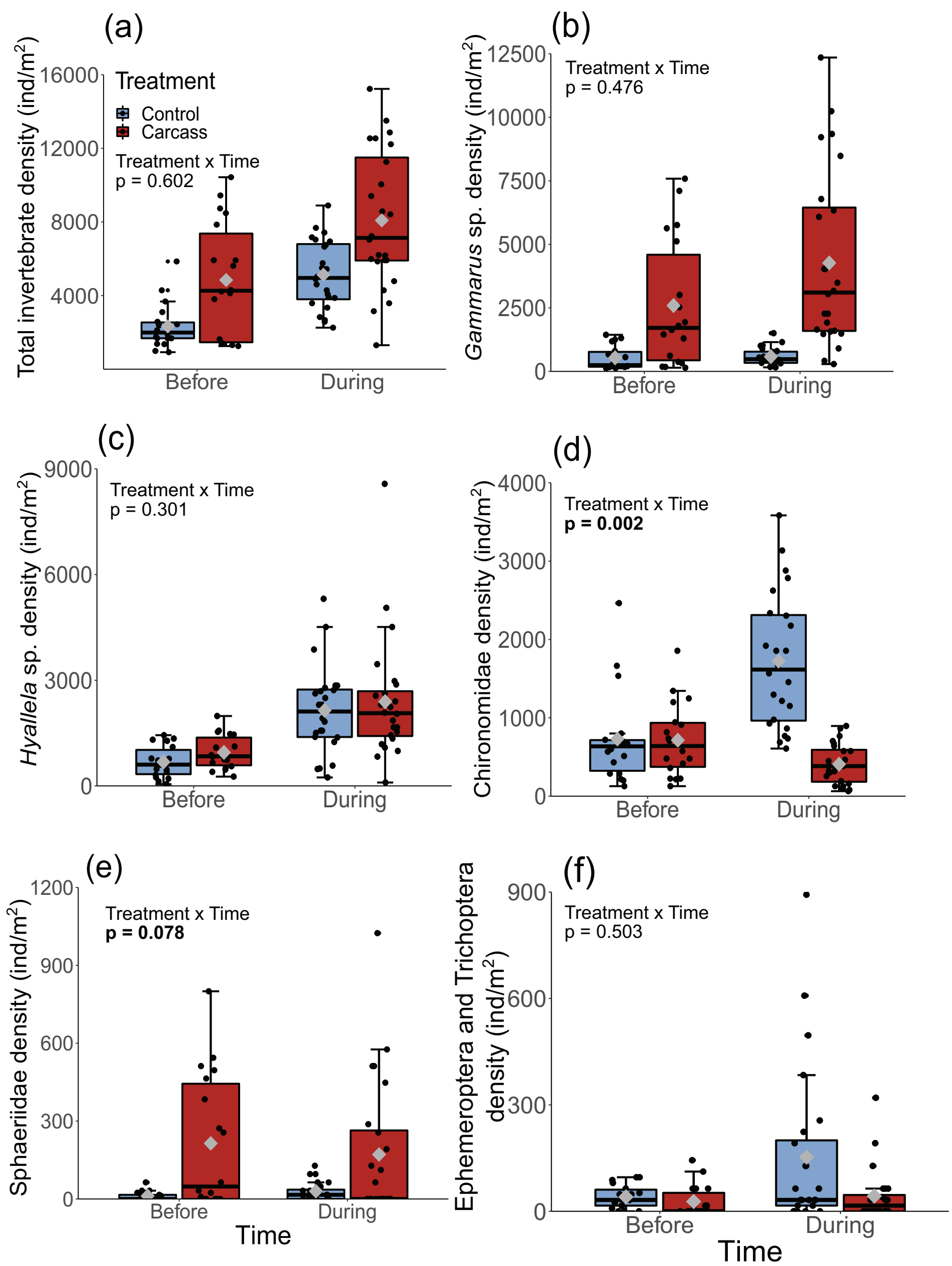

FIGURE 3 Density (ind/m^2) for (a) total invertebrates, (b) *Gammarus* sp., (c) *Hyallela* sp., (d) non-Tanypodinae Chironomidae, (e) Sphaeriidae, and (f) Ephemeroptera and Trichoptera at control sites and carcass treatment sites before (June 17–August 11, 2019) and during (August 12–October 1, 2019) the carcass treatment period. Gray diamonds indicate mean values. *p*-Values are shown for the interaction term between treatment and time and refer to model results, while the figures show raw data. *p*-Values that are significant at the $\alpha = 0.10$ level are shown in bold. Abbreviation: ind, individuals

