Hydrobiologia
https://doi.org/10.1007/s10750-023-05450-w

PRIMARY RESEARCH PAPER

Novel technique for suppressing an invasive apex predator minimally alters nitrogen dynamics in Yellowstone Lake, Wyoming, USA

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Received: 4 February 2023 / Revised: 7 December 2023 / Accepted: 8 December 2023

Abstract Non-native species have invaded most ecosystems and methods are needed to manage them, especially in locations with sensitive species where they cannot be easily extirpated. Gillnetting for invasive lake trout [*Salvelinus namaycush* (Walbaum, 1792)] in Yellowstone Lake, Yellowstone National Park, USA began in 1995 and their carcasses are deposited into deep areas. This suppression method was recently supplemented by adding carcasses to shallow (< 20 m) spawning sites during the autumn spawning period to decrease dissolved oxygen through decomposition, suffocating lake trout embryos. We measured ammonium concentrations (shallow and deep sites), algal biomass, and ammonium uptake by phytoplankton and periphyton (shallow sites only) to investigate the degree to which carcasses caused bottom-up effects. Ammonium concentrations increased in autumn and were higher at deep sites than shallow sites. Algal biomass and ammonium uptake did not increase after adding carcasses, suggesting minimal effects. Periphyton biomass was 9 times higher than phytoplankton, but phytoplankton demanded 4.5 times more ammonium. Returning lake trout carcasses to deep areas of the lake may cause a second algal bloom. Assessing how novel management techniques alter the environment helps managers develop the most successful mitigation strategies that are effective without causing adverse effects to other portions of the ecosystem.

Handling editor: Zhengwen Liu

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-023-05450-w.

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Published online: 19 January 2024

Keywords Nutrients · Algae · Fish · Uptake · Benthic vs. pelagic · Carcasses

Introduction

Mass mortality can have large effects on ecosystems (e.g., Subalusky et al., 2017a, b, 2020); however, we are only beginning to understand the degree to which these events can alter freshwater ecosystems (Benbow et al., 2020). Animal carcasses can fertilize streams, lakes, and wetlands from aquatic (autochthonous) and terrestrial (allochthonous) sources continuously, seasonally or periodically. Decomposing carcasses can increase nutrient concentrations, increase algal biomass, increase invertebrate growth rates and be integrated into all trophic levels of a food web (e.g., Cederholm et al., 1999; Claeson et al., 2006). The most well-known example is salmon transporting marine nutrients seasonally to freshwater ecosystems during spawning (Cederholm et al., 1999). Mass mortality events can occur regularly in freshwater from sedimentation of zooplankton (Tang et al., 2014), winter fish kills (Schoenebeck et al., 2012), and drowning of wildebeest [*Connochaetes taurinus* (Burchell, 1923)] while migrating (Subalusky et al., 2017a, b, 2020). Most of the literature investigating the mass mortality of animals focused on natural events and fewer studies assessed mass mortality from management actions (see review by Benbow et al., 2020) such as the control of invasive species.

Successful mitigation of invasive species is crucial for reclaiming and restoring ecosystems to their natural configurations (Clavero & Garcia-Berthou, 2005), yet we know little about the effects of management actions on non-target organisms and the ecosystem. Non-native species have pervaded most aquatic ecosystems across the globe (Gallardo et al., 2016) and invasive animals can affect ecosystems by altering food webs (e.g., trophic cascade), introducing disease and altering habitats (Dayer et al., 2020). Invasive fish can hybridize (Mandeville et al., 2019), compete with (Guy et al., 2011), or prey on native fish (Tronstad et al., 2010; Koel et al., 2019). Various methods are used to manage or eradicate invasive animals including chemical removal (e.g., rotenone), physical removal (e.g., electrofishing or netting), and biological controls (e.g., introducing a predator; Rytwinski et al., 2019). Using two methods simultaneously can increase the success of controlling invasive species (Buktenica et al., 2013). Multiple studies estimated the success of control programs (summarized by Rytwinski et al., 2019), but few studies investigated if the mitigation strategies affected the ecosystem more than the invasive species themselves (Kettenring and Adams 2011; Ballari et al., 2016). For example, while rotenone can eliminate non-native fish, native fishes, and other gill-breathing animals may also be removed (Billman et al., 2012; Dalu et al., 2015). The fate of invasive carcasses is a major consideration for invasive species removal programs, and partially depends on the methods used. For example, incentives for anglers to retain carcasses sometimes removes them from the ecosystem, chemical and biological methods leave carcasses in ecosystems, and carcasses can be returned or removed from the ecosystem when physical methods are used (Sorenson, 2021). Management strategies can alter species and ecosystem processes in unexpected ways; therefore, investigating possible responses in other trophic levels is critical to avoid unexpected outcomes (Zavaleta et al., 2001).

Introduced species and the management strategies used to control them may alter nutrient dynamics. Disruptions to food webs can alter all trophic levels (Carpenter et al., 1985), including primary producers (Carpenter et al., 2001) that result in altered nutrient cycling (Tronstad et al., 2015). Lake food webs are complex integrating pelagic and benthic energy pathways that should be studied concomitantly (Vander Zanden et al., 2011). For example, gizzard shad [*Dorosoma cepedianum* (Lesueur, 1818)] were introduced to ponds and increased phosphorus concentrations and nutrient uptake (Schaus & Vanni, 2000). Nutrient uptake is the demand for a required element (i.e., nitrogen or phosphorus) by fungi, bacteria and primary producers. Nutrient uptake is commonly measured in streams and the pelagic zones of lakes, but less is known about fluxes in the benthic zone of lakes (Vadeboncoeur & Steinman, 2002). Nutrient uptake by periphyton can dominate in some lakes (Axler & Reuter, 1996) although these fluxes have seldom been compared. Nutrient uptake can be sensitive to ecosystem changes because uptake is affected by factors such as nutrient concentrations, nutrient inputs, food web configuration, temperature, algal biomass, and light (Carpenter et al., 1985; Vadeboncoeur & Steinman, 2002; Griffiths, 2006; Deininger et al., 2017). Strategies to eliminate or reduce an invasive fish have

the potential to alter stocks and flows of nutrients in an ecosystem, but these have seldom been measured.

