NON-TARGET EFFECTS OF A NOVEL INVASIVE SPECIES MANAGEMENT STRATEGY: BENTHIC INVERTEBRATE RESPONSES TO LAKE TROUT EMBRYO SUPPRESSION IN YELLOWSTONE LAKE, WYOMING

by

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TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES CONTINUED

ABSTRACT

Invasive species threaten native biodiversity and ecosystem function, and suppression is often required to reduce these effects. However, invasive species management actions can cause harmful, unintended consequences for non-target taxa. In Yellowstone Lake, Wyoming, invasive lake trout (*Salvelinus namaycush*) have reduced abundance of the native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*), decreasing availability of an important food source for aquatic and terrestrial predators. Gillnets are used to suppress adult lake trout, and the lake trout carcasses are then deposited onto spawning sites in the littoral zone to cause embryo mortality by reducing dissolved oxygen concentrations as they decay. However, this management action may have non-target effects on organisms in the lake, including benthic invertebrates, which comprise a large portion of native trout diets. Some taxa of invertebrates may benefit from the addition of nutrients to the littoral zone, while other taxa may experience mortality in response to low dissolved oxygen conditions caused by carcass decay. We conducted two field experiments to understand how carcass treatment affects benthic invertebrates in Yellowstone Lake. First, we conducted an *in situ* experiment with individual invertebrates housed in small chambers covered by carcasses to determine if carcass treatment causes mortality of hypoxia-tolerant amphipods and hypoxia-sensitive caddisflies. We found that carcass treatment caused increased mortality in caddisflies but not amphipods. Second, we conducted a field experiment to investigate how carcass treatment affects invertebrate communities when applied at entire spawning sites. We also compared invertebrate communities at cobble-dominated lake trout spawning sites to macrophyte-dominated sites to determine if carcass treatment could alter food web dynamics at a lake-wide scale. We found that carcass treatment causes non-target effects on benthic invertebrates, specifically reducing immobile taxa, hypoxia-sensitive taxa, and Chironomidae, and altering community structure. Areas dominated by macrophytes had more abundant and larger invertebrates than spawning sites. Due to the small spatial extent of spawning sites and the higher abundance of invertebrates at other habitats in the lake, we conclude carcass treatment can have localized non-target effects at a local scale but is unlikely to alter food-web dynamics at a lake-wide scale.

CHAPTER 1

CARCASS DEPOSITION TO SUPPRESS INVASIVE LAKE TROUT CAUSES DIFFERENTIAL MORTALITY OF TWO COMMON BENTHIC INVERTEBRATES IN YELLOWSTONE LAKE, WYOMING

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CARCASS DEPOSITION TO SUPPRESS INVASIVE LAKE TROUT CAUSES DIFFERENTIAL MORTALIY OF TWO COMMON BENTHIC INVERTEBRATES IN YELLOWSTONE LAKE

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Abstract

Invasive species require management to mitigate their harmful effects on native biodiversity and ecosystem processes. However, such management can also have negative, unintended consequences on non-target taxa, ecosystem processes, and food web dynamics. In Yellowstone Lake, invasive lake trout (*Salvelinus namaycush*) have caused a decline in the native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) population. To suppress the invader, lake trout carcasses are deposited on the species' spawning sites, causing embryo mortality by

reducing dissolved oxygen as they decay. The non-target effects of carcass deposition are unknown, but benthic invertebrates may be sensitive to reductions in dissolved oxygen. Benthic invertebrate taxa have varying hypoxia tolerances; caddisflies of the family Limnephilidae are hypoxia sensitive whereas the amphipods *Gammarus lacustris* and *Hyalella azteca* are hypoxia tolerant. Both taxa are widespread and abundant in Yellowstone Lake and comprise a large proportion of fish diets, and changes in their abundances could therefore alter food web dynamics. We conducted an in situ experiment to determine if carcass deposition causes mortality in these two benthic invertebrate taxa. The probability of mortality for caddisflies was 3.15 times higher in carcass treatments compared to controls, while amphipod mortality did not change in response to carcass treatment. Amphipods, which contribute most significantly to fish diets, are unlikely to be reduced in response to carcass deposition, which is confined to a small fraction of the lake where lake trout spawn, limiting the possibility for lake-wide effects. We conclude that carcass deposition is unlikely to alter the availability of invertebrates as a food source for fish in Yellowstone Lake.

Keywords: Amphipoda; anoxic; caddisfly; fish carcass; hypoxic; invasive species management; non-target taxa; Trichoptera

Introduction

Invasive species threaten native biodiversity and ecosystem processes on a global scale (Sala et al. 2000; Clavero & García-Berthou 2005). As the frequency and severity of biological invasions increases, the management and removal of invasive species is becoming increasingly important (Simberloff et al. 2013). However, invasive species management can cause unintended, negative ecological effects (Zavaleta et al. 2001) including mortality of native

species as a byproduct of the invasive species removal method (Eason et al. 2002); trophic cascades caused by the removal of an invasive predator (Bergstrom et al. 2009); and opportunities for secondary invasions (Skurski et al. 2013). Thus, it is important to consider non-target effects in the design and implementation of invasive species management actions taken to support biodiversity and ecosystem function.

In Yellowstone Lake, Wyoming, an intensive management program has been established to combat the effects of lake trout (*Salvelinus namaycush*), an invasive predatory fish that has altered the ecosystem and its aquatic and terrestrial species (Koel et al. 2019). By preying on native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*), lake trout have dramatically reduced native trout abundance (Koel et al. 2019), thereby reducing the availability of an important prey item for native aquatic and terrestrial predators. The reduction in cutthroat trout has also caused a trophic cascade in Yellowstone Lake, altering the biomass of lower trophic levels including zooplankton and phytoplankton (Tronstad et al. 2010). To mitigate the pervasive influence of lake trout invasion on this iconic ecosystem and to promote the recovery of Yellowstone cutthroat trout, the National Park Service (NPS) removes adult lake trout by gillnetting (Koel et al. 2020a) and is exploring other control methods (Doepke et al. 2017). For example, the NPS deposits carcasses from gillnetting onto lake trout spawning sites over a period of weeks during the autumn spawning season (late September to early October) to induce embryo mortality (Thomas et al. 2019; Poole et al. 2020). Carcass deposition at densities of ≥ 7 kg m^{-2} reduces dissolved oxygen (DO) to hypoxic concentrations for a period of several days, leading to embryo suffocation (Thomas et al. 2019; Poole et al. 2020).

Carcasses are deposited at lake trout spawning sites, characterized by cobble substrates, in the littoral zone of Yellowstone Lake (Bigelow 2009; Koel et al. 2020b; Williams 2019), where other organisms may also respond to their application. In particular, benthic invertebrates inhabit the littoral zone and comprise a large proportion of the diets of both native Yellowstone cutthroat trout and invasive lake trout (Syslo et al. 2016). Benthic invertebrates have taxon-specific oxygen requirements, and many are sensitive to low DO concentrations (Nebeker 1972). In river ecosystems, fish carcasses can reduce oxygen concentrations and alter benthic invertebrate populations (Chaloner & Wipfli 2002; Holtgrieve & Schindler 2011; Fellman et al. 2019), but their effects in lake ecosystems are largely unknown. Potential responses of invertebrates to carcass-induced low-oxygen conditions include mortality, reduced growth, delays or absence of insect emergence, and reduced reproduction (Nebeker et al. 1992; Connolly et al. 2004). It is important to understand benthic invertebrate responses to carcass deposition, because changes to their populations may alter food web dynamics and ecosystem function.

We conducted an in situ experiment in Yellowstone Lake to determine if carcass deposition causes mortality in two benthic invertebrate taxa: amphipods (*Gammarus lacustris* and *Hyalella azteca*) and caddisflies (family Limnephilidae). We selected these two amphipods because they dominate benthic invertebrate biomass in Yellowstone Lake (Wilmot et al. 2016) and make a substantial contribution to trout diets (Syslo et al. 2016). Benthic amphipods are moderately tolerant of hypoxia (Nebeker et al. 1992) and we thus compared their responses with a caddisfly family which is also common in Yellowstone Lake but more sensitive to hypoxia (Nebeker et al. 1996; Wilmot et al. 2016). Our objectives were to examine the effects of carcass deposition on (1) DO concentrations on the lake bed, and (2) mortality in invertebrate taxa with different

oxygen requirements. We predicted that carcasses would reduce DO concentrations, increasing mortality in both invertebrate taxa, but that mortality would be higher in caddisfly larvae compared to amphipods due to higher oxygen requirements. Understanding the potential non-target effects of carcass deposition as a suppression method for invasive fish will inform future management actions that support biodiversity in functional lake ecosystems.

Methods

Study area

Yellowstone Lake is located in Yellowstone National Park in northwestern Wyoming at an elevation of 2,357 m (Fig. 1A). With a surface area of 340 km^2, it is the largest high-elevation lake (above 2,000 m) in North America. It has complex bathymetry, with a mean depth of 43 m, a maximum depth of 148 m, and geothermal features distributed throughout the northern and western portions (Kaplinski 1991). Yellowstone Lake is a mesotrophic, dimictic lake which is thermally stratified in the summer (Kilham et al. 1996) and usually ice-covered from late December to mid-May (Koel et al. 2020a). Mixing events occur in mid-May, after the ice thaws, and in late September, when thermal stratification ends (Koel et al. 2020a). DO concentrations measured at the substrate surface in the littoral zone using miniDOT loggers in 2018 and 2019 ranged from 8.0–10.0 mg l^{-1} in early summer, and water temperatures typically range from 5.0–9.0ºC in early summer and from 8.0–10.0ºC in the autumn during the lake trout spawning season (Koel et al. 2020a).

Experimental design and data collection

The experiment was conducted at the Flat Mountain Mid lake trout spawning site located in the southwestern portion of Yellowstone Lake (Fig. 1A) from June 10–27, 2019. The site is

characterized by cobble substrates and varies in depth from 0 to 5 m. Scuba divers anchored polypropylene rope to the substrate to delineate six 1.5 m × 1.5 m experimental plots at 2 m intervals in a line parallel to the shore at approximately 2 m depth (Fig. 1B).

Invertebrates were collected on the day the experiment was initiated (day 0). To collect *H. azteca* and *G. lacustris* amphipods, we deployed three emergent fry traps at the site two days before day 0. The traps are constructed of steel mesh cones (73-cm diameter) that rest on the substrate surface (Simard 2017). Amphipods are collected in a 1 l bottle containing an inverted funnel mounted on top of each trap. Caddisflies (family Limnephilidae) were collected by wading from the northern shore of Yellowstone Lake and removing large-bodied individuals from the substrate by hand. Collected invertebrates were transported to the site in buckets of lake water at ambient temperature and oxygenated with aerators.

Each invertebrate was placed into an individual chamber constructed from PVC pipe (length 7.6 cm, diameter 3.8 cm) with 500-µm mesh covering both ends. The mesh allowed water and dissolved and fine particulate matter to passively move through the chambers. Food was not placed in the chambers to reduce the possibility of fungal and/or bacterial contamination. Preliminary tests showed that both taxa, collected using these methods, survived for >3 weeks confined in chambers without food. We tied chambers together in groups of six, with three containing one amphipod and three containing one caddisfly. Grouping chambers allowed removal of individual chamber groups on different dates without disturbing other chambers. Six chamber groups were randomly placed on the substrate in each experimental plot by divers, resulting in each plot containing 18 amphipods and 18 caddisflies (Fig. 1C, Fig. 2A). The ropes used to gather each group were connected to a surface buoy to facilitate retrieval. We placed one

calibrated miniDOT logger (Precision Measurement Engineering, California, USA) on the substrate surface in each plot to measure DO concentrations (mg l^{-1}) and temperature (ºC) at 15-min intervals throughout the experiment.

We obtained lake trout carcasses from NPS gillnetting crews and shredded the carcasses using a fish grinder (Poole et al. 2020). To establish the experimental treatments, we applied ~60 kg of carcass material to each treatment plot (26.7 kg m^{-2}) by dumping the material off the side of a boat. This carcass application rate has been shown to reduce DO concentrations and cause embryo mortality (Poole et al. 2020). Carcass material was placed on the three easternmost plots to minimize the drift of material from treatment plots onto control plots. The day after carcass material was deposited (day 1), divers ensured it covered all chambers and loggers in treatment plots and that there was no carcass material in control plots.

The experiment lasted for 17 days, a period over which DO concentrations would be reduced and return to ambient levels (Thomas et al. 2019; Poole et al. 2020). On days 3, 5, 7, 10, 14, and 17 of the experiment, one randomly selected group of chambers (three containing an amphipod and three containing a caddisfly) was removed from the plot using a boat hook. We immediately determined if the invertebrates in these chambers were alive or dead by visual inspection and did not return the invertebrates to the plots.

Variation in dissolved oxygen response to carcass treatment

We further investigated how DO concentrations responded to carcass treatment by measuring DO concentrations (mg l^{-1}) and temperature (ºC) in multiple locations within a single plot at 15-minute intervals for 17 days, from July 24 to August 10, 2019. We established one carcass treatment plot as described for the experimental site, with six miniDOT loggers spaced out

evenly on the substrate surface. These measurements characterized patterns in DO concentrations at a fine spatial scale, providing additional context for the concentrations observed during the experiment.

Data analysis

We calculated the mean, median, minimum, and mean daily range of DO concentrations recorded in each plot, and used a two-sided t-test to compare the minimum concentrations recorded in treatment and control plots. We used generalized linear mixed-effect models (GLMMs) with a binomial distribution to estimate the effects of carcass treatment on amphipod and caddisfly mortality. We included carcass treatment, a two-level categorical variable, as an explanatory variable in the model but did not include DO concentrations because these variables are not independent from carcass treatment. Our models included day of experiment, treatment, and invertebrate taxa as explanatory variables and chamber group nested within plot as random effects. We constructed nine models including all combinations of interactions between our three explanatory variables, each of which could plausibly be related to invertebrate mortality. Model assumptions were tested and met. We used Akaike's Information Criterion corrected for small sample sizes (AICc) for model selection. Out of the models with ΔAICc < 2, we selected the most parsimonious model as our final model. We used the output from the final model to estimate the probability of mortality for amphipods and caddisflies in treatment and control plots on each day of the experiment. All analyses were conducted in R version 3.6.2 (R Core Team 2019) and GLMMs were fitted using the lme4 package (Bates et al. 2015).

Results

Carcass treatment reduced DO concentrations, but reductions were inconsistent across treatment plots. Minimum DO concentrations were lower and more variable in carcass treatments compared to controls, ($t = 13.41$, $df = 2.48$, $p = 0.002$; Table 1, Fig. 3). Two carcass treatment plots had both mean and median DO concentrations >8.5 mg l^{-1}, and only one consistently had DO concentrations <3.4 mg l^{-1}. Mean temperature during the experiment was 6.6ºC. In the single oxygen measurement plot, DO concentrations were also highly variable (Table 2, Fig. 4). Five of six loggers recorded mean DO concentrations <3.4 mg l^{-1}. The time required for DO concentrations to decline to <3.4 mg l^{-1} within the plot varied from 1 to 9 days. Mean temperature in the plot was 14.9ºC.

Invertebrates responded to carcass treatment, but the response magnitude differed between taxa. The final model using carcass treatment to predict mortality included day of experiment, treatment, invertebrate taxa, and an interaction term between treatment and taxa as explanatory variables (conditional $R^2 = 0.269$, marginal $R^2 = 0.252$; Table 3). There was a positive relationship between day of experiment and mortality for both invertebrate taxa in both control and treatment plots, ($p = 0.0014$; Fig. 6). An interaction between taxa and treatment ($p = 0.0046$) indicated that amphipods and caddisflies responded differently to carcass treatment. Amphipod mortality did not differ between the control and carcass treatments. On the final day of the 17-day experiment, the predicted probability of mortality for an individual amphipod in the carcass and control treatments was 0.56 (95% CI 0.35–0.75) and 0.40 (95% CI 0.22–0.61), respectively (Fig. 6A). Caddisflies in the carcass treatment experienced higher mortality than those in the control treatments on day 3 (Fig. 5B), and their mortality remained higher in treatment plots throughout the experiment. On the final day of the experiment, the probability of mortality for an

individual caddisfly in the carcass and control treatments was 0.82 (95% CI 0.65–0.92) and 0.26 (0.13–0.47), respectively (Fig. 6B).

Discussion

Management actions to control invasive species can influence non-target taxa and ecosystem functioning. Lake trout carcass deposition is used to suppress invasive lake trout embryos in Yellowstone Lake. To evaluate potential non-target consequences of this management action, we investigated the effects of carcass deposition on dissolved oxygen concentrations and benthic invertebrate mortality in a 17-day in situ experiment. Our results indicate that carcass deposition can reduce DO concentrations, but these reductions vary at small spatial scales. We found evidence that carcass deposition increases mortality in caddisflies but not amphipods, which dominate benthic invertebrate communities in Yellowstone Lake and are an important food source for fish.

Dissolved oxygen response to carcass deposition

The physical characteristics of our study site likely contributed to the spatially variable response of DO concentrations to carcass treatment. Water temperature, sunlight, biological oxygen demand, and wind are tightly coupled with DO concentrations in lakes (Hanson et al. 2006; Langman et al. 2010). Water temperatures recorded during our experiment were lower than is typical during the autumn lake trout spawning season, which may have contributed to higher DO concentrations than recorded in previous carcass deposition studies (Thomas et al. 2019; Poole et al. 2020). Our study was conducted at a confirmed lake trout spawning site, characterized by cobble-dominated substrates with large interstitial spaces. Due to the shallow depth of the site, wave action could induce water flow (Barton 1981) and move well-oxygenated water across the substrate surface and into interstitial spaces, even in areas with carcass material

present. Higher flow velocities and larger interstitial spaces increase the availability of oxygen to developing salmonid embryos in streams (Greig et al. 2007) and lake trout select spawning sites with large interstitial spaces and adequate wave action to provide oxygenated water to, and remove fine sediment from, developing embryos (Bigelow 2009; Marsden et al. 1995). Although depositing carcass material can increase biological oxygen demand and dramatically reduce DO concentrations at spawning sites (Thomas et al. 2019), the physical characteristics of our study site likely allowed some oxygenated water to access the substrate surface.

Invertebrate response to carcass deposition

Caddisflies experienced higher mortality in response to carcasses within three days of treatment, and their mortality remained higher than for amphipods exposed to carcass treatment throughout the experiment. Caddisflies of the family Limnephilidae have been shown to experience 50% mortality at DO concentrations of 2.0 mg l^{-1} in four-day exposures, and 30% mortality when exposed to DO concentrations of 8.1 mg l^{-1} for 21 days (Nebeker et al. 1996). These previous results indicate that caddisfly larvae experience mortality during both short periods of very low DO concentrations and longer periods of slightly reduced DO concentrations, which both occurred in our carcass treatments. The Limnephilidae are a large and diverse family with varying oxygen tolerances, and within-family variation may have influenced our results if responses to carcass treatment varied among multiple genera or species (Bonada et al. 2004).

In contrast to caddisfly larvae, amphipods did not experience increased mortality in our carcass treatments. There are conflicting estimates of hypoxia tolerances of *Gammarus* and *Hyalella* amphipods. Mortality of 50% can occur in these genera at DO concentrations between

1.0–2.0 mg l^{-1} in 2–5 day exposures (Hoback & Barnhart 1996; Irving et al. 2004); equally, up to 80% of gammarid individuals may survive concentrations of <1.0 mg l^{-1} for 7 days (Nebeker et al. 1992). This evidence that amphipods can tolerate prolonged exposure to hypoxia aligns with our results and indicates that reduced DO resulting from carcass deposition is unlikely to cause amphipod mortality.

Caddisflies experienced increased mortality but reductions in DO concentrations were variable, which suggests that additional mechanisms may have contributed to mortality of non-target taxa in response to carcass deposition. Carcass treatment may have increased fungal and bacterial growth on chambers and the surrounding substrate (Yoder et al. 2006; Fenoglio et al 2010), reducing water quality and leading to invertebrate mortality. The high density of carcass material may have reduced food availability in our experiment by limiting the flow of particulate material into chambers or reducing periphyton growth by blocking light (Qinr et al. 2007). Additionally, carcass material may limit availability of preferred hard-surface substrate for colonization by invertebrates (Mackay 1992). Recent experiments documenting the effectiveness of manufactured analog pellets intended to simulate fish carcass material and suppress lake trout embryos by reducing oxygen concentrations also showed unexpected results, suggesting the concurrent influence of other mechanisms (Koel et al. 2020b). Treatments of ≤14 kg m^{-2} of carcass analog pellets did not reduce DO concentrations at the substrate surface but still resulted in high mortality in lake trout embryos, which was attributed in part to elevated carbon dioxide concentrations and fungal growth resulting from decomposing organic material (Koel et al. 2020b). DO reductions within the substrate are possible when carcasses are placed on the

substrate surface (Koel et al. 2020b), but the effects on invertebrates within the substrate are unknown.

Invertebrate movement and differential mobility among taxa might lead to variable responses to carcass treatment among taxa with different traits. Our experiment confined invertebrates within chambers, preventing them from moving away from carcass material and ensuring their continuous exposure to the environmental conditions caused by carcass treatment. Amphipods are strong swimmers that move away from anoxic and hypoxic waters (Nebeker et al. 1992; Henry & Danielopol 1999) associated with dense carcass cover, reducing their susceptibility to mortality from carcass deposition in natural environments. Cased caddisflies, which experienced mortality in response to carcass treatment, are less mobile than amphipods (Poff et al. 2006), potentially increasing their susceptibility to mortality from carcasses. Many limnephilid caddisflies crawl slowly (<1 m h^{-1}), with some taxa moving <3 m d^{-1} (Erman 1986; Poff et al. 2006). This low mobility may limit their ability to move away from low DO conditions caused by carcass deposition at spawning sites (which range in size from 0.5–2.0 ha; Koel et al. 2020b) before dying – which can occur within three days. Immobile taxa that remain buried beneath carcass material would be highly affected by carcass treatment, but further research is required to characterize the responses of such taxa.

Beyond mortality, benthic invertebrates may show additional responses to carcass deposition at individual, population, and community levels. At the individual level, hypoxia can cause other negative, sub-lethal physiological responses, such as reductions in growth and reproduction (Nebeker 1972; Winter et al. 1996; Connolly et al. 2004). Carcass deposition could reduce food resources for some taxa, while others may benefit from carcass material by consuming it. When

carcass deposition covers entire lake trout spawning sites, population and community responses could become evident. At the population level, insect taxa may experience changes in abundance, biomass, and timing or magnitude of emergence. At the community level, varying taxon-specific responses may alter structure and diversity. Salmon carcasses in streams can alter invertebrate community structure by differentially increasing abundances and growth rates of different taxa (Chaloner & Wipfli 2002; Janetski et al. 2009), but effects vary depending on carcass density and duration of application (Benjamin et al. 2020). It is unknown how the high-density, short-term carcass treatments required to induce mortality of invasive fish embryos will affect community structure or taxa not studied in this experiment. Better characterization of population and community responses to carcass deposition at entire spawning sites could inform implementation of lake trout embryo suppression programs and support effective management of their ecological consequences.

Conclusions and management implications

Understanding potential non-target effects is vital for managers implementing invasive species control programs. Our results suggest that carcass deposition to induce lake trout embryo mortality is unlikely to alter lake-scale food availability for native trout in Yellowstone Lake, because this management action only occurs at lake trout spawning sites, which comprise 0.03% of its total surface area (Koel et al. 2020b) and 0.12% of the surface area above waters <30 m deep (Bigelow 2009). Although carcass deposition could cause localized reductions in hypoxia-sensitive, slow-moving taxa such as caddisflies, it is unlikely to alter amphipod populations, which are the most abundant benthic invertebrates in Yellowstone Lake (Wilmot et al. 2016) and contribute most notably to fish diets (Syslo et al. 2016). Thus, the availability of amphipods as

prey for native fish such as the Yellowstone cutthroat trout is unlikely to be reduced by carcass deposition. Abundant amphipods also play key ecological roles by processing organic matter and transferring energy between trophic levels (Wallace & Webster 1996; Covich et al. 1999), so reductions in their populations could alter ecosystem functioning. Carcass deposition can suppress lake trout embryos without reducing the abundance of dominant benthic invertebrates and this management strategy is thus unlikely to compromise lake-wide ecosystem function.

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Author Contributions

All authors contributed to conceptualization and experimental design; MAB and DRL conducted the field work; MAB analyzed data; MAB and LKA wrote the original draft of the manuscript; all authors contributed to later versions of this manuscript.

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Tables

Table 1. Minimum, median, mean, standard error of the mean (SE), coefficient of variation, and mean daily range for dissolved oxygen concentrations recorded in each plot over the 17-day experimental period

Plot number	Plot treatment	Minimum (mg l^{-1})	Median (mg l^{-1})	Mean (mg l^{-1})	SE	Coefficient of variation	Mean daily range (mg l^{-1})
1	Control	7.82	9.62	9.36	0.007	0.029	1.06
2	Control	8.42	9.57	9.59	0.006	0.025	0.86
3	Control	8.17	9.79	9.77	0.006	0.026	0.93
4	Treatment	1.60	9.24	8.82	0.030	0.14	3.65
5	Treatment	1.49	9.31	9.32	0.021	0.093	2.53
6	Treatment	0.05	0.08	1.11	0.060	2.17	2.77

Table 2. Minimum, median, mean, standard error of the mean (SE), coefficient of variation, and mean daily range for dissolved oxygen concentrations recorded by each logger in the oxygen measurement plot over the 17-day measurement period.

Logger number	Minimum (mg l^{-1})	Median (mg l^{-1})	Mean (mg l^{-1})	SE	Coefficient of variation	Mean daily range (mg l^{-1})
1	0.06	0.07	0.72	0.040	2.31	2.67
2	0.05	0.14	0.59	0.044	3.14	1.21
3	0.05	0.08	1.01	0.057	2.34	1.65
4	0.06	7.24	6.22	0.079	0.53	6.88
5	0.05	0.08	0.67	0.044	2.74	2.17
6	0.05	0.06	1.91	0.073	1.58	2.18

Table 3. Nine candidate models presented with AICc scores and ΔAICc scores

Model	Number of parameters	AIC_c	ΔAIC_c
Invertebrate × treatment + day	7	239.62	0
Invertebrate × treatment + treatment × day	8	240.62	1.00
Invertebrate × treatment + invertebrate × day	8	241.56	1.95
Invertebrate × treatment + invertebrate × day + day × treatment	9	242.63	3.01
Invertebrate × treatment × day	10	243.65	4.04
Invertebrate + treatment + day	6	245.84	6.23
Day × treatment + invertebrate	7	247.08	7.46
Invertebrate × day + treatment	7	247.96	8.34
Day x treatment + invertebrate × day	8	249.23	9.62

Figure Legends

Figure 1. (A) The location of the experiment site, Flat Mountain Mid (44.3721, -110.3993), within Yellowstone Lake, Wyoming and the location of Yellowstone Lake in North America; (B) the arrangement of experimental plots at the site; and (C) the arrangement of chambers containing amphipods and caddisflies and the dissolved oxygen logger within each plot. B and C are not shown to scale.

Figure 2. (A) A control plot, with 36 chambers containing invertebrates and one dissolved oxygen logger; (B) a carcass treatment plot, with chambers and logger covered in carcass material.

Figure 3. Mean dissolved oxygen concentrations for control and treatment plots during the 17-day experiment. The gray shaded areas indicate the standard error.

Figure 4. Dissolved oxygen concentrations for the six loggers in the oxygen measurement plot over 17 days and their arrangement within the 1.5m × 1.5m plot.

Figure 5. Mean ± standard error (SE) % mortality of (A) amphipods and (B) caddisflies during the 17-day experiment. For points without error bars, SE = 0, i.e. % mortality was the same in all plots.

Figure 6. Predicted probability of mortality for (A) amphipods and (B) caddisflies in carcass treatment and control plots during the 17-day experiment, with 95% confidence intervals.

Figures

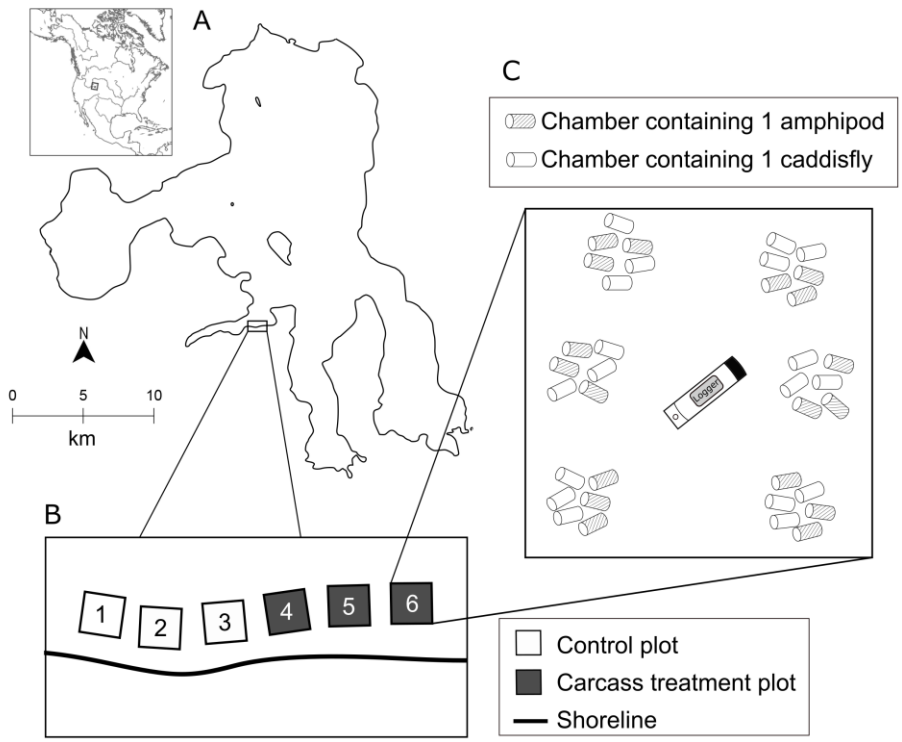

Figure 1

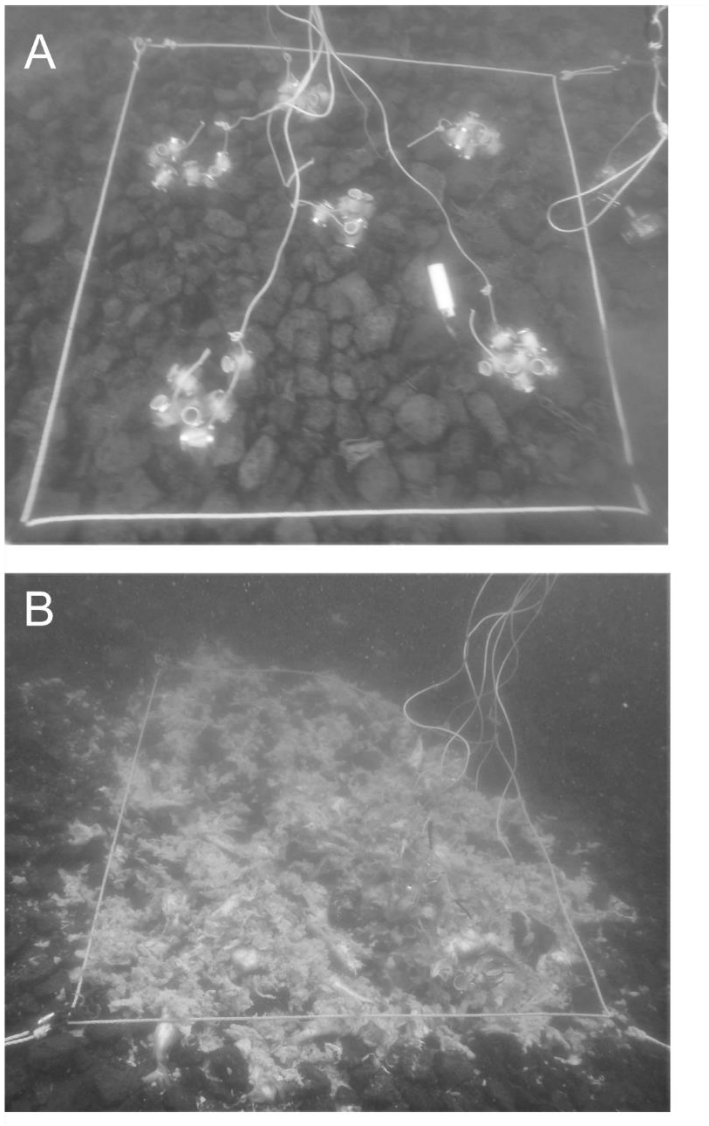

Figure 2

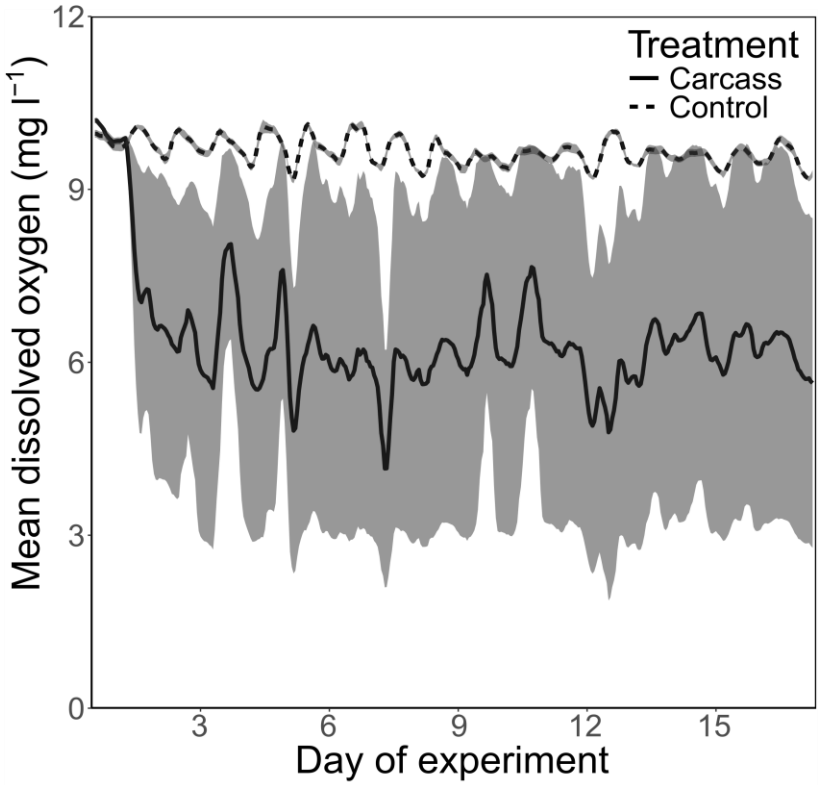
Treatment
Carcass
Control
Mean dissolved oxygen (mg l−1)
Day of experiment
0
3
6
9
12
3
6
9
12
15

Figure 3

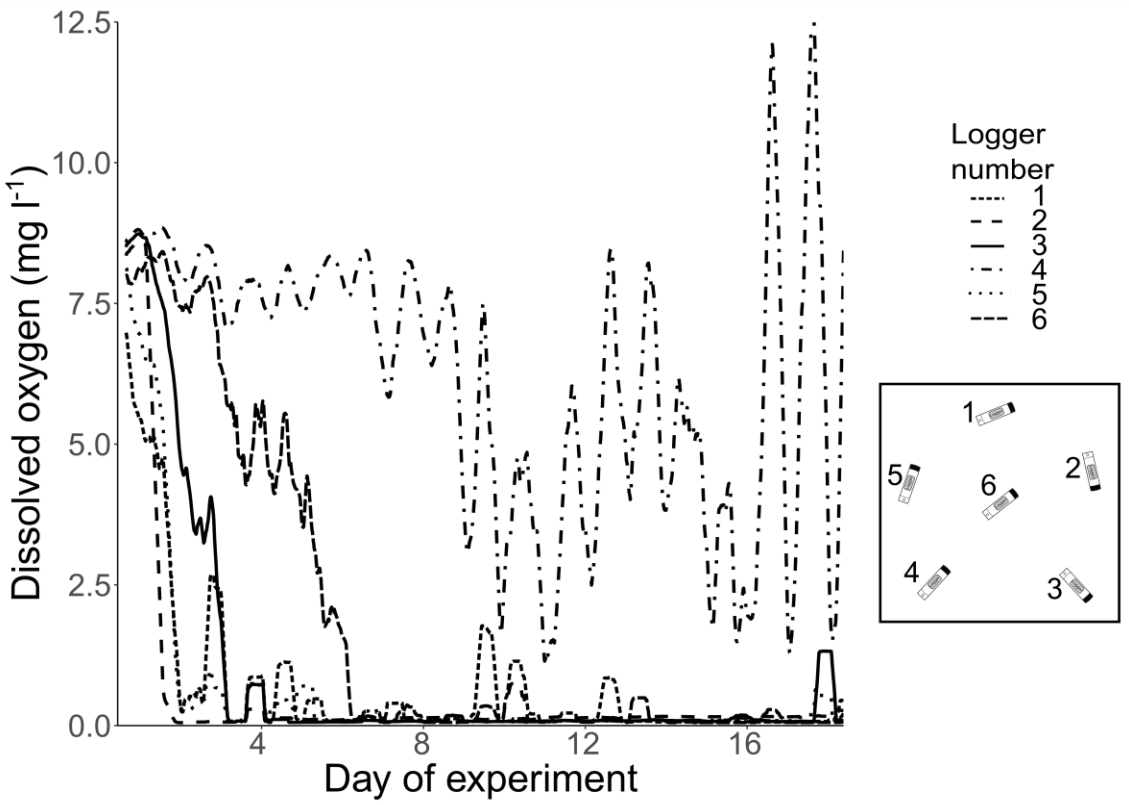
12.5
10.0
7.5
5.0
2.5
0.0
Dissolved oxygen (mg l-1)
4
8
12
16
Day of experiment
Logger number
1
2
3
4
5
6
1
2
3
4
5
6

Figure 4

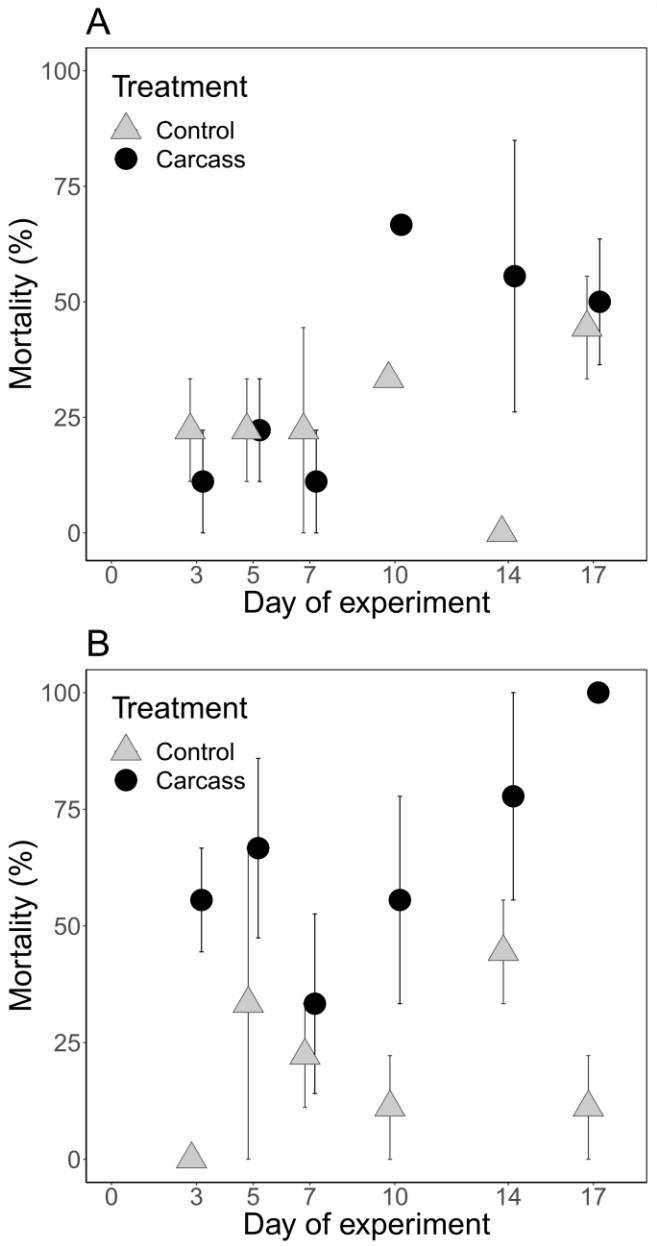
A
Treatment
Control
Carcass
Mortality (%)
100
75
50
25
0
0
3
5
7
10
14
17
Day of experiment
B
Treatment
Control
Carcass
Mortality (%)
100
75
50
25
0
0
3
5
7
10
14
17
Day of experiment

Figure 5

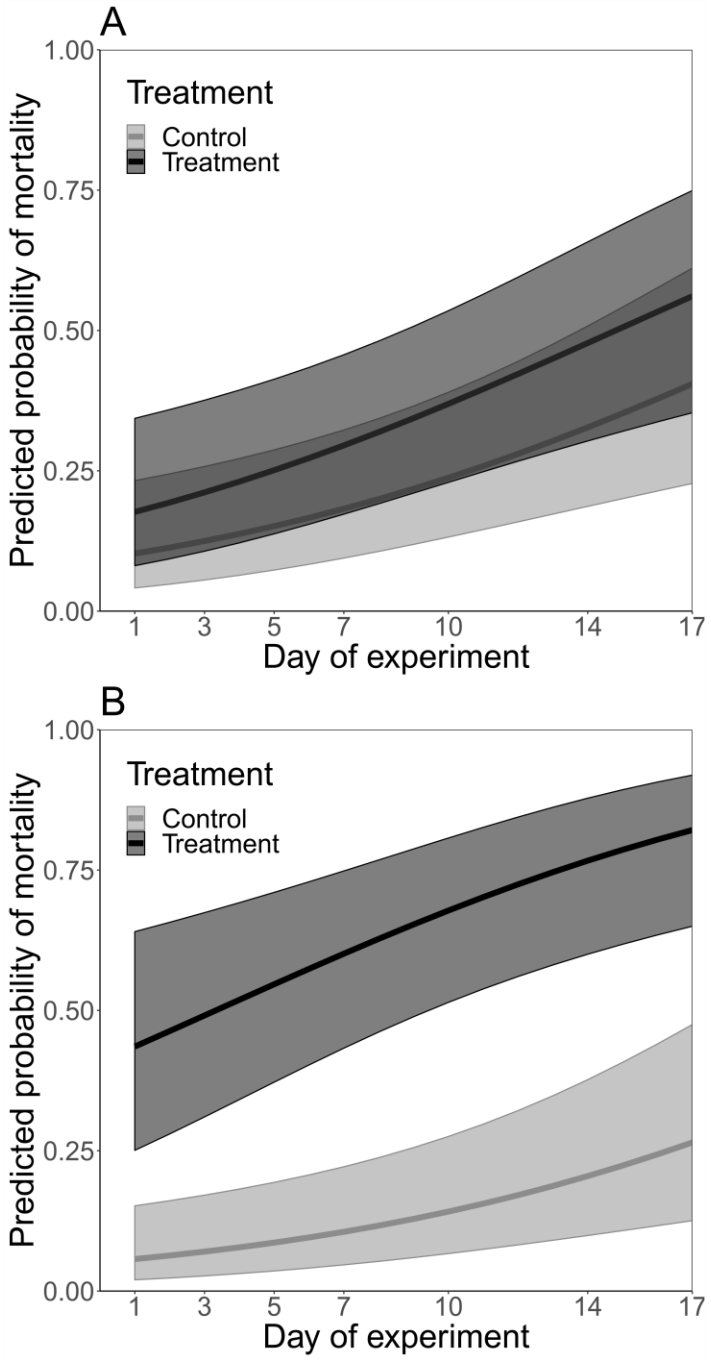
A
Treatment
Control
Treatment
Predicted probability of mortality
1.00
0.75
0.50
0.25
0.00
1
3
5
7
10
14
17
Day of experiment
B
Treatment
Control
Treatment
Predicted probability of mortality
1.00
0.75
0.50
0.25
0.00
1
3
5
7
10
14
17
Day of experiment

Figure 6

CHAPTER 2

NON-TARGET EFFECTS OF A NOVEL SUPPRESSION TECHNIQUE FOR INVASIVE FISHES: RESPONSES OF BENTHIC INVERTEBRATE COMMUNITIES

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Contributions: Conceptualization and experimental design; conducted field work, analyzed data, wrote original draft of manuscript, contributed to later versions of the manuscript

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Contributions: Conceptualization and experimental design, wrote original draft of the manuscript, contributed to later versions of the manuscript

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Co-Author: Lusha M. Tronstad

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Contributions: Conceptualization and experimental design, contributed to later versions of the manuscript

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NON-TARGET EFFECTS OF A NOVEL SUPPRESSION TECHNIQUE FOR INVASIVE FISHES: RESPONSES OF BENTHIC INVERTEBRATE COMMUNITIES

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Abstract

Invasive species threaten native biodiversity and ecosystem function, and suppression is often required to reduce these impacts. However, these management actions can cause negative, unintended effects on non-target taxa. Across the USA, lake trout (*Salvelinus namaycush*) are invasive in many freshwater ecosystems, harming native fishes through predation and competition. In Yellowstone Lake, Wyoming, lake trout invasion caused a decline in abundance of native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*) and cascading changes to the ecosystem. In an integrated pest management approach, embryos of this invasive fish are suppressed by depositing lake trout carcasses onto spawning sites, causing embryo mortality by reducing dissolved oxygen concentrations as they decay. Carcass addition is commonly used as a fertilization technique in rivers, and their use for suppression in lakes is largely unknown. This management action may have non-target effects on organisms in a lake's littoral zone, including benthic invertebrates, which comprise a large portion of native trout diets. Some taxa of invertebrates may benefit from the large addition of nutrients to the littoral zone, while other taxa may experience mortality in response to low DO conditions. We conducted a field experiment to investigate the non-target effects of carcass treatment on benthic invertebrates. We also compared invertebrate assemblages at cobble-dominated lake trout spawning sites and macrophyte-dominated sites to determine if carcass treatment is likely to alter food web dynamics at a lake-wide scale. While total invertebrate as well as amphipod density and biomass did not respond to carcass treatment, Chironomidae and fingernail clams (Sphaeriidae) decreased in abundance. Carcass treatment also altered invertebrate community structure based on density, but not on biomass. Invertebrates at cobble-dominated lake trout spawning sites were less

abundant and have smaller body sizes than at macrophyte-dominated sites. Carcass treatment does have localized non-target effects on benthic invertebrates, which should be monitored as this novel management strategy is implemented in other systems. However, due to the small spatial extent of carcass treatment, restricted only to spawning sites with cobble substrate, and high abundance of invertebrates at other habitat types, we conclude it is unlikely that carcass treatment will alter food availability for native fishes.

Keywords: *Invasive species management; fish carcass addition; applied limnology; lake trout; Yellowstone Lake*

Introduction

Invasive species are among the greatest threats to native biodiversity, and as invasive species continue to spread globally, these threats are becoming increasingly severe and widespread (McNeely et al. 2001, Clavero and Garciaberthou 2005). In concert with threats to native biodiversity, invasive species jeopardize ecosystem processes, with significant economic and cultural ramifications (Pimentel et al. 2005, Pejchar and Mooney 2009, Paini et al. 2016). For example, invasive dreissenid mussels reduce ecosystem services associated with clean water, cause millions of dollars in damage to infrastructure, and dramatically alter ecosystem structure and function (Pejchar and Mooney 2009, Higgins and Vander Zanden 2010). Invasive plants such as salt cedar (*Tamarix* sp.) can cause long-term changes to habitat, outcompete native vegetation, and reduce fresh water availability (Di Tomaso 1998, Strayer et al. 2006).

To mitigate harmful effects of invasive species, managers implement suppression actions, but management actions can have unintended, negative consequences on the ecosystem (Zavaleta et al. 2001, Simberloff et al. 2013). Non-target effects of invasive species management are

extensive and include mortality of native species in response to the suppression method (Mangum and Madrigal 1999); trophic cascades caused by the removal of an invasive predator in multiply invaded systems (Bergstrom et al. 2009); the opportunity for secondary invasions (Peterson et al. 2020); and the loss of habitat for native species when highly 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 programs is the lake trout (*Salvelinus namaycush*), a top-level predatory fish invasive in over 200 waterbodies throughout the U.S. Lake trout alter ecosystems by predating on and competing with native fishes, with cascading consequences for both aquatic and terrestrial food webs (Martinez et al. 2009, Koel et al. 2019). In Yellowstone Lake, Wyoming, invasive lake trout consume native Yellowstone cutthroat trout (*Oncorhynchus clarkii bouvieri*), reducing the availability of this key prey item for its other 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 of lake trout (Doepke et al. 2017, Koel et al. 2020a). To suppress embryos, NPS deposits carcasses from gill netting onto lake trout spawning sites in the littoral zone during the autumn spawning period (late September to early October, Thomas et al. 2019, Poole et al. 2020). When applied at densities of $\geq$7 kg m^{-2}, the carcasses reduce dissolved oxygen (DO) concentrations as they decay, causing up to 100% mortality in lake trout embryos (Thomas et al. 2019, Poole et al. 2020).

It is unknown how the addition of carcasses, which alter water chemistry and are a major source of limiting nutrients, will affect organisms in a littoral zone, such as benthic invertebrates (Theriot et al. 1997, Lujan 2020). In river ecosystems, fish carcass additions are commonly used to stimulate stream productivity in response to reduced salmon runs. This management strategy has been successful in increasing periphyton and benthic invertebrate biomass, consumption of invertebrates by fish, and fish production (Wipfli et al. 2004, Collins et al. 2016). Salmon carcasses provide direct and indirect food sources for benthic invertebrates, which can increase growth rates, biomass, and abundance of some taxa (Wipfli et al. 1998, Chaloner and Wipfli 2002). 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 systems (Ambrose et al. 2004, Chaloner et al. 2007, Bellmore et al. 2014). Almost all research to date on carcass additions has been performed in rivers, and their non-target effects in lakes are unknown. Non-target influence on aquatic benthic invertebrates could have major consequences since invertebrates are important components of food webs and contribute to nutrient cycling, energy transfer, and decomposition (Covich et al. 1999).

Benthic invertebrate taxa in particular could show changes to population metrics and altered community structure if carcass treatment differentially affects abundance and biomass of taxa depending on their traits (Dolédec et al. 2011). Many invertebrate taxa are sensitive to low DO conditions and may experience mortality or reductions in growth or reproduction (Nebeker 1972, Connolly et al. 2004). Sessile taxa may be particularly susceptible to mortality in response to carcass treatment due to an inability to move away from unfavorable conditions caused by carcass decay, such as reduced DO and poor water quality due to fungal and bacterial growth

(Fenoglio et al. 2010, Poole et al. 2020). Some invertebrate taxa, particularly those tolerant of poor environmental conditions and likely to consume carcass material, may benefit from the addition of nutrients into the littoral zone (Chaloner and Wipfli 2002, Collins et al. 2016). In Yellowstone Lake, benthic invertebrates, and specifically 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. However, invertebrates may be in relatively low abundances on cobble-dominated lake trout spawning sites where carcasses are deposited compared to other lake habitats such as macrophyte beds, so any changes to invertebrates there may be minimal for the lake as a whole (Wilmot et al. 2016). It is unknown how short-term, high density carcass treatments in a lake system will alter benthic invertebrate communities and the implications this may have for ecosystem function.

We conducted a field experiment in Yellowstone Lake to determine how carcass treatment to induce lake trout embryo mortality affects invertebrate communities. To determine how effectively carcass treatment was implemented, we quantified the amount of carcass material present at treatment sites and measured changes in dissolved oxygen. We determined whether carcass treatment altered invertebrate density, biomass, and community structure. We characterized general trends in invertebrate communities and looked specifically at relatively abundant taxa, hypoxia-sensitive taxa, and immobile taxa. We compared invertebrate assemblages at sites dominated by macrophytes to invertebrate assemblages at carcass treatment and control sites dominated by cobble substrate to determine how carcass treatment might influence food web dynamics at a lake-wide scale. Our findings provide some of the first

description of potential non-target effects of invasive fish suppression using carcass material in lake ecosystems.

Methods

Study area

Yellowstone Lake is located in Yellowstone National Park in northwestern Wyoming at an elevation of 2,357 m. With a surface area of 340 km^2, it is the largest high-elevation lake above 2,000 m 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 geothermal features distributed throughout the northern and western portions (Kaplinski 1991). Benthic invertebrate assemblages are dominated by two amphipod species, *Hyallela azteca* and *Gammarus lacustris*, which together comprise approximately 55% of invertebrate biomass (Wilmot et al. 2016).

Carcass treatment

Carcass treatment occurred at two lake trout spawning sites, Flat Mountain Hump and Snipe Point, from August 12 – October 2, 2019 (Fig. 1). Carcass treatment sites were selected from confirmed lake trout spawning sites that were deep enough to avoid attracting terrestrial wildlife (Thomas et al. 2019), and two control sites were selected based on similar depths and substrate type. Substrate at both carcass treatment and control sites was dominated by bedrock or hard cobble (< 250 mm), and the sites varied from 2.5 to 9.5 m deep. 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.

We secured one miniDOT logger (Precision Measurement Engineering) to the substrate surface at each carcass treatment and control site while scuba diving to measure dissolved oxygen (mg L^{-1}) at 60-minute increments throughout the entire sampling period (June 17 – October 1, 2019). To monitor carcass cover at the carcass treatment sites, we photographed a 1 m^2 quadrat placed on the substrate surface using a GoPro camera. We took five adjacent photographs of the quadrat along a 0º heading, starting directly north of the concrete anchor marking the site, and we took five additional photographs along a 180º 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 two weeks during the carcass treatment period, for a total of four measurements per site.

Invertebrate collection and vegetation measurement

At each carcass treatment and control site, three replicate benthic invertebrate samples were collected monthly before carcass treatment started (June 17 – August 11, 2019) and every two weeks after carcass treatment started (August 12 – October 1, 2019), totaling three sampling dates before and four sampling dates during carcass treatment. To quantitatively sample benthic invertebrates, we used a diver-operated suction sampler constructed from a bilge pump mounted on a plastic cutting board with a 500 µm mesh collection net. We randomly placed a 0.25 m^2 quadrat on the lakebed 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 bias. After surfacing, we rinsed all contents of the collection nets into a 500 µm sieve and preserved all material that was retained by the sieve in 75% ethanol.

We selected three macrophyte sites: two were selected from historical sampling locations, and the third was selected based on the presence of macrophytes and proximity to other sites to facilitate sampling. We used a Ponar grab sampler (Wildco, 524 cm^2 sampling area) mounted on a boat via a winch and crane to collect three replicate benthic invertebrates once per month from June – October, 2019 at each site. We rinsed all material collected by the grab sampler into a 500 µm sieve and preserved all material that was retained by the sieve in 75% ethanol.

In the laboratory, we subsampled our invertebrate samples to the smallest fraction that included ≥100 individuals, sorted invertebrates from debris and organic material, and identified individuals to the lowest practical taxonomic level using dichotomous keys, which was often genus or family and occasionally order (Merritt et al. 2008). We measured 25 randomly selected individuals of each taxon to calculate biomass. We used published length-mass regressions to calculate biomass (AFDM) of each taxon (Bottrell et al. 1976, Benke et al. 1999, Méthot et al. 2012).

After removing invertebrates from samples collected at macrophyte sites, we elutriated the sample to separate vegetation from inorganic detritus. We then dried the vegetation in a drying oven to determine the dry mass of vegetation in each sample. At carcass and control sites, we

took photographs of each quadrat immediately before invertebrate collection to estimate the percent cover of vegetation in each sampling area.

Data analysis

To determine if invertebrate density and biomass changed in response to carcass treatment, we looked for an 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. We expected the control and treatment sites to change over time due to seasonal variation, so we used the interaction between time and treatment as evidence that carcasses are altering invertebrate communities differently than they are being altered in the controls due to seasonal variation. We focused on the three most abundant taxa (*Gammarus* sp. and *Hyallela* sp. amphipods and non-Tanypodinae Chironomidae), 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 some sites but not others, our analyses of Ephemeroptera and Trichoptera density and biomass were each combined and only included taxa observed at control and carcass sites. Our models included treatment, time, and their interaction as fixed effects, and sampling date nested with site as random effects to account for temporal and spatial autocorrelation. We used linear mixed effects models for most metrics, and we log-transformed response variables when necessary to meet model assumptions. 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 did not perform statistical analysis

on Ephemeroptera and Trichoptera biomass and 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 models. Statistical significance was tested with an alpha value of 0.1 due to the high amount of variation expected from such a large-scale experiment where replication was low, and to improve our detection of invertebrate responses. All statistical analyses were conducted in R version 3.6.2 (Team 2019).We fit linear mixed effects models using the lme4 package (Bates et al. 2015) and zero-inflated negative binomial models using the glmmTMB package (Brooks et al. 2017).

We used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities to visualize how invertebrate community structure based on untransformed density and biomass responded to carcass treatment. To test whether invertebrate community structure changed in response to carcass treatment, we used a two-way mixed effects PERMANOVA including time, treatment, and their interaction as fixed effects and site as a random effect. We used 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. Community analysis was conducted using the vegan package (Oksanen et al. 2019).

We used linear mixed effects models to compare density, biomass, and individual body size of invertebrates at spawning sites to macrophyte sites. Our models included habitat type as a fixed effect and sampling date nested within site as random effects, and response variables were log-transformed to meet model assumptions. We excluded samples collected at carcass treatment sites during the carcass treatment period from these analyses. To determine the relationship between invertebrate abundance and vegetation density at macrophyte sites, we used a linear

mixed effects model with total invertebrate density as our response variable, vegetation dry mass as a fixed effect, and sampling date nested within site as random effects. Total invertebrate density was log-transformed to meet model assumptions.

Results

Dissolved oxygen and carcass cover

Carcass treatment at the scale of whole spawning sites altered water chemistry, leading to a decline in DO concentrations at carcass treatment sites (Fig. 2a, b). At Flat Mountain Hump, mean daily DO concentrations declined below 3.4 mg L^{-1}, a threshold known to cause lake trout embryo mortality (Koel et al. 2020b), 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^{-1} after 5 weeks of carcass treatment and then fluctuated from 2.0 to 6.6 mg L^{-1} until the eighth week of treatment, when DO concentrations were consistently hypoxic at <1.0 mg L^{-1}. Mean percent carcass cover at Flat Mountain Hump was 21.6% and 20.1% on the second and eighth weeks of carcass treatment, respectively (Fig. 2c). At Snipe Point, carcass material did not accumulate as quickly, and carcass cover was more variable (Fig. 2d). Mean carcass cover at Snipe Point was <1.0% on the second week of treatment but increased to 30.0% on the eighth week of treatment.

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 abundant *Gammarus* sp. and *Hyallela* sp. amphipods, and density of Ephemeroptera and Trichoptera did not change due to carcass treatment (Figs. 3a-c, f). Carcass treatment was associated with a decrease in the

density of non-Tanypodinae Chironomidae (df = 22, t = -3.51, p = 0.002, Fig. 3d), with predicted densities decreasing from 567.7 individuals (ind) m^{-2} (90% CI 382.4 – 2,286.1) to 320.5 ind m^{-2} (90% CI 227.7 – 4,816.5) 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 1,080.1 – 3,920.0) at control sites during the same time period. Density of Sphaeriidae also decreased in response to carcass treatment (z = -1.76, p = 0.078, Fig. 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 (Figs. 4a-c). Biomass of non-Tanypodinae Chironomidae decreased in response to carcass treatment (df = 22, t = -3.07, p = 0.006, Fig. 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 (Fig. 4f).

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 x time p = 0.012, Fig. 5). Specifically, invertebrate communities at control and treatment sites had low dissimilarity and high overlap before carcass treatment (Fig. 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. These changes were driven by the three most abundant taxa: *Gammarus* sp. and *Hyallela* sp. (Order: Amphipoda), and non-Tanypodinae Chironomidae (Order: Diptera) (Table 1). Non-Tanypodinae Chironomidae showed a reduction in relative abundance while *Gammarus* amphipods showed an increase in relative abundance at carcass treatment sites compared to control sites (Fig. 6). Invertebrate community structure based on biomass did not change in response to carcass treatment.

Comparison of macrophyte and spawning sites

Total invertebrate density and biomass were higher at macrophyte sites than at spawning sites (density df = 5, t = -3.39, p = 0.020, biomass df = 5, t = -4.25, p = 0.008, Tables 2, 3). Median invertebrate density was 2.87 (90% CI 1.53 – 5.39) times higher at macrophyte sites than spawning sites, and median invertebrate biomass was 4.26 (90% CI 2.14 – 8.48) times higher at macrophyte sites than spawning sites. The higher invertebrate density at macrophytes was primarily driven by higher densities of non-Tanypodinae Chironomidae, which had a median density 6.99 (90% CI 2.78 – 17.56) times higher at macrophyte than spawning sites (df = 5, t = -4.25, p = 0.008, Table 2). Macrophyte sites had a 5.51 (90% CI 2.14 – 14.19) times higher median biomass of *Gammarus* (df = 5, t = -3.64, p = 0.015) and a 10.58 (90% CI 4.00 – 27.95) times higher median biomass of non-Tanypodinae Chironomidae (df = 5, t = -6.24, p = 0.002) than spawning sites (Table 3). Mean *Gammarus* body size was over twice as large at macrophyte

sites than spawning sites, and predicted median body size was 4.80 (90% CI 2.4 – 9.60) times higher (df = 6, t = -4.40, p = 0.004, Table 4). The difference in body size, rather than a difference in density, explains the higher *Gammarus* biomass at macrophyte sites. *Hyallela*, non-Tanypodinae Chironomidae, and Sphaeriidae also had larger body size at macrophyte sites than at spawning sites (*Hyallela* df = 6, t = -3.48, p = 0.013; Chironomidae df = 6, t = -3.36, p = 0.015; Sphaeriidae df = 6, t = -2.63, p = 0.039, Table 4).

Invertebrate density was positively related to vegetation dry mass at macrophyte sites (df = 27, t-value = 2.98, p = 0.006, Fig. 7), with an estimated 4.0% increase in median invertebrate density for each 1 g increase in vegetation dry mass per m^2. Mean cover of vegetation at control and carcass sites during the entire sampling period was estimated at 1.5%.

Discussion

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

We predicted that carcass treatment would add a source of nutrients to the littoral zone and increase benthic invertebrate density and biomass (Wipfli et al. 1998, Janetski et al. 2009,

Collins et al. 2016), particularly for taxa that are likely to consume carcass material directly, such as amphipods and Chironomidae (Chaloner and Wipfli 2002). 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, but neither density nor biomass of *Gammarus* sp. or *Hyallela* sp. amphipods increased in response to carcass treatment. Amphipods can take advantage of many food sources, including fish carcasses, and high quality food such as carcass material can increase growth and fecundity (MacNeil 1997, Cruz-Rivera and Hay 2000, Ito 2003). Chironomidae density and biomass actually declined in response to carcass treatment, a surprising outcome, because we predicted abundance would increase. Chironomidae are generally considered to be tolerant of poor environmental conditions (Barbour et al. 1999), and have consistently shown positive responses to fish carcass additions in streams (Wipfli et al. 1999, Chaloner et al. 2002, Minakawa et al. 2002). Although we cannot conclusively identify the mechanism, several factors may have influenced the decline. Chironomidae may be susceptible to mortality related to fungal contamination from carcass material, or alternatively, increased fitness due to carcass treatment may have caused increased or earlier emergence at carcass treatment sites, leading to lower larval abundance. Overall, these results indicate that carcass treatment in Yellowstone Lake did not cause a rapid increase benthic invertebrate populations, which we predicted would occur in response to increased primary productivity stimulated by the presence of carcass material.

We examined responses of both hypoxia-sensitive taxa and immobile taxa, because we predicted they would be particularly susceptible to the low-oxygen conditions that cause

mortality in lake trout embryos (Thomas et al. 2019, Poole et al. 2020). Ephemeroptera and Trichoptera taxa can experience mortality due to low oxygen conditions in less than four days (Nebeker 1972), and carcass treatment in our experiment reduced DO concentrations below ambient levels for over three weeks at both sites. 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 caused by low oxygen conditions, or changes in the timing or magnitude of emergence (Nebeker et al. 1996, Connolly et al. 2004). Hypoxia sensitive taxa may have avoided lethal effects by locating patches of substrate free from carcass material where environmental conditions would be more favorable. 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. The density of fingernail clams (family Sphaeriidae) decreased in response to carcass treatment. This sessile taxa was exposed to low DO conditions, and carcass decay can also create 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 trait-based reductions in hypoxia-sensitive and 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.

The timescale of our experiment may have prevented us from detecting responses that take more than eight 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 two 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 eight 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.

Maintaining high-density carcass cover throughout the treatment period is challenging due to limitations in supply and transportation of lake trout carcasses, so implementation focuses on small areas of the lakebed. 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 unfavorable 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 (Wipfli et

al. 1999, Chaloner et al. 2002, Collins et al. 2016). Distributing carcasses across the entire aquatic habitat, rather than treating confined areas of a lakebed, may explain some differences in invertebrate responses between our study and previous research. Future implementation of carcass treatment should 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 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, which may have been larger than any responses to carcass treatment. Additionally, carcass treatment occurs in the fall, as water temperatures are declining and photoperiod is decreasing, which may limit the use of these excess nutrient inputs by the ecosystem (Ambrose et al. 2004). Wind, wave action, and wildlife can contribute to the rapid dispersal of carcass material (Thomas et al. 2019, Poole et al. 2020), which can reduce the effects of additions or cause a faster return to baseline levels (Ambrose et al. 2004, Benjamin et al. 2020).

The confinement of carcass treatment to cobble-dominated spawning sites reduces the possibility for lake-wide effects. Lake trout spawning sites are generally small (0.3 – 2.0 ha each) and comprise just 0.03% of the total area (Koel et al. 2020b) 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. Invertebrate density, biomass, and body size were larger in areas dominated by macrophytes compared to cobble-dominated

spawning sites, and there was a positive relationship between invertebrate density and macrophyte abundance. In particular, Chironomidae, which decreased in abundance in response to carcass treatment in the experiment, were over seven times more abundant at macrophyte sites. Additionally, *Gammarus* sp. amphipods, a preferred food source for native Yellowstone cutthroat trout (Syslo et al. 2016) were over twice as large at macrophyte sites. Yellowstone cutthroat trout preferentially feed on larger amphipods (Wilmot et al. 2016), so high abundances of large bodied amphipods and other invertebrates at macrophyte sites may represent a more important food source for native trout than at spawning sites. While the area of the littoral zone dominated by macrophytes in Yellowstone Lake is unknown, it is likely equal to or larger than the area of confirmed lake trout spawning sites. Due to the abundance of food resources at other habitat types and the limited spatial extent of carcass treatment, we conclude it is unlikely that this management action will reduce food availability for native trout at a lake-wide scale. The effects of this management strategy on benthic communities in lakes with a larger fraction of cobble substrate relative to macrophyte beds remains to be evaluated.

Here, we determined that carcass treatment to suppress invasive lake trout embryos causes non-target effects on benthic invertebrate communities at the site scale, with relatively uncommon and immobile taxa showing the strongest responses. Changes to these taxa could locally alter nutrient cycling and primary productivity. However, these effects are unlikely to alter food availability for native trout in Yellowstone Lake because 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 fish were not altered.

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, system-wide invasive species management strategies 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.

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Author Contributions

All authors contributed to conceptualization and experimental design; MAB and DRL conducted the field work; MAB analyzed data; MAB and LKA wrote the original draft of the manuscript; all authors contributed to later versions of this manuscript.

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Tables

Table 1. Results of 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.

Control before treatment vs. control after treatment

Taxon	Percent cumulative contribution	Mean abundance, control before (ind m^{-2})	Mean abundance, control after (ind m^{-2})
Hyallela	37.81	679.8	2,146.0
Non-Tanypodinae	66.01	729.8	1,724.0
Gammarus	77.46	535.3	580.7

Control before treatment vs. carcass before treatment

Taxon	Percent cumulative contribution	Mean abundance, control before (ind m^{-2})	Mean abundance, carcass before (ind m^{-2})
Gammarus	47.45	535.3	2,592.9
Hyallela	63.59	679.8	950.7
Non-Tanypodinae	7.92	729.8	714.7

Carcass before treatment v. carcass after treatment

Taxon	Percent cumulative contribution	Mean abundance, carcass before (ind m^{-2})	Mean abundance, carcass after (ind m^{-2})
Gammarus	48.93	2,592.9	4,268.33
Hyallela	74.05	950.7	2,392.0
Non-Tanypodinae	8.14	714.7	408.7

Control after treatment vs. carcass after treatment

Taxon	Percent cumulative contribution	Mean abundance, control after (ind m^{-2})	Mean abundance, carcass after (ind m^{-2})
Gammarus	43.14	580.7	4,268.3
Hyallela	63.83	2,146.0	2,392.0
Non-Tanypodinae	81.39	1724.0	408.7

Table 2. Mean and median density of invertebrates at macrophyte sites and spawning sites with 90% bootstrapped confidence intervals. Rows in boldface indicate a significant difference in the density of that taxon between habitat types. Samples collected at carcass sites after carcass treatment began were excluded from this analysis.

	Density at macrophyte sites		**Density at spawning sites**	
Taxa	Mean (90% CI) (ind m^{-2})	Median (ind m^{-2})	Mean (90% CI) (ind m^{-2})	Median (ind m^{-2})
All invertebrates	**12,445 (10,457 – 14,327)**	**10,458**	**4,205 (3,682 – 4,712)**	**3,904**
Gammarus	1,963 (1,621 – 2,272)	1,565	1,171 (799 – 1,499)	568
Hyallela	1,173 (832 – 1,485)	534.35	1,348 (1,113 – 1,566)	1,112
Chironomidae (Non-tanypodinae)	**8,165 (6,346 – 9,839)**	**5,916**	**1,123 (943 – 1,295)**	**808**
Sphaeriidae	120.44 (71.2 – 163.7)	76.34	79.80 (43.8 – 113.0)	16
Ephemeroptera and Trichoptera	110.69 (74.2 – 143.8)	76.34	121.27 (72.9 – 164.7)	32

Table 3. Mean and median biomass of invertebrates at macrophyte sites and spawning sites with 90% bootstrapped confidence intervals. Rows in boldface indicate a significant difference in biomass of that taxon between the habitat types. Samples collected at carcass sites after carcass treatment began were excluded from this analysis.

	Biomass at macrophyte sites		**Biomass at spawning sites**	
Taxa	Mean (90% CI) (mg m^{-2})	Median (mg m^{-2})	Mean (90% CI) (mg m^{-2})	Median (mg m^{-2})
All invertebrates	**54,511.48 (40,414 – 65,868)**	**38,085.06**	**10,417.96 (9,072 – 11,699)**	**8,778.74**
Gammarus	**45,130.72 (31,833 – 55,841)**	**29,539.31**	**7,249.71 (5,885 – 8,519)**	**5,583.23**
Hyallela	2,556.11 (1,857 – 3,225)	1,319.59	2,112.10 (1,779 – 2,441)	1,559.86
Chironomidae (Non-tanypodinae)	**4,176.79 (3,255 – 5,013)**	**2,889.78**	**380.22 (298.1 – 454.8)**	**239.49**
Sphaeriidae	17.02 (9.6 – 23.5)	7.72	8.80 (4.8 – 12.6)	0.65
Ephemeroptera and Trichoptera	349.39 (129 – 506)	205.23	249.62 (161.1 – 330.9)	65.84

Table 4. Mean and median individual body size at macrophyte and spawning sites by taxa. Rows in boldface indicate a significant difference in individual body size between habitat types.

	Body size at macrophyte sites		**Body size at spawning sites**	
Taxa	Mean (90% CI) (mg DM)	Median (mg DM)	Mean (90% CI) (mg DM)	Median (mg DM)
Gammarus	**21.300 (19.870 – 22.710)**	**5.881**	**9.450 (8.828 – 10.070)**	**1.102**
Hyallela	**2.287 (2.106 – 2.456)**	**1.413**	**1.613 (1.556 – 1.665)**	**1.413**
Chironomidae (non-tanypodinae)	**0.568 (0.544 – 0.591)**	**0.468**	**0.333 (0.321 – 0.346)**	**0.214**
Sphaeriidae	**0.141 (0.130 – 0.153)**	**0.158**	**0.126 (0.108 – 0.142)**	**0.0907**
Ephemeroptera and Trichoptera	3.629 (2.667 – 4.458)	1.881	2.029 (1.831 – 2.215)	1.253

Figures

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

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 two 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. Mean 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. Error bars indicate bootstrapped 90% confidence intervals. 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.

Figure 4. Mean 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. Error bars indicate bootstrapped 90% confidence intervals. 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.

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 abundance of the three most abundant taxa, Gammarus sp., Hyallela sp., and Chironomidae (non-tanypodinae) at (a) control sites and (b) carcass treatment sites before and during the carcass treatment period.

Figure 7. Dry mass of vegetation and total invertebrate density at macrophyte sites collected from June – October, 2019.

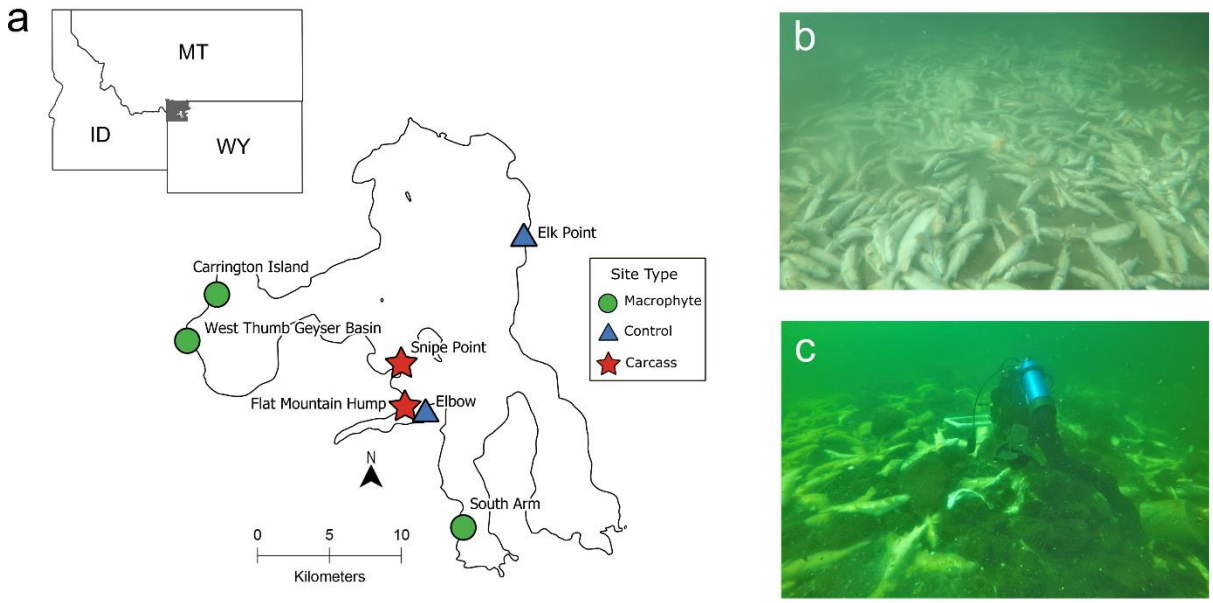
a
MT
ID
WY
Elk Point
Carrington Island
West Thumb Geyser Basin
Snipe Point
Flat Mountain Hump
Elbow
South Arm
Site Type
Macrophyte
Control
Carcass
N
0
5
10
Kilometers
b
c

Figure 1

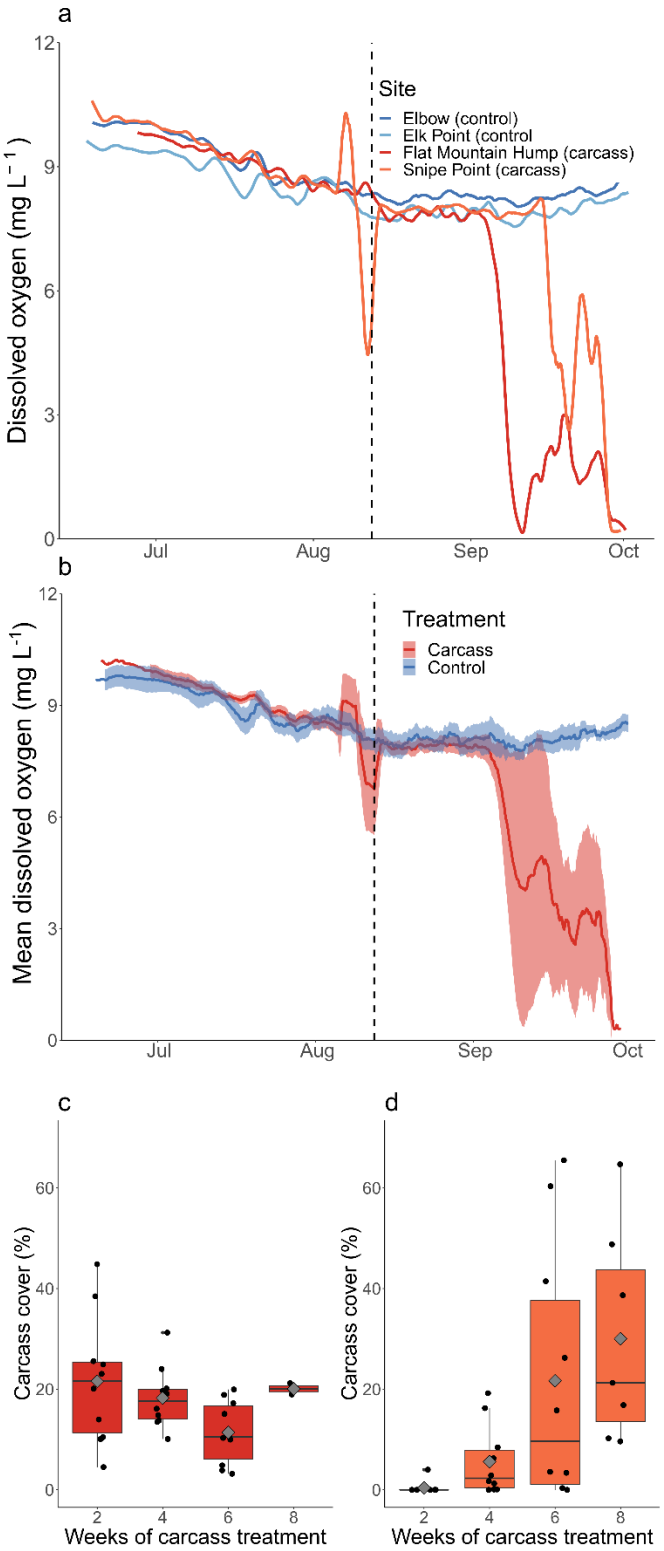
a
Dissolved oxygen (mg L⁻¹)
Site
Elbow (control)
Elk Point (control
Flat Mountain Hump (carcass)
Snipe Point (carcass)
Jul
Aug
Sep
Oct
b
Mean dissolved oxygen (mg L-1)
Treatment
Carcass
Control
c
Carcass cover (%)
Weeks of carcass treatment
d
Carcass cover (%)
Weeks of carcass treatment

Figure 2

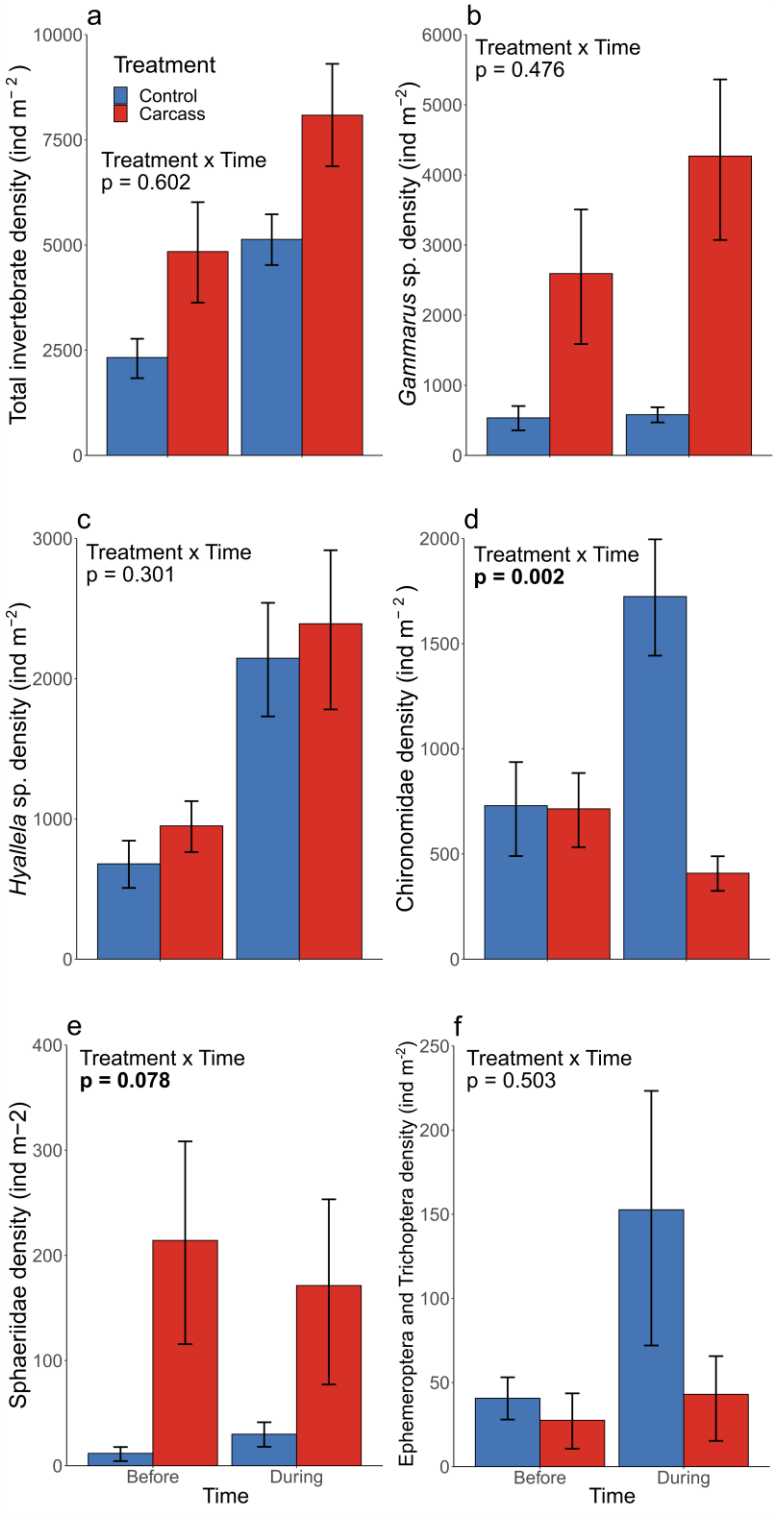
a
Treatment
Control
Carcass
Treatment x Time
p = 0.602
Total invertebrate density (ind m⁻²)
b
Treatment x Time
p = 0.476
Gammarus sp. density (ind m⁻²)
c
Treatment x Time
p = 0.301
Hyallela sp. density (ind m⁻²)
d
Treatment x Time
p = 0.002
Chironomidae density (ind m⁻²)
e
Treatment x Time
p = 0.078
Sphaeriidae density (ind m−2)
f
Treatment x Time
p = 0.503
Ephemeroptera and Trichoptera density (ind m⁻²)
Before
During
Time

Figure 3

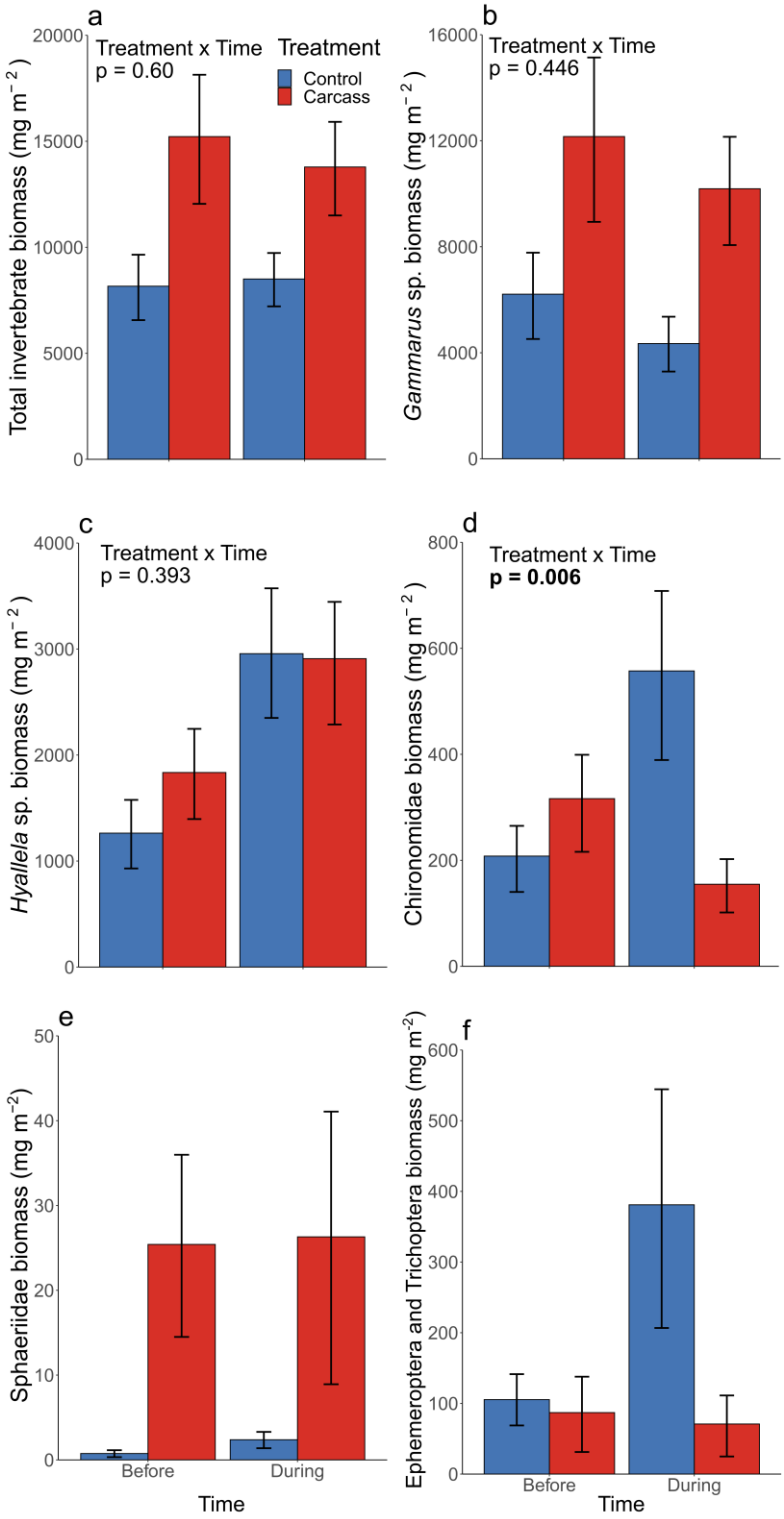
a
Treatment x Time
p = 0.60
Treatment
Control
Carcass
Total invertebrate biomass (mg m^{-2})
20000
15000
10000
5000
0
b
Treatment x Time
p = 0.446
Gammarus sp. biomass (mg m^{-2})
16000
12000
8000
4000
0
c
Treatment x Time
p = 0.393
Hyallela sp. biomass (mg m^{-2})
4000
3000
2000
1000
0
d
Treatment x Time
p = 0.006
Chironomidae biomass (mg m^{-2})
800
600
400
200
0
e
Sphaeriidae biomass (mg m^{-2})
50
40
30
20
10
0
Before
During
Time
f
Ephemeroptera and Trichoptera biomass (mg m^{-2})
600
500
400
300
200
100
0
Before
During
Time

Figure 4

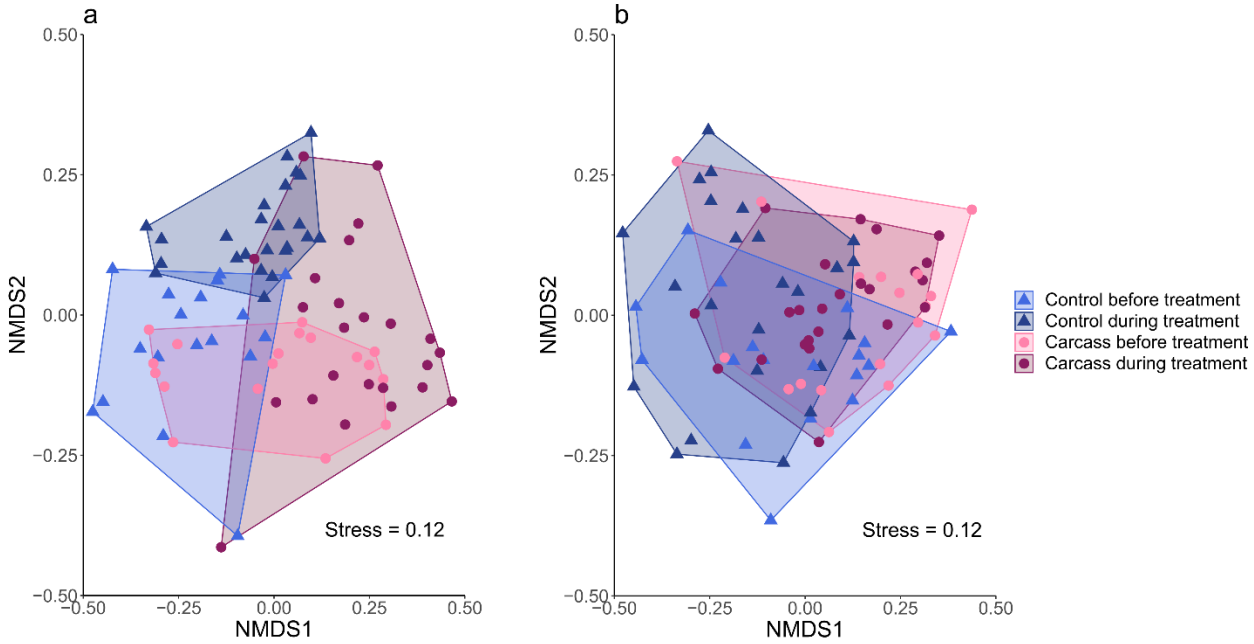
a
b
NMDS2
NMDS1
0.50
0.25
0.00
−0.25
−0.50
Stress = 0.12
Control before treatment
Control during treatment
Carcass before treatment
Carcass during treatment

Figure 5

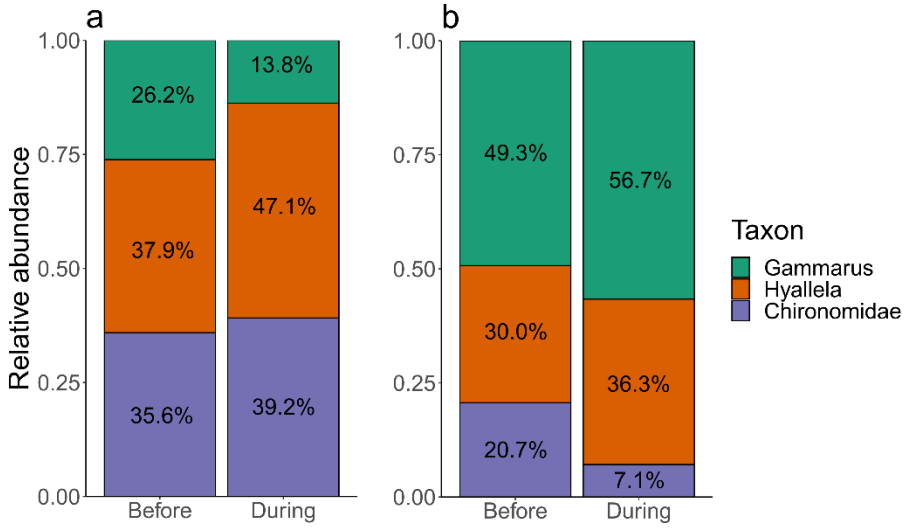
a
b
Relative abundance
1.00
0.75
0.50
0.25
0.00
26.2%
37.9%
35.6%
13.8%
47.1%
39.2%
49.3%
30.0%
20.7%
56.7%
36.3%
7.1%
Before
During
Taxon
Gammarus
Hyallela
Chironomidae

Figure 6

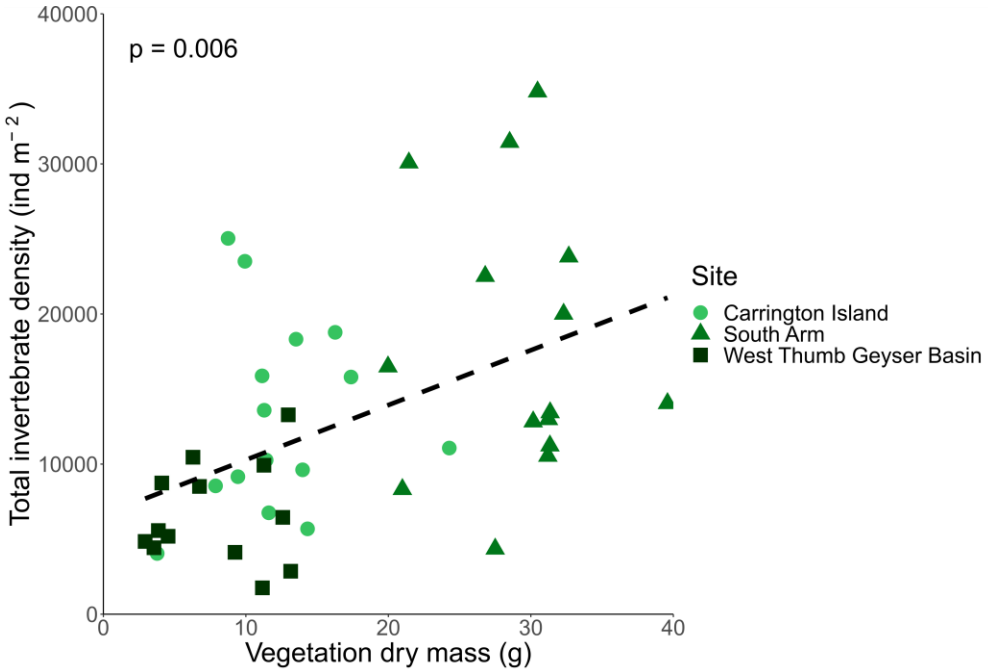
p = 0.006
Total invertebrate density (ind m^{-2})
Vegetation dry mass (g)
0
10000
20000
30000
40000
0
10
20
30
40
Site
Carrington Island
South Arm
West Thumb Geyser Basin

Figure 7

Supplementary Table 1: Mean biomass and density of all invertebrate taxa collected at lake trout spawning sites during this study. Mean values were calculated from four sites and seven sampling dates. Zooplankton were likely collected from the water column and not the substrate, and the sampling method was not designed to quantitatively sample these taxa.

Taxon	Biomass		Density	
	Mean (mg m^{-2})	Standard deviation	Mean (ind m^{-2})	Standard deviation
Crustacea				
Amphipoda				
Gammarus sp.	8,089.55	6,332.13	2,056	2,693
Hyallela sp.	2,339.86	1,642.96	1,646	1,366
Cladocera (Non-Daphnia)	0.0876	0.433	20	100
Daphnia sp.	0.220	0.510	38	89
Copepoda	0.427	0.510	61	72
Ostracoda			9	31
Insecta				
Diptera				
Non-tanypodinae				
Chironomidae	315.83	338.16	919	780
Tanypodinae Chironomidae	8.12	35.12	16	53
Chironomidae pupae	8.57	14.26	45	75
Ephemeroptera				
Baetidae	7.36	33.77	4	14
Ephemerellidae	25.21	71.18	11	34
Heptageniidae	4.01	27.86	0.8	5
Leptophlebiidae	23.50	90.39	27	114
Trichoptera				
Brachycentridae	0.0111	0.102	0.2	2
Leptoceridae	3.81	15.76	4	11
Limnephilidae	111.92	315.90	41	133
Molannidae	21.47	70.78	8	21
Trichoptera pupae	0.546	4.97	1	6
Elmidae	0.145	1.32	0.2	2
Mollusca				
Physidae	197.71	613.89	36.29	68.98
Planorbidae	10.65	40.83	3.95	11.89
Sphaeriidae	13.80	31.14	105.95	200.95
Annelida				
Hirudinea	11.75	20.57	28.05	38.65
Oligochaeta	13.48	21.60	125.29	221.01
Acari	0.0559	0.0746	55.86	74.60
Turbellaria	0.229	1.15	2.67	10.99

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