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Article

Carcass deposition to suppress invasive lake trout causes differential mortality of two common benthic invertebrates in Yellowstone Lake

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With 6 figures and 3 tables

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 (Za-

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valeta 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 $\geq 7\,\mathrm{kg\ m^{-2}}$ 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}, and water temperatures typically range from 5.0–9.0 °C in early summer and from 8.0–10.0 °C in the autumn during the lake trout spawning season (Koel et al. 2020a).

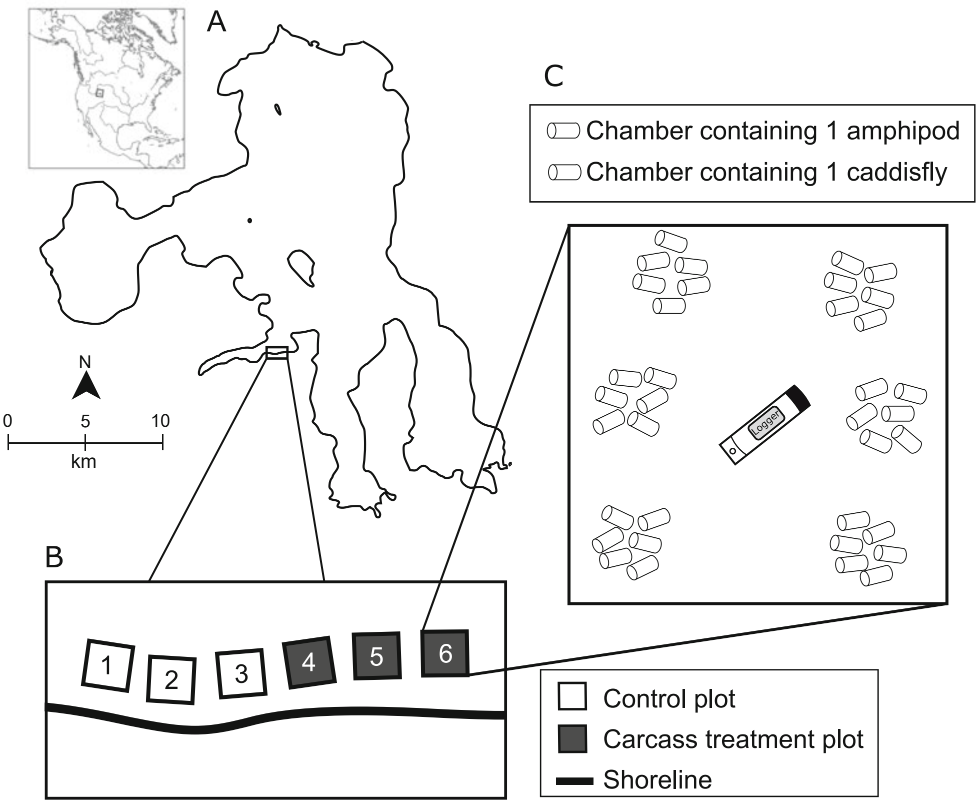

Fig. 1. **(A)** The location of the experiment site, Flat Mountain Mid (44.3721, -110.3993), within Yellowstone Lake, Wyoming and the location of Yellowstone Lake in North America; **(B)** the arrangement of experimental plots at the site; and **(C)** the arrangement of chambers containing amphipods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

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 (°C) 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.

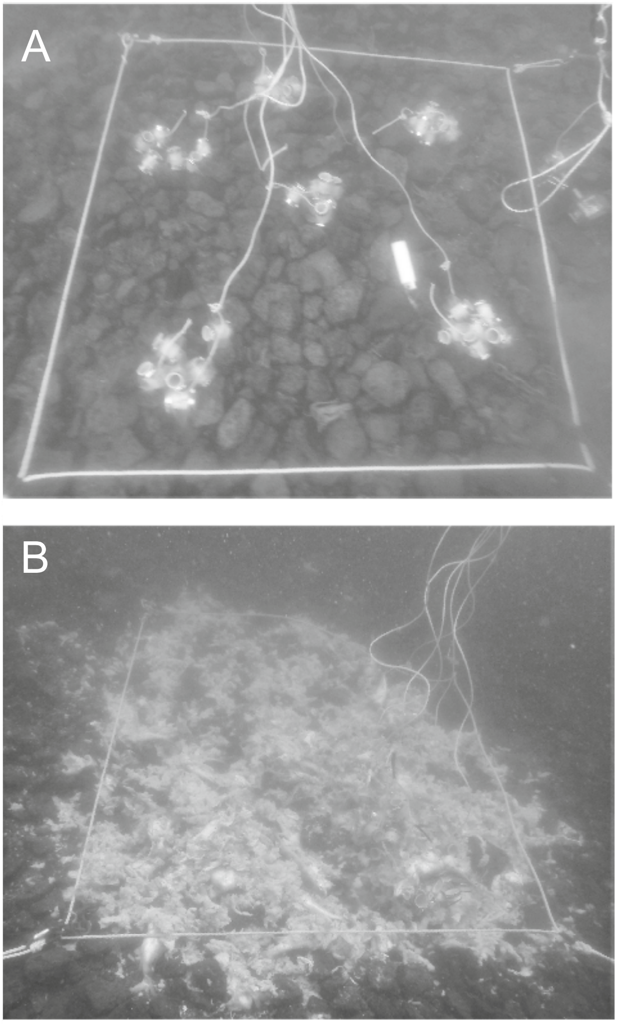

Fig. 2. **(A)** A control plot, with 36 chambers containing invertebrates and one dissolved oxygen logger; **(B)** a carcass treatment plot, with chambers and logger covered in carcass material.

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 (°C) 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 Development 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 6.6 °C. 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 14.9 °C.

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

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

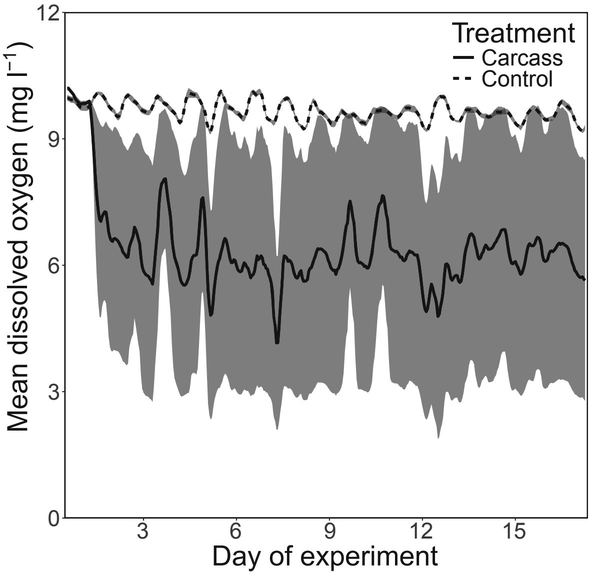

Fig. 3. Mean dissolved oxygen concentrations for control and treatment plots during the 17-day experiment. The gray shaded areas indicate the standard error.

for both invertebrate taxa in both control and treatment plots, ($p = 0.0014$; Fig. 5). 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 em-

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 dailyrange (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

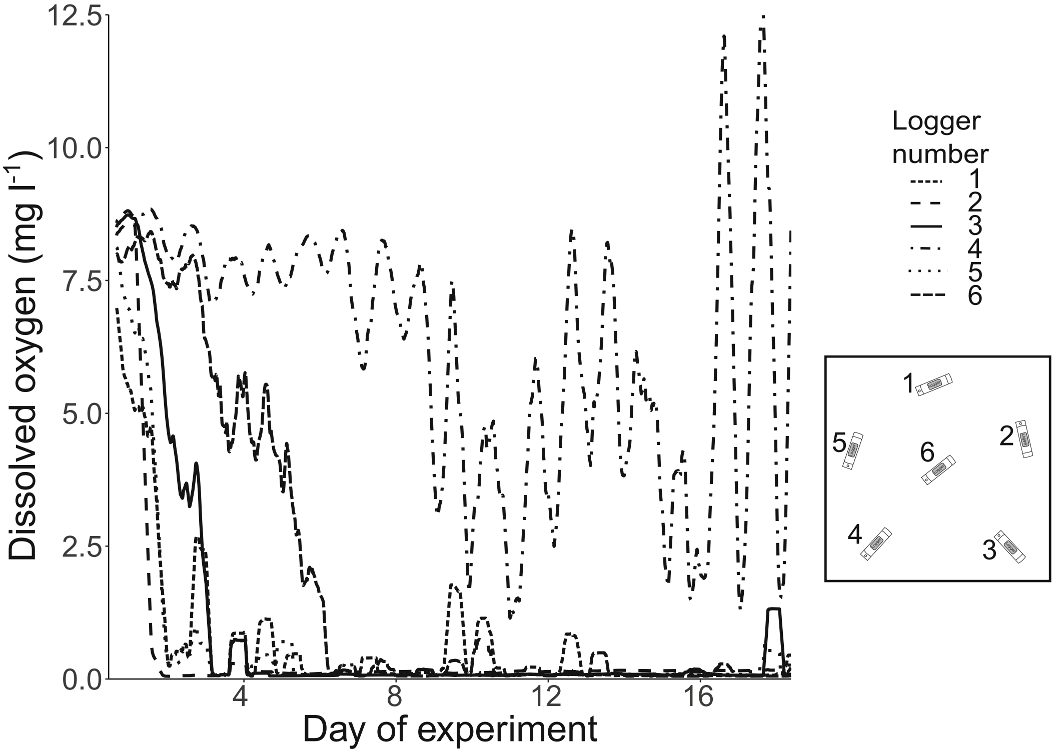

Fig. 4. Dissolved oxygen concentrations for the six loggers in the oxygen measurement plot over 17 days and their arrangement within the 1.5 m × 1.5 m plot.

bryos 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 (Marsden et al. 1995; Bigelow 2009). 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

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

Model	Number of parameters	AICc	ΔAICc
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 × treatment + invertebrate × day	8	249.23	9.62

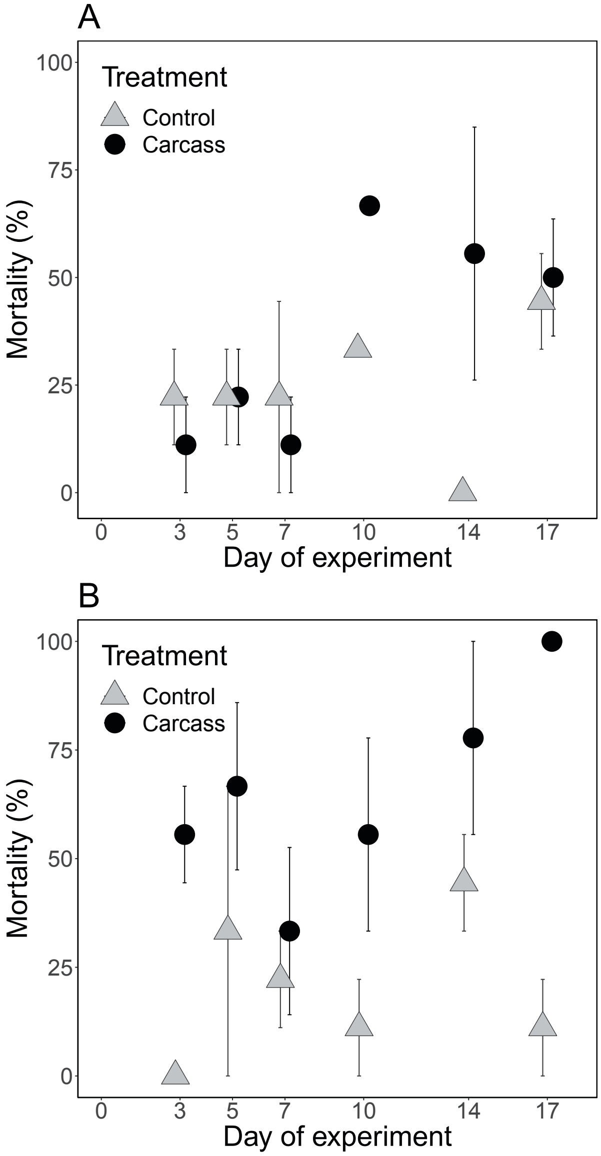

Fig. 5. Mean ± standard error (SE) % mortality of **(A)** amphipods and **(B)** caddisflies during the 17-day experiment. For points without error bars, SE = 0, i.e. % mortality was the same in all plots.

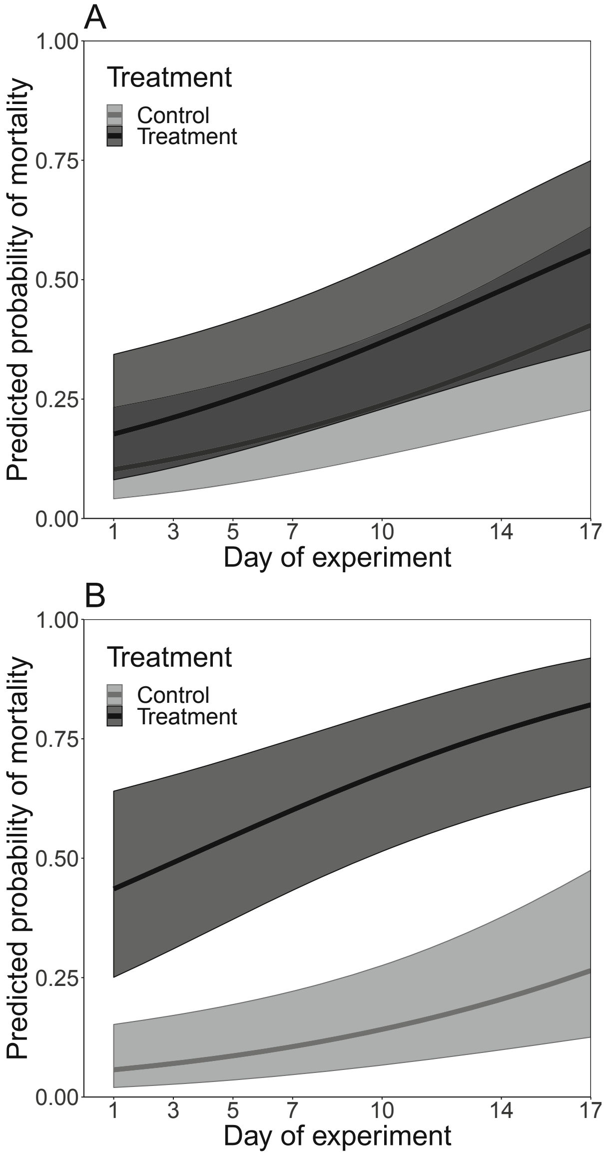

Fig. 6. Predicted probability of mortality for **(A)** amphipods and **(B)** caddisflies in carcass treatment and control plots during the 17-day experiment, with 95 % confidence intervals.

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 (Qin 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 1998) 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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Authors' 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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