Yellowstone Lake is home to the largest population of Yellowstone cutthroat trout [*Oncorhynchus clarki bouvieri* (Jordan & Gilbert, 1883)] in their native range, but their numbers drastically declined following the invasion of predatory lake trout (Koel et al., 2019). The invasive of lake trout and decline of Yellowstone cutthroat trout caused a trophic cascade that altered the structure of the zooplankton assemblage with large-bodied *Daphnia* dominating and decreased algal biomass (Tronstad et al., 2010). After lake trout were discovered, Yellowstone National Park began gillnetting in 1995 to conserve native cutthroat trout (Kaeding et al., 1994). The suppression program grew over time (Koel et al., 2020a) and most lake trout carcasses were deposited in deep areas of the lake (> 70 m) to return nutrients to the ecosystem. Although adult lake trout have been reduced by > 80% since 2012, the recruitment of juvenile lake trout remained high (Koel et al., 2020a). Yellowstone National Park experimented with small-scale trials where lake trout carcasses were added to spawning areas in shallow water (< 20 m) and 99% of embryos were killed due to low dissolved oxygen concentrations (Thomas et al., 2019; Poole et al., 2020). After their success, the park tested the management strategy on a larger scale using carcasses at lake trout spawning sites (Koel et al., 2020a, b). Even though salmonid carcasses or analog pellets have been used to supplement streams and lakes when reduced fish populations decreased nutrient cycling (Hyatt & Stockner, 1985; Ebel et al., 2014; Marcarelli et al., 2014; Kaylor et al., 2020), we are not aware of any studies that have used carcasses as a method to control invasive species.

Our goal was to measure the degree to which adding carcasses to a large lake would alter nutrient cycling and algal biomass. Our specific questions were: (1) to what degree did nutrient concentrations increase after adding fish carcasses to the hypolimnion and littoral zone in Yellowstone Lake, (2) how much did algal biomass of phytoplankton or periphyton increase from depositing carcasses at shallow sites, (3) to what degree did ammonium (NH_4^+) uptake increase by phytoplankton and periphyton during carcass additions in the littoral zone and (4) how much did depositing carcasses in the depths of the lake alter NH_4^+ concentrations, algal biomass, and NH_4^+ uptake when the lake turned over? We predicted that periphyton biomass and uptake would increase in response to adding carcasses to spawning sites, but we did not expect a response by phytoplankton because of the large volume of the lake and water currents moving plankton. We hypothesized that adding ~ 300,000 lake trout to the depths of Yellowstone Lake each summer would increase nutrient concentrations, phytoplankton biomass, and phytoplankton uptake after autumn turnover. To answer our questions, we measured nutrient concentrations at three deep sites where lake trout carcasses were deposited daily from the adult suppression program and one deep reference site. We also measured nitrogen (N) concentrations, algal biomass, and NH_4^+ uptake at two shallow treatment sites and one reference site to estimate how strategies to control an invasive apex predator altered nutrient dynamics.

Methods

Study area

Yellowstone Lake, Yellowstone National Park, Wyoming, USA, is the largest high elevation (> 2000 m) lake in North America (Gresswell et al., 1997) with a surface area of 341 km^2 and a volume of 16.54 km^3 (Kaplinski, 1991). The littoral zone (< 20 m deep) encompasses 23% of the lake area (Benson, 1961), the average depth is 43 m, and the maximum measured depth is 137 m (Kaplinski, 1991; Koel et al., 2020a). The lake is mesotrophic (Kilham et al., 1996), dimictic, and ice-covered from late December through late May to early June each year. Stratification generally occurs from mid-July through mid-September and surface water temperatures vary between 9 and 18°C during this time (Koel et al., 2019). The lake turns over in late May to early June and in mid to late September annually, delivering a surge of nutrients to shallow waters. Nitrogen limited phytoplankton (Interlandi et al., 1999) and periphyton were co-limited by N and phosphorus (P; Lujan et al., 2022). Strong currents circulate water throughout the lake (Benson, 1961) and the predominately southwestern winds blow across the 26 km fetch (Kaplinski, 1991).

The fish of Yellowstone Lake consist of few species. Two fish are native to Yellowstone Lake [Yellowstone cutthroat trout and longnose dace, *Rhinichthys*

cataractae (Valenciennes, 1842)]. As adults, Yellowstone cutthroat trout (cutthroat trout hereafter) reside in the littoral zone of Yellowstone Lake and spawn in tributary streams each spring. Five fish are non-native and lake trout are the most abundant non-native species (Gresswell et al., 1997; Koel et al., 2020a). Lake trout reside in the depths of Yellowstone Lake, feed at shallow depths, and spawn each autumn on angular rock, bedrock, volcanic (hydrothermal) deposits, and embedded cobble substrate within the littoral zone (Koel et al., 2020b). Lake trout tend to return to spawning sites used in previous years, which allowed spawning sites to be located from gillnetting efforts and radio telemetry studies (Bigelow, 2009; Williams et al., 2021).