Figure 3e), with predicted densities decreasing from 49.5 ind/m^2 (90% CI 7.0–352.2) to 34.7 ind/m^2 (90% CI 4.9–247.5) at carcass sites and increasing from 16.6 ind/m^2 (90% CI 2.2–124) to 35.6 ind/m^2 (90% CI 4.9–256.0) at control sites.

Total invertebrate biomass and biomass of *Gammarus* sp. and *Hyallela* sp. amphipods did not change in response to carcass treatment (Figure 4a–c; Figure S2). Biomass of non-Tanypodinae Chironomidae decreased in response to carcass treatment ($df = 22$, $t = -3.07$, $p = 0.006$, Figure 4d), with predicted biomass decreasing from 246.3 mg/m^2 (90% CI 148.3–419.2) to 101.8 mg/m^2 (90% CI 64.9–159.6) at carcass sites and increasing from 155.5 mg/m^2 (90% CI 92.5–261.4) to 389.1 mg/m^2 (90% CI 248.1–610.2) at control sites. Mean biomass of Ephemeroptera and Trichoptera decreased from 87.0 mg/m^2 (90% CI 31.2–137.9) to 70.9 mg/m^2 (90% CI 24.9–111.2) at carcass sites and increased from 105.4 mg/m^2 (90% CI 68.8–141.4) to 381.0 mg/m^2 (90% CI 206.7–544.5) at control sites, indicating a possible reduction in response to carcass treatment (Figure 4f).

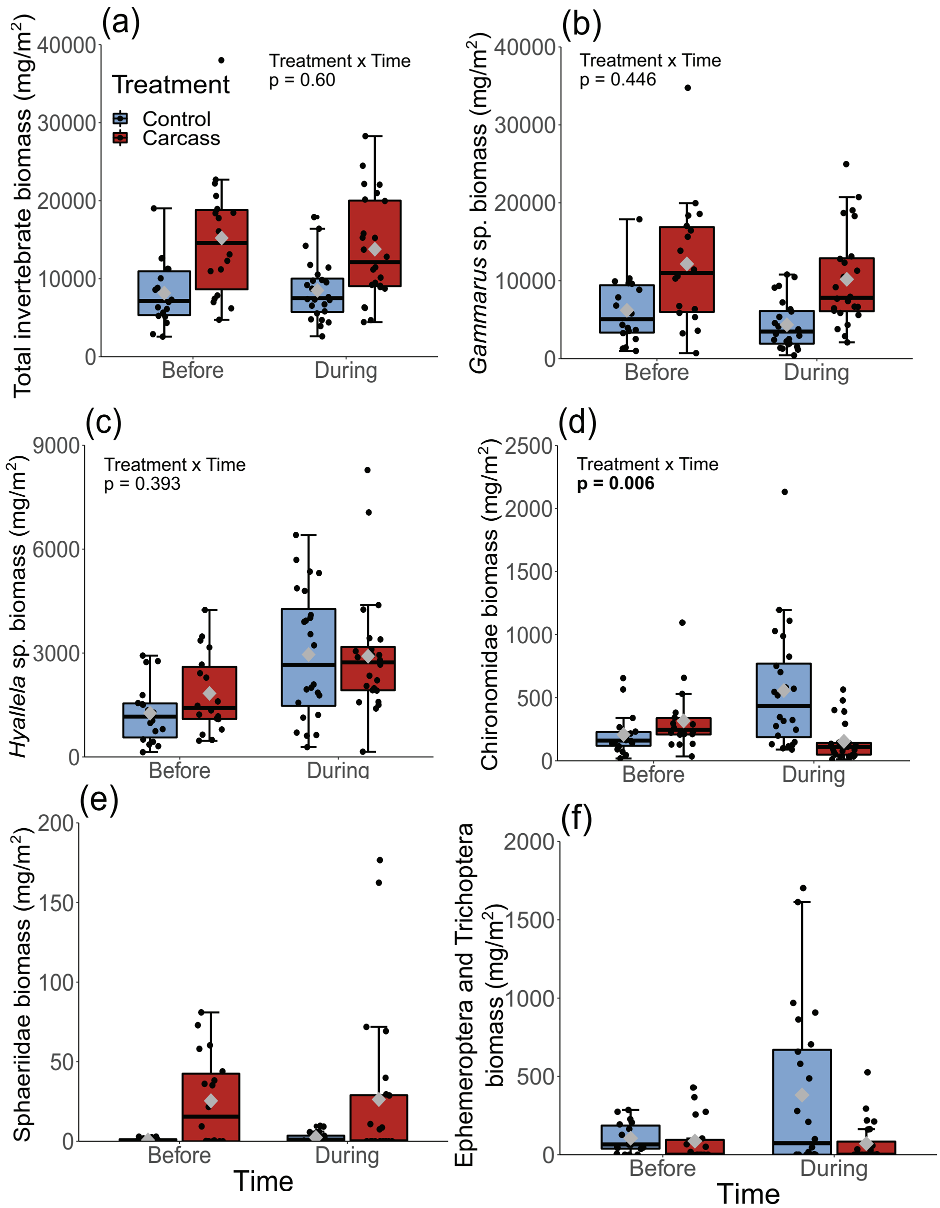

FIGURE 4 Biomass (mg AFDM/m^2) for (a) total invertebrates, (b) *Gammarus* sp., (c) *Hyallela* sp., and (d) non-Tanypodinae Chironomidae, (e) Sphaeriidae, and (f) Ephemeroptera and Trichoptera at control sites and carcass sites before and during the carcass treatment period. Gray diamonds indicate mean values. *p*-Values are shown for the interaction term between treatment and time and refer to model results, while the figures show raw data. *p*-Values that are significant at the $\alpha = 0.10$ level are shown in bold.

Invertebrate community structure based on density changed differently over time at carcass treatment sites compared to control sites, indicating a possible response to carcass treatment (treatment × time $p = 0.012$, Figure 5). Specifically, invertebrate communities at control and treatment sites had low dissimilarity and high overlap before carcass treatment (Figure 5a). Invertebrate communities at control sites became more dissimilar from each other over time, while invertebrate communities at carcass treatment sites maintained low dissimilarity to each other over time. Additionally, overlap between multivariate position representing invertebrate communities at control sites and treatment sites decreased after carcass treatment was initiated. The results of SIMPER analysis indicated that these changes were driven by the three most abundant taxa: *Gammarus* sp., *Hyallela* sp. (Order: Amphipoda), and non-Tanypodinae Chironomidae (Order: Diptera; Table 1). Non-Tanypodinae Chironomidae showed a reduction in relative frequency while *Gammarus* amphipods showed an increase in relative frequency at carcass treatment sites compared to control sites (Figure 6). Invertebrate community structure based on biomass did not change in response to carcass treatment.

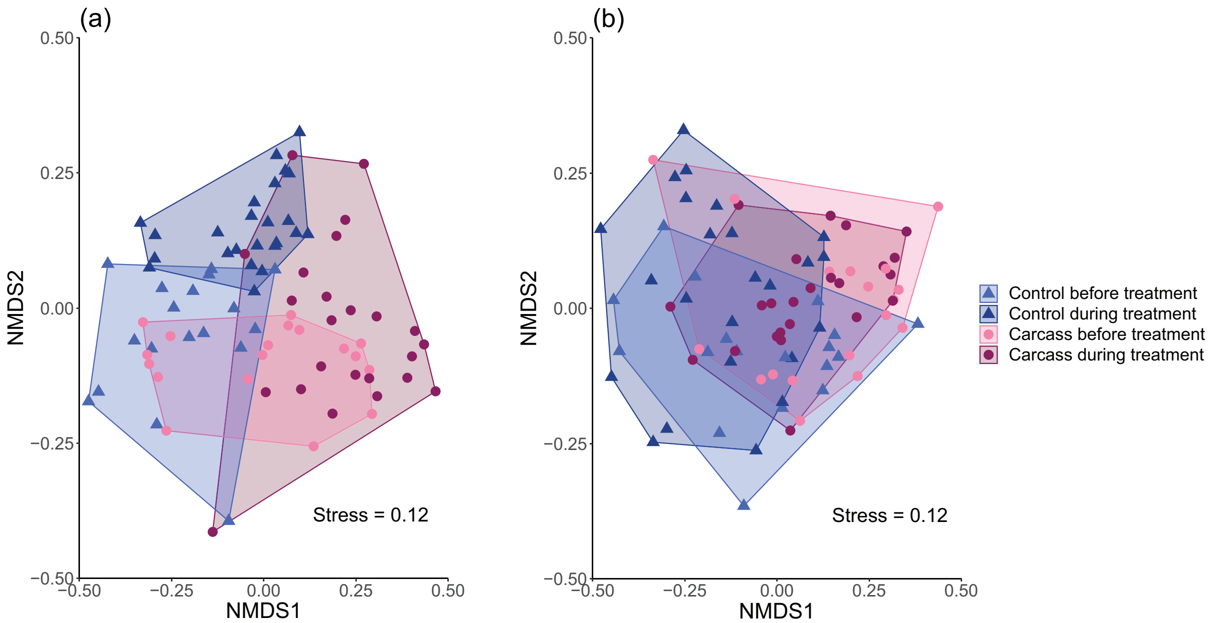

FIGURE 5 Non-metric multidimensional scaling based on Bray–Curtis dissimilarities from invertebrate (a) density and (b) biomass, grouped by treatment and time

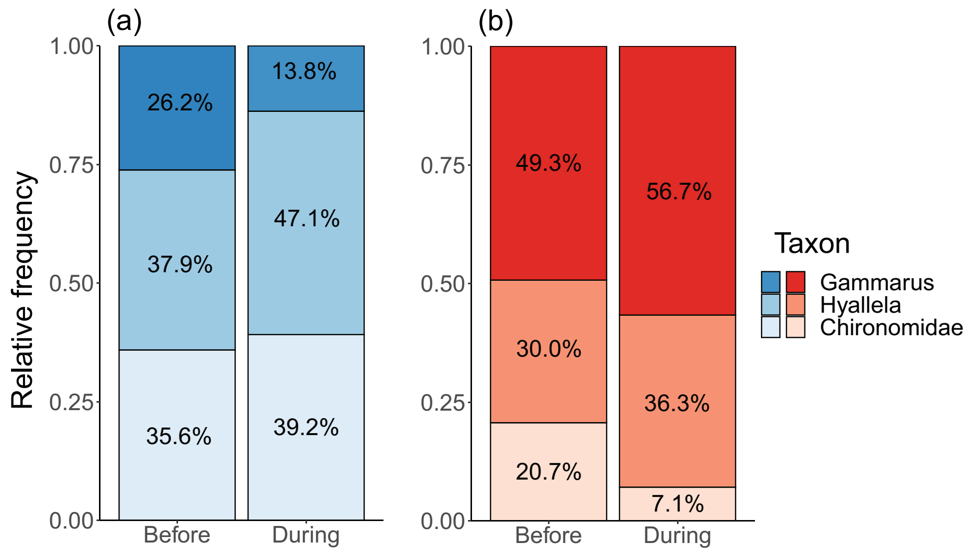

FIGURE 6 Mean relative frequency of the three most abundant taxa, *Gammarus* sp., *Hyallela* sp., and Chironomidae (non-tanypodinae) at (a) control sites (blue) and (b) carcass treatment sites (red) before and during the carcass treatment period

4 | DISCUSSION

Non-target effects of invasive species management can alter ecosystems and harm native species, and they should be considered when management strategies are developed (Zavaleta et al., 2001). We conducted an in situ experiment to investigate the non-target effects of a novel strategy to suppress invasive fish embryos on invertebrates. High carcass cover and low DO concentrations indicated effective implementation of the management strategy and the potential to cause high mortality of lake trout embryos (Poole et al., 2020; Thomas et al., 2019). Carcass treatment did not cause changes in populations of highly abundant *Gammarus* sp. and *Hyallela* sp. amphipods or a change in invertebrate community structure based on biomass; however, carcass treatment altered benthic invertebrate communities by changing community structure based on density and by reducing abundance of Chironomidae and Sphaeriidae.

TABLE 1 Results of similarity percentages (SIMPER) analysis comparing invertebrate communities based on density at carcass and control sites before and during treatment. Results show the percent cumulative contribution to dissimilarities between groups for the three taxa with the highest contributions, as well as the average abundance of each taxon by group

Taxon	Percent cumulative contribution	Mean abundance (ind/m^2)	Mean abundance (ind/m^2)
Control before treatment vs. control after treatment			
		Control before	Control after
Hyallela sp.	37.81	679.8	2146.0
Non-Tanypodinae	66.01	729.8	1724.0
Gammarus sp.	77.46	535.3	580.7
Control before treatment vs. carcass before treatment			
		Control before	Carcass before
Gammarus sp.	47.45	535.3	2592.9
Hyallela sp.	63.59	679.8	950.7
Non-Tanypodinae	79.16	729.8	714.7
Carcass before treatment vs. carcass after treatment			
		Carcass before	Carcass after
Gammarus sp.	48.93	2592.9	4268.33
Hyallela sp.	74.05	950.7	2392.0
Non-Tanypodinae	81.43	714.7	408.7
Control after treatment vs. carcass after treatment			
		Control after	Carcass after
Gammarus sp.	43.14	580.7	4268.3
Hyallela sp.	63.83	2146.0	2392.0
Non-Tanypodinae	81.39	1724.0	408.7

Abbreviation: ind, individuals.

4.1 | Response of amphipods and Chironomidae

Previous research in lotic systems has documented increases in benthic invertebrate density and biomass in response to carcass treatment (Collins et al., 2016; Janetski et al., 2009; Wipfli et al., 1998), particularly for taxa that are likely to colonize carcasses or consume carcass material directly, such as amphipods and Chironomidae (Chaloner et al., 2002; Kline et al., 1997). However, we did not detect increases in total invertebrate density or biomass in response to carcass treatment. We observed amphipods, the dominant benthic invertebrate, on top of lake trout carcasses, suggesting potential for direct consumption. Amphipods consume many food resources, and high-quality food resources such as carcass material can increase growth and fecundity (Cruz-Rivera & Hay, 2000; Ito 2003; Kusano & Ito, 2005; MacNeil et al., 1997). Additionally, mobile taxa such as amphipods may immigrate to sites treated with carcass material and colonize the carcasses, which could cause increases in density and biomass evident at relatively short timescales (Chaloner et al., 2002). However, neither density nor biomass of *Gammarus* sp. or *Hyallela* sp. amphipods increased in response to carcass treatment. Chironomidae density and biomass declined in response to carcass treatment. Many Chironomidae taxa are considered to be tolerant of poor environmental conditions such as low DO and pollutants (Barbour et al., 1999) and have consistently shown positive responses to fish carcass additions in streams (Chaloner et al., 2002; Minakawa et al., 2002; Wipfli et al., 1999). Although we cannot conclusively identify the mechanism, the decline in Chironomidae abundance may have been caused by mortality related to fungal contamination from decomposing carcass material or by individuals dispersing away from treatment sites (Garman, 1992). Additionally, identifying Chironomidae to a higher taxonomic resolution may reveal differential responses by genus or species, as tolerance to low DO and poor water quality associated with carcass decomposition may vary (Wright & Burgin, 2009; Odume & Muller, 2011). Overall, these results indicate that carcass treatment in Yellowstone Lake did not cause a rapid increase in benthic invertebrate populations.

4.2 | Response of hypoxia-sensitive and immobile taxa

We examined responses of hypoxia-sensitive taxa because they may be particularly susceptible to the low-oxygen conditions that cause mortality in lake trout embryos (Poole et al., 2020; Thomas et al., 2019). Ephemeroptera and Trichoptera taxa can experience mortality due to low oxygen conditions in less than 4 days (Nebeker, 1972), and in an experimental setting, carcass treatment in Yellowstone Lake increased mortality in captive Trichoptera within 3 days (Briggs et al., 2021). Carcass treatment in our experiment reduced DO concentrations below 3.4 mg/L, a threshold known to cause mortality in lake trout embryos, for multiple days at both sites (Koel, Thomas, et al., 2020). Several Ephemeroptera and Trichoptera taxa can survive at lower oxygen concentrations (Nebeker, 1972; Nebeker et al., 1996), indicating that carcass treatment may be able to induce embryo mortality without causing widespread mortality in hypoxia-sensitive invertebrates. While we did not detect a decrease in density of Ephemeroptera and Trichoptera in response to carcass treatment, we did observe a possible reduction in biomass in both taxa in response to carcass treatment. These results could indicate a reduction in growth or recruitment, which can occur under moderately hypoxic conditions as observed in our study (Connolly et al., 2004; Nebeker et al., 1996). Hypoxia-sensitive taxa may have avoided lethal effects by locating patches of substrate free from carcass material where environmental conditions would be more favourable. Additionally, these taxa are relatively uncommon in Yellowstone Lake and were absent from many samples in the experiment, which may have limited our ability to detect changes in density and biomass. Further research could investigate the hypoxia tolerances of invertebrate taxa in Yellowstone Lake to predict both lethal and non-lethal responses to future carcass treatment.

In addition to hypoxia-sensitive taxa, we also examined the responses of immobile taxa to carcass treatment. The density of fingernail clams (family Sphaeriidae) decreased in response to carcass treatment. This sessile taxon was exposed to low DO conditions, and carcass decay likely caused poor water quality due to fungal and bacterial growth (Fenoglio et al., 2010). Without the ability to move from these conditions, Sphaeriidae may have experienced mortality due to suffocation or an inability to filter feed in poor water quality. These results provide evidence of reductions in immobile taxa due to carcass treatment. Further study of non-target effects on these taxa is warranted, particularly in systems where they comprise a larger portion of the invertebrate community.

4.3 | Influence of spatial scale, temporal scale, and seasonal variation

The timescale of our experiment prevented us from detecting responses that take more than 8 weeks after the beginning of treatment to manifest. Some taxa may experience increases in fitness or fecundity due to high-quality food which would not become apparent at the population level for one or more generations. Invertebrate responses to carcass additions via indirect pathways may take 2 months or more to become evident (Claeson et al., 2006). Alternatively, sub-lethal, negative effects of carcass treatment due to low DO concentrations, such as reduced fecundity or emergence, would not be apparent in our 8-week sampling period (Connolly et al., 2004). Many benthic invertebrates are univoltine, so changes in fecundity and emergence would not be detected during our relatively short autumn sampling period (Poff et al., 2006). Long-term monitoring at carcass treatment sites would provide information to fully understand non-target effects over longer timescales. Additional monitoring will be particularly informative if carcass treatment is implemented at the same sites for multiple years, which may cause greater changes in invertebrate communities than a single year of carcass treatment (Collins et al., 2016).

Maintaining high-density carcass cover throughout the treatment period is challenging due to limitations in supply and transportation of lake trout carcasses. To accumulate enough carcass material to reduce DO and cause mortality in lake trout embryos, carcasses were deposited in a concentrated area of approximately 10-m diameter. This approach did not cover the entire extent of cobble substrate at the spawning sites. The small spatial extent of carcass treatment that is feasible to achieve in a large lake is likely to minimize non-target effects on invertebrate populations. Invertebrates may disperse to and from the edges of the spawning sites, where carcass cover is the lightest, masking changes in abundance in response to carcass treatment. This outcome is particularly pertinent to highly mobile invertebrates, such as amphipods. Carcass cover was also variable within the treated area, and invertebrates could have found refuge from unfavourable conditions in patches with low carcass cover. Many studies examining the effects of carcass additions have been conducted in small streams, with carcasses distributed across the entire wetted width (Chaloner et al., 2002; Collins et al., 2016; Wipfli et al., 1999). Distributing carcasses across the entire aquatic habitat, rather than treating confined areas of a lakebed, as well as differences between lotic and lentic habitats, may explain some differences in invertebrate responses between our study and previous research. Future implementation of carcass treatment could consider spatial scale and how treating large areas of substrate may cause changes in invertebrate populations due to decreased opportunities for dispersal from untreated areas.

The timing and duration of carcass treatment will also influence the non-target effects of this management action. Seasonal variation in benthic invertebrate populations may exceed responses to carcass treatment (Morley et al., 2016). In this study, we observed increases in invertebrate abundance throughout the season. Collecting an entire year of before-treatment data at all sites was infeasible in our system, so we accounted for seasonal variation in our analysis. Even when accounting for seasonal changes, high natural variation and population trends can make the detection of treatment effects more difficult (Rassweiler et al., 2021), which underscores the need for additional, long-term monitoring to fully understand the non-target effects of carcass treatment. Additionally, carcass treatment occurs in autumn, as water temperatures are declining and photoperiod is decreasing, which may limit the uptake of these excess nutrient inputs by the ecosystem

(Ambrose et al., 2004). Wind and wave action can contribute to the rapid dispersal of carcass material (Poole et al., 2020; Thomas et al., 2019), which can reduce the effects of additions and cause a faster return to baseline conditions (Ambrose et al., 2004; Benjamin et al., 2020).

4.4 | Management implications

The confinement of carcass treatment to cobble-dominated spawning sites reduces the possibility for large changes to the food web in Yellowstone Lake. Lake trout spawning sites are generally small (0.3–2.0 ha each) and comprise 0.03% of the total surface area (Koel, Thomas et al., 2020) and 0.12% of the area <30 m deep in Yellowstone Lake (Bigelow, 2009). Thus, even carcass treatment on every spawning site would cover only a fraction of the lakebed in the littoral zone. Due to the limited spatial extent of carcass treatment and the abundance of invertebrates at other habitats in the lake, we conclude it is unlikely that this management action will reduce food availability for fishes in Yellowstone Lake. Additionally, given that amphipods are the preferred and dominant prey item of Yellowstone cutthroat trout and are also commonly consumed by lake trout (Glassic, 2022; Syslo et al., 2016), the non-target effects of carcass treatment observed in this study are unlikely to alter food resources for native Yellowstone cutthroat trout or invasive lake trout in Yellowstone Lake. Chironomidae comprise a large proportion of the diets of minnow species in Yellowstone Lake, so carcass treatment may cause localized, short-term reductions in food availability for these fishes at treatment sites (Glassic et al., 2021). However, replication in our experiment was low, and additional monitoring will be required to determine if our results extend to other locations within Yellowstone Lake as well as in other lakes, particularly where spawning habitat is more extensive and carcass treatment may be applied over a larger fraction of the lakebed.

5 | CONCLUSIONS

Our results indicate that non-target effects caused by carcass treatment are unlikely to alter food availability for native cutthroat trout in Yellowstone Lake. The abundant taxa that comprise the majority of fish diets did not show changes in response to carcass treatment. Additionally, carcass treatment did not change invertebrate biomass and community structure based on biomass, providing further evidence that food resources for native fish were not altered. Non-target effects on benthic invertebrate communities were detected at the site scale, with relatively uncommon and immobile taxa showing the strongest responses. Carcass treatment is a promising strategy for the suppression of invasive fishes, but the non-target effects must be considered to ensure implementation effectively supports native fish conservation. Given the increasing rate of species invasions and other global change such as alterations to climate and land use, the use of novel invasive species suppression strategies in an integrated pest management approach is becoming increasingly important. When non-target effects are identified and understood, these management actions can offer exciting and effective tools to conserve and restore native biodiversity and ecosystem function.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

ETHICS STATEMENT

This work was completed under Yellowstone National Park Scientific Research and Collecting Permit #8050 and followed National Park Service guidelines and policies.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be openly available at https://doi.org/10.5061/dryad.c866t1g9m.

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SUPPORTING INFORMATION

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

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