The introduction of lake trout in Yellowstone Lake caused a trophic cascade that altered all trophic levels (Tronstad et al., 2010; Koel et al., 2019). Historically, cutthroat trout were the top trophic level and fed on zooplankton and benthic invertebrates (Benson, 1961); however, lake trout consumed cutthroat trout and reduced their abundance altering lower trophic levels. The zooplankton assemblage was dominated by copepods but shifted to larger species (e.g., *Daphnia* spp.) after the invasion of lake trout (Tronstad et al., 2010). The decline of cutthroat trout also increased the individual size and total biomass of amphipods in the benthos (Wilmot et al., 2015). Additionally, phytoplankton biomass and biovolume decreased after the invasion of lake trout, and water clarity increased (Secchi disk depths; Tronstad et al., 2010, Koel et al., 2019). Algal biomass was highest after spring turnover and did not increase after autumn turnover (Tronstad et al., 2010). Phytoplankton uptake of NH_4^+ peaked mid-summer (405 µg N m^{-3} h^{-1}) and zooplankton excreted 86% of the N-NH_4^+ demanded by phytoplankton (Tronstad et al., 2015). Atmospheric deposition (9 µg N m^{-2} h^{-1}) contributed little N compared to internal sources (Tronstad et al., 2015).

Lake trout removal program

Gillnetting efforts to remove lake trout and conserve cutthroat trout began in 1995 (Koel et al., 2020a). Small-mesh (25–38 mm bar measure) and large-mesh (44–76 mm bar measure) gillnets were used to target lake trout 2 years and older at depths > 20 m to avoid bycatch of native cutthroat trout (Koel et al., 2019). Between 1995 and 2009, 444,491 lake trout were caught and their carcasses returned to the depths of Yellowstone Lake (Koel et al., 2020a). In 2009, contract gillnetting began supplementing Yellowstone National Park gillnetting, increasing the number of lake trout removed annually to 250,000–300,000 fish (Koel et al., 2020a). The decomposition rate of whole lake trout carcasses in the depths of Yellowstone Lake was -0.0075 day^{-1} and the half-life of carcasses was 91 days (Glassic et al., in press). Yellowstone National Park experimented with other methods to control early life stages of lake trout to reduce gillnetting costs and reduce juvenile survival. In 2018 and 2019, carcasses were added to entire spawning sites to estimate the effectiveness of the method allowing us to measure how algae and uptake responded.

Overview of study design

We investigated N dynamics at deep and shallow sites in Yellowstone Lake. We measured nutrient concentrations at three deep sites (> 70 m depth; West Thumb, South Dot, and Promontory Point; deep sites hereafter; Fig. 1) that received lake trout carcasses daily from June–September and one deep reference site, East Frank, where no fish were deposited. We also investigated N cycling at two shallow sites (< 20 m depth; Snipe Point and Olson Reef) that received lake trout carcasses in the autumn to suffocate lake trout embryos. Snipe Point (early season site hereafter; 20,000 m^2) was treated with carcasses before spawning began to deter lake trout from spawning there. Carcasses were added beginning on 29 August 2018 (week 15) and 10 August 2019 (week 12). Boat operators added fewer carcasses to our experimental sites in 2018 than in 2019; our sites were made a higher priority in 2019 resulting in more added carcasses. Olson Reef (late season site hereafter; 3000 m^2) was treated with carcasses on 1 October 2018 and 2019 (week 20) after spawning occurred. We collected fewer samples at Olson Reef because of the late timing and unsafe conditions on the lake in autumn. Both shallow treatment sites were confirmed spawning locations and received minimal to no carcass additions in the past. SCUBA divers and a remote operated vehicle confirmed spawning sites by observing viable embryos. Wolf Point was the shallow reference site in 2018 and Elk Point was the shallow reference site in 2019. We moved our

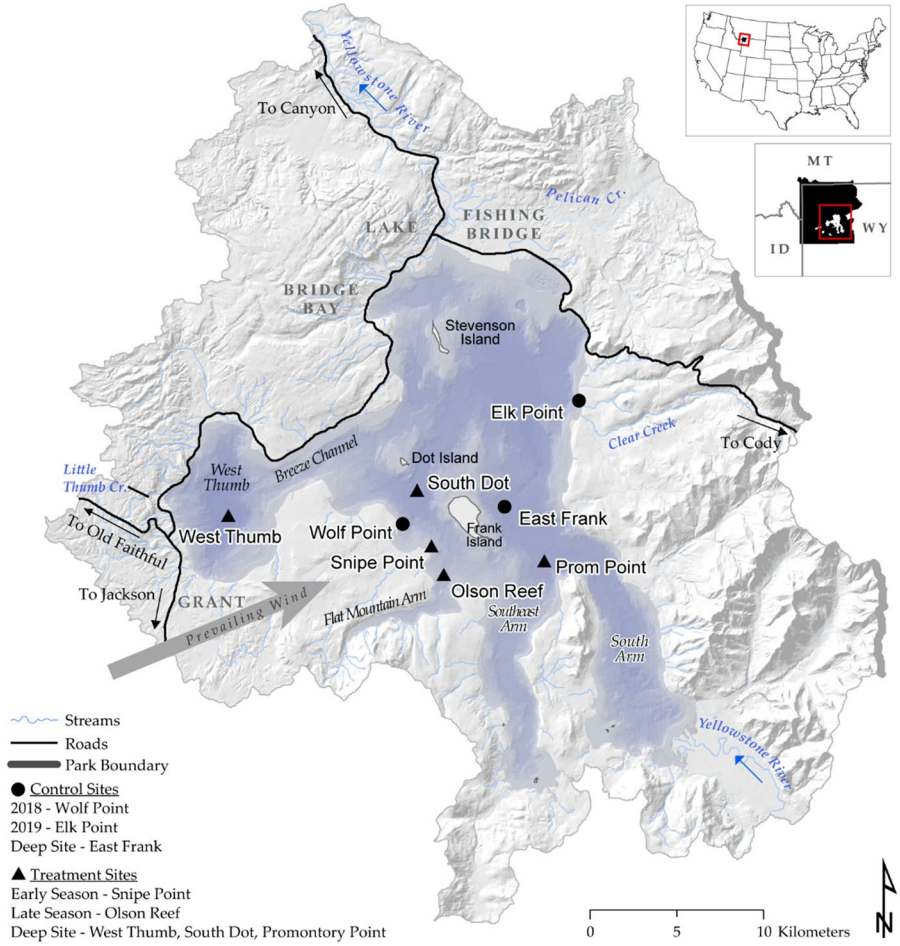

Fig. 1 We measured how deposited carcasses used to suppress lake trout embryos at three confirmed spawning sites and a reference site altered nutrient concentrations, algal biomass and nitrogen cycling. We moved our shallow reference site in 2019 from Wolf Point to Elk Point because the proximity and frequent gillnetting at the original site may have altered our results. Carcasses were added to the early season site beginning in mid-August as a potential deterrent for spawning lake trout and to have a longer time frame to measure effects. Carcasses were added to the late season site beginning 1 October after lake trout spawned. Three deep sites were used to measure the nutrients added by daily gillnetting operations and East Frank was a reference

reference site in 2019 because the proximity of Wolf Point to one of our treatment sites and because gillnetting operations may have altered our results in 2018. Reference sites had suitable substrate for lake trout spawning but no eggs have been observed there (Bigelow, 2009).

General measurements

We measured water chemistry and dissolved oxygen concentrations at each site and date, and we grouped observations by week. Week 1 is the last week of May when gillnetting began, and gillnetting ended in mid- to late October (weeks 20–22). At the shallow sites, we measured specific conductivity (SPC; µS cm^{-1}) and pH using a Yellow Springs Instrument (YSI) Professional Plus multiprobe that was calibrated weekly. Dissolved oxygen (DO; percent saturation and mg l^{-1}) and water temperature (°C) were measured hourly with a miniDOT logger (Precision Measurement Engineering) placed on the substrate at each site for the entire sampling season (June–October). We reported average values of each measurement before and during carcass additions at each site, but see Briggs et al. (2022) for hourly DO concentrations in 2019.

Nutrient concentrations

We collected water above the substrate and measured NH_4^+ and nitrate (NO_3^-) concentrations at deep and shallow sites. At the deep sites ($n = 4$–5 measurements annually), we measured nutrient concentrations by collecting 400 ml water near the substrate with a remote operated vehicle (ROV). Deep sites were marked with mooring buoys and the ROV followed ropes down to the lake bottom. Once the ROV reached the bottom, we searched the site for carcasses

and collected water with a 100 ml syringe attached to the ROV (four trips). Two replicates from each site were collected for NH_4^+ concentrations (µg N l^{-1}) and processed the same day on a fluorometer (method detection limit = 0.2 µg N l^{-1}; Turner Designs TD-700) according to Taylor et al. (2007). Nitrate and PO_4^{3-} were measured using a ThermoFisher ICS-5000 ion chromatograph equipped with an AS23 anion separation column and suppressed conductivity detection (method detection limit; NO_3^- = 24.5 µg N l^{-1}). We do not report PO_4^{3-} concentrations due to values that were below the detection limit (135 µg P l^{-1}).

We measured several characteristics at shallow sites including nutrient concentrations, water clarity, water depth, and the mass of carcasses deposited (n = 7–17 weeks annually). We estimated nutrient concentrations at shallow sites by collecting water above the substrate using a beta bottle (2.2 l; Wildco) and water was analyzed using the same methods as for the deep sites. Water clarity was recorded by lowering a Secchi disk off the shaded side of the boat and recording the depth at which the disk was no longer visible. Site depth was measured with the Lowrance depth finder mounted on the boat. We estimated the mass of carcasses deposited at shallow sites by recording the net mesh size used to capture lake trout and the number of bins (containers used to hold lake trout carcasses) amended to each site. We measured the mass of full bins from each net mesh size (n = 2–8) and calculated the biomass of fish (kg) added to the site in wet mass (WM). Dry mass (DM) was calculated as 22% of WM (Cyr & Peters, 1996) and N was calculated as 11% of DM (Griffiths, 2006). We estimated the total amount of N returned to the depths of Yellowstone Lake based on the number of lake trout caught annually through gillnetting, and the average length (373 mm total length; Koel et al., 2020a) and mass (464 g WM; Piccolo et al., 1993) of lake trout captured.

Algal biomass

We estimated algal biomass of phytoplankton and periphyton at the shallow sites through the open water season (June–October). We measured planktonic chlorophyll *a* (3–7 m depth) concentrations to estimate phytoplankton biomass during the open water season (biweekly from June–July, weekly August–October). We collected two 1-l samples at each site and date. Samples were stored in a cooler until we returned to the laboratory where samples were filtered onto type-A/E glass-fiber filters (Pall Life Sciences, Port Washington, New York). Chlorophyll *a* was extracted by incubating filters overnight in 90% ethanol buffered with $MgCO_3$. We measured chlorophyll *a* concentrations using the acid method with a pheopigment correction (Nusch, 1980) on a TD-700 fluorometer (Turner Designs, Sunnyvale, California). Benthic chlorophyll *a* concentrations were estimated from three rocks haphazardly collected from each site and date by SCUBA divers. Rocks were stored in plastic bags and returned to the laboratory where they were scrubbed using a brush and traced to estimate their two-dimensional area (cm^2). The slurry was filtered onto type A/E glass-fiber filters and chlorophyll *a* was extracted using the same method used for pelagic chlorophyll *a*.

Benthic uptake

We estimated benthic and pelagic NH_4^+ uptake to compare the demand for N before and after carcasses were added to spawning sites. We measured benthic NH_4^+ uptake by incubating rocks collected from their respective sites in 2-l polycarbonate containers. SCUBA divers collected four rocks at each site and date, placed them in plastic bags and transported them to the northern shore in a cooler. One rock was placed into each container and filled with lake water. Each container was spiked with 200 µl of 0.5 µg N-$^{15}NH_4Cl$ and lids were tightly sealed (Wozniak et al., 2008). One container was used to estimate the initial ^{15}N value (time zero) by spiking the water, mixing and immediately collecting a biofilm sample. The remaining rocks were incubated for 3 h while submerged underwater in the lake. Biofilm samples were collected from rocks by scrubbing the entire surface with a brush about 20 min after incubation ended. A subsample of the slurry was filtered onto 25 mm type A/E glass-fiber filters and analyzed for $\delta^{15}N$ and the mass of N at the University of Wyoming Stable Isotope Facility. We measured the volume of water displaced by each rock in a 2-l graduated cylinder to calculate the volume of water in each chamber.

Phytoplankton uptake

We measured phytoplankton NH_4^+ uptake at each site and date to estimate the demand for N throughout the open water season (Tronstad et al., 2015). In 2018, we collected water at 5, 10, and 15-m depths. We collected the 5 m depth water sample directly over the site and we gradually moved east until we reached the target depth where we collected the water sample. This allowed us to sample from an undisturbed water column. We filled three 2.5-l Nalgene polycarbonate bottles with lake water from each depth and added 0.5 µg N-$^{15}NH_4Cl$. One bottle was immediately filtered to estimate the ^{15}N value (time zero) at the beginning of the experiment to account for adsorption. We suspended the remaining bottles at their respective depths to incubate for 3 h. After 3 h, we retrieved the bottles and placed them in an ice-filled, dark cooler to transport them back to the laboratory. We collected phytoplankton by filtering 1.2 l of water through ashed 25-mm PALL type A/E glass-fiber filters (1 µm pore size). In 2019, we used the same procedures except we only collected water from directly over the treatment site.

Stable isotope calculations for uptake

We used N stable isotopes incorporated into periphyton and phytoplankton biomass during incubation to measure the uptake fluxes (all samples; Tronstad et al., 2015). We calculated the amount of ^{15}N taken up in each bottle or chamber as the fraction of excess ^{15}N in each sample (^{15}N/total N; atomic fraction; F), $F_{xs} = F_{3hr} - F_{t=0}$, where F_{xs} is the F excess, F_{3hr} is the F after 3 h of incubating, and $F_{t=0}$ is the F at time zero (sample taken immediately after ^{15}N was added). Total ^{15}N uptake flux ($^{15}N_{TU}$; µg N l^{-1} h^{-1} for phytoplankton or µg N m^{-2} h^{-1} for periphyton) was calculated by $^{15}N_{TU} = (N_S \times F_{xs}/ta) \times S$, where N_S is the sample mass of N on filters (µg), t is the incubation time (h), a is the volume of water filtered (l) or surface area of the rock (m^2), and S is the ratio of $^{14}N/F_{xs}$. The residence time (R; h) of an NH_4^+ molecule was calculated by $R = 1/(^{15}N_{TU}/C_{15N})$ where C_{15N} is the mean concentration of ^{15}N excess in the bottle or chamber (µg ^{15}N l^{-1}). We converted volumetric uptake (µg m^{-3} h^{-1}) by phytoplankton to areal uptake (µg m^{-2} h^{-1}) by multiplying by the depth of each site to compare periphyton and phytoplankton uptake in a 1 m^2 column of water at each site. The calculations assume that our estimate of phytoplankton and periphyton uptake are representative of the water column and benthos. Shallow sites were ≤ 7 m depth and we measured nutrient concentrations each day we measured uptake.

Statistical approach

We estimated what factors influenced NH_4^+ concentrations, algal biomass, and NH_4^+ uptake using generalized linear models (glm) in Program R (R Core Development Team, 2017). We analyzed all NH_4^+ concentrations by depth (deep or shallow), week (time since ice-off) and year to estimate how concentrations differed between deep and shallow sites. We evaluated deep NH_4^+ concentrations by week (time since ice-off), year and site to assess differences among deep sites. We analyzed shallow NH_4^+ concentrations by week, treatment (before or during carcass additions), year, site and an interaction term between site and treatment to estimate the degree to which these variable affected concentrations in the littoral zone. We investigated algal biomass (chlorophyll *a*) by habitat (shallow versus deep), week, year, site and an interaction term between site and treatment. We analyzed NH_4^+ uptake by habitat, week, year, treatment, site and an interaction term between site and treatment. An interaction term ($P \leq 0.05$) between site and treatment can indicate that treating sites with carcasses altered nutrient concentrations, algal biomass or uptake. The data were not normally distributed so we used the fitdistplus package (Delignette-Muller & Dutang, 2015) to select the gamma distribution to analyze the data. Each level of a categorical variable receives a *t*- and *P*-value for which we report a range of values. We used emmeans (Lenth, 2021) to estimate differences among levels for each categorical variable when they had ≥ 3 levels.

Results

General conditions

Dissolved oxygen was the only abiotic factor that varied due to adding carcasses and other parameters differed little among sites or treatment (Tables 1, 2). Water temperatures peaked in early August resulting

Table 1 Average values measured for site depth, ammonium (NH_4^+) and nitrate (NO_3^-) concentrations

	East Frank (reference)	Promontory point	West thumb	South dot
2018				
Depth (m)	79	79	91	79
NH_4^+ (µg N l^{-1})	6.4 ± 1.4	28.9 ± 5.3	9.3 ± 1.5	8.4 ± 0.63
NO_3^- (µg N l^{-1})	180 ± 55	110 ± 17	200 ± 12	120 ± 16
N from carcasses (kg)	0	633	336	526
2019				
Depth (m)	79	79	91	79
NH_4^+ (µg N l^{-1})	5.7 ± 1.0	9.5 ± 1.0	6.0 ± 0.2	9.7 ± 1.2
NO_3^- (µg N l^{-1})	< 50	< 50	177 ± 6.9	< 50
N from carcasses (kg)	0	321	1035	357

Standard error was calculated for nutrient concentrations when at least three measurements were above detection limit. We estimated the dry mass (DM) and nitrogen (N) from lake trout carcasses deposited at deep sites during the open water season in Yellowstone Lake (see section "Methods" for details)

Table 2 Average values for measured benthic water temperature, water depth, Secchi disk depth, ammonium (NH_4^+) and nitrate (NO_3^-) concentrations, dissolved oxygen (DO; mg l^{-1} and % saturation), specific conductivity (SPC), and pH at each shallow site before (pre) and during (treatment) carcass additions at reference, early season (treated prior to spawning) and late season (treated after spawning) sites

	Reference		Early		Late	
	Pre	Treatment	Pre	Treatment	Pre	Treatment
2018						
Temperature (°C)	11.7	13.5	10.8	11.4	7.8	10.3
Depth (m)	5	5	5	5	12	12
Secchi (m)	7	8.2	6	8.5	8	10
NH_4^+ (µg N l^{-1})	4.6 ± 0.47	5.6 ± 0.32	3.4 ± 0.46	6.9 ± 0.24	3.5 ± 0.49	5.5 ± 0.11
NO_3^- (µg N l^{-1})	78 ± 41	120 ± 49	70	120 ± 48	< 50	50 ± 1.6
DO (mg l^{-1})	8.7	8.4	8.5	5.9	9.0	8.0
DO (% saturation)	111.4	108.6	99.7	74.0	101.3	95.3
N carcasses (kg)	0	0	0	52	0	11
g N m^{-2}	0	0	0	2.6	0	3.6
2019						
Temperature (°C)	11.5	13.2	10.5	13.8	7.8	10.3
Depth (m)	7	7	5	5	12	12
Secchi (m)	7.5	11.25	8.75	10	9.5	10
NH_4^+ (µg N l^{-1})	4.8 ± 1.3	6.5 ± 1.2	3.7 ± 1.5	6.6 ± 0.64	3.2 ± 0.83	3.9 ± 0.72
NO_3^- (µg N l^{-1})	< 50	< 50	< 50	< 50	< 50	< 50
DO (mg l^{-1})	8.9	8.1	9.2	6.6	9.0	8.0
DO (% saturation)	108.5	102.9	110.2	86.4	101.3	95.3
SPC (µS cm^{-1})	120.8 ± 35	92.0 ± 0.3	126.1 ± 36	91.9 ± 0.4	92.2 ± 0.62	91.7 ± 0.43
pH	7.3	7.1	6.8	7.7	7.6	7.2
N carcasses (kg)	0	0	0	144	0	10
g N m^{-2}	0	0	0	7.2	0	3.3

Standard error was calculated for nutrient concentrations when at least three measurements were above detection limit. The estimated amount of lake trout carcass material as nitrogen (N) and per unit of area (g N m^{-2}) added to the early and late season sites (see section "Methods" for more details). Specific conductivity and pH were not collected in 2018 because of equipment failure

in a mean water temperature that was cooler pre-treatment and warmer post-treatment. Adding carcasses at the early season site decreased dissolved oxygen to nearly 0 mg l^{-1} (see Briggs et al., 2022 for hourly 2019 measurements at Snipe Point). Secchi disk depths were deeper at all sites post-treatment (10 m) compared to pre-treatment (7.8 m; $t=2.9$, $P<0.0001$) as typically occurs throughout the open water season because phytoplankton becomes sparser (Tronstad et al., 2010). Specific conductivity was higher pre-treatment (116 µS cm^{-1}; $t=5.4$, $P<0.0001$) compared to post-treatment (93 µS cm^{-1}), but values did not differ among sites ($t=0.76$–2.4, $P=0.02$–0.53; emmeans, $P=0.08$–0.99). pH did not differ pre- (7.5) versus post-treatment (7.2; $t=1.1$, $P=0.28$) or among sites ($t=1.1$–1.7, $P=0.08$–0.27; emmeans, $P=0.30$–0.99; Table 2).

Carcass deposition

Lake-wide, approximately 3369 kg N (9.9 kg N km^{-2}) were returned via carcasses to Yellowstone Lake in 2018 and 3182 kg N (9.3 kg N km^{-2}) were returned in 2019. The deep sites measured in our study averaged ~ 20,600 kg WM in 2018 and ~ 23,600 kg WM of carcasses in 2019 (Table 1), resulting in nearly 1500 kg N deposited at the lake bottom at these three sites in 2018 and > 1700 kg N deposited in 2019 (Fig. 2). Carcasses were added to other deep areas throughout the lake explaining the discrepancy between our deep sites and total N returned lake wide. The deep sites received nearly 9.5 times more carcass material than the shallow spawning sites. Carcasses were added to the deep sites during the entire ice-free season, and carcasses were added to shallow sites only in the late summer and autumn to deter spawning lake trout or increase embryo mortality. Additionally, more lake trout were captured earlier in the year when carcasses were added to deep sites. At the shallow sites, the early season site received ~ 2200 kg WM in 2018 and ~ 5900 kg WM of carcasses in 2019 (Table 2), resulting in 52 kg N (2.6 g N m^{-2}) added to the site in 2018 and 144 kg N (7.2 g N m^{-2}) added in 2019 starting annually in August (Fig. 3). The late season site received ~ 440 kg WM in 2018 and ~ 400 kg WM of carcasses in 2019, adding 11 kg N (3.6 g N m^{-2}) in 2018 and 10 kg N (3.3 g N m^{-2}) in 2019 beginning annually in October (Fig. 3; Table 2).

Ammonium concentrations

Ammonium concentrations were higher at deep sites (8.1 ± 0.75 µg N l^{-1}; mean ± SE; Fig. 2) compared to shallow spawning sites (5.0 ± 0.24 µg N l^{-1}; 4.9t = 2.4, $P=0.015$; Fig. 3). Concentrations at deep sites varied over time ($t=4.9$, $P<0.0001$), but concentrations did not differ between years ($t=0.7$, $P=0.48$). Concentrations at shallow sites were highest in the spring and autumn after the lake turned over ($t=2.8$, $P=0.004$; Fig. 3). An interaction term between site and treatment indicated that adding carcasses changed NH_4^+ concentrations by site ($t=2.2$–3.9, $P=0.0001$–0.03). Concentrations of NH_4^+ were higher when carcasses were added to the early season site (emmeans, $P=0.015$), but concentrations at the reference site did not differ during this period (emmeans, $P=0.99$). Ammonium concentrations peaked at all sites when the lake turned over in autumn (7.3 ± 0.32 µg N l^{-1}; week 18) and concentrations doubled compared to weeks 7–9 (3.2 ± 0.25 µg N l^{-1}).

Periphyton and phytoplankton biomass

Periphyton in the littoral zone of Yellowstone Lake had much higher chlorophyll *a* concentrations, an indicator of algal biomass, compared to phytoplankton. On average, periphyton biomass was nine times higher than phytoplankton biomass ($t=18.2$, $P<0.0001$). Algal biomass did not change over time ($t=0.8$, $p=0.43$), but periphyton generally had higher concentrations in autumn (Fig. 4a, c, e). Phytoplankton biomass was highest after the lake turned over (Fig. 4b, d, f). Periphyton biomass was four times higher and phytoplankton biomass was 2.5 times higher in 2019 compared to 2018 ($t=8.8$, $P<0.0001$). An interaction term between site and treatment indicated that adding carcasses altered algal biomass differently among sites ($t=0.3$–3.3, $P=0.001$–0.79). Phytoplankton biomass was higher at the late season site compared to the other shallow sites post-treatment (emmeans, $P \leq 0.03$), but phytoplankton biomass at the late season site did not differ pre- versus post-treatment (emmeans, $P=0.2$) indicating that phytoplankton biomass was higher at that site throughout the period. Phytoplankton biomass at the early season site did not differ from the reference site post-treatment (emmeans, $P=0.44$). Similarly, phytoplankton biomass at the early season

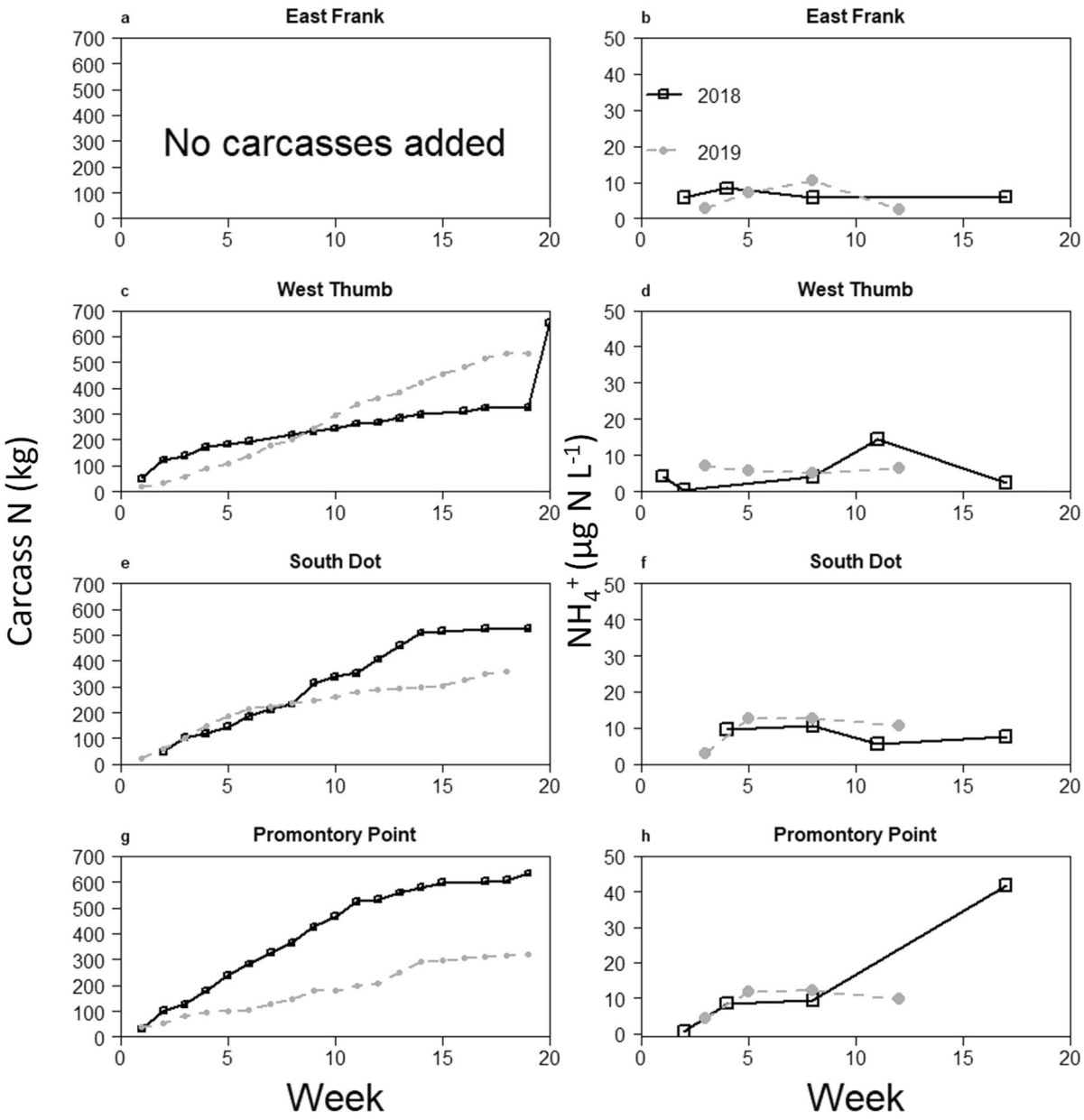

Fig. 2 Nitrogen (N; **a**, **c**, **d**, **f**) added to deep sites from adding lake trout carcasses calculated from the wet mass of carcasses deposited. We measured ammonium concentrations (µg N l^{-1}; **b**, **d**, **f**, **g**) to assess changes in available N at deep sites East Frank (**a**, **b**; reference), West Thumb (**c**, **d**), South Dot (**e**, **f**), and Promontory Point (**g**, **h**) during 2018 and 2019. No carcasses were added to the reference site (**a**) resulting in no N from carcasses. Week 1 is the last week of May when gillnetting began and week 20 is the end of October when gillnetting finished

site did not differ pre- and post-treatment (emmeans, $P=0.15$), suggesting that adding carcasses did not alter phytoplankton biomass. Phytoplankton biomass was higher post-treatment compared to pre-treatment at the reference site (emmeans, $P=0.004$) supporting the idea that mineralized nutrients from decomposing lake trout carcasses in the hypolimnion are brought to surface waters each autumn during turnover affecting all sites, including our reference site. Periphyton biomass did differ at the early season site

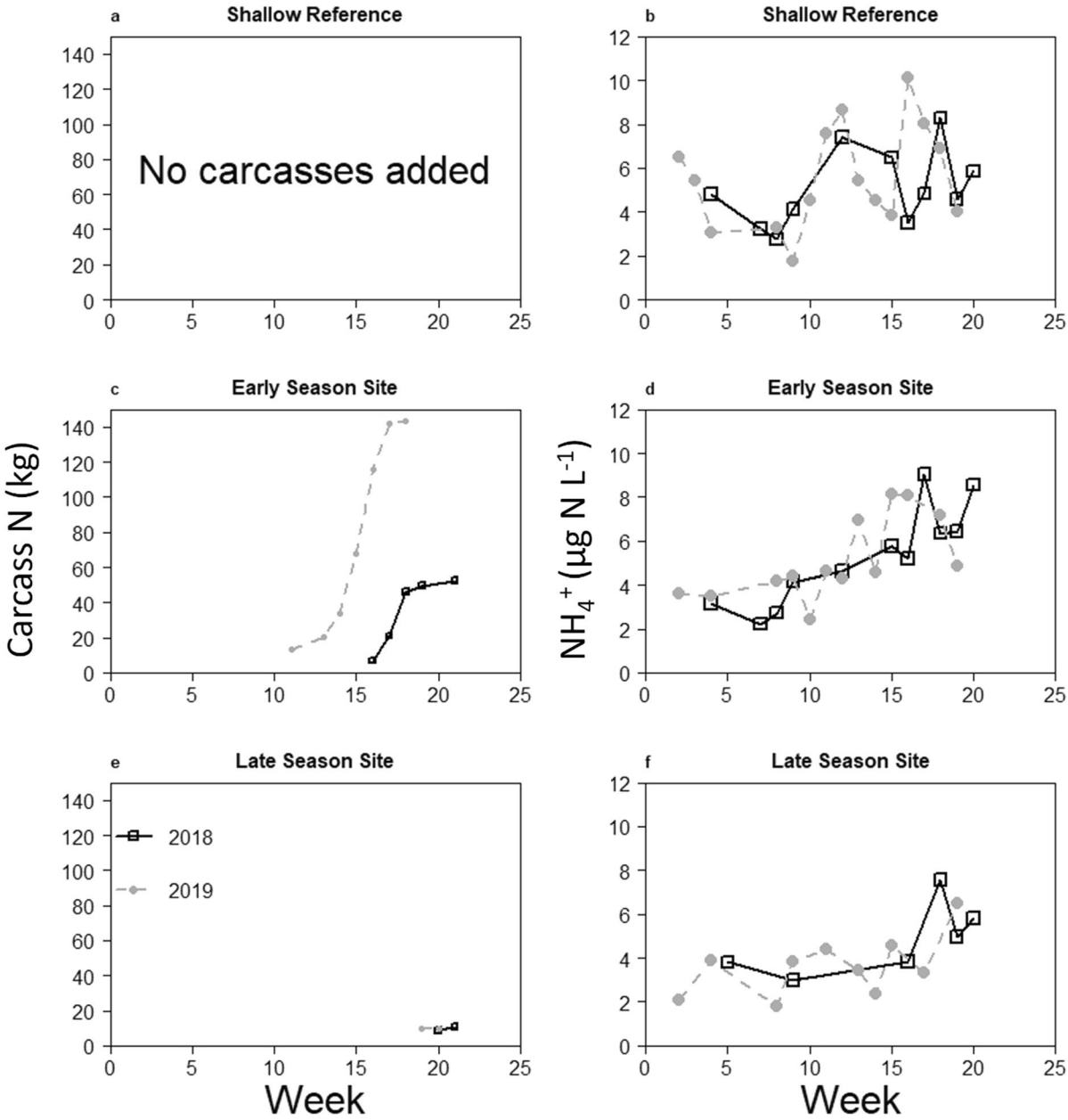

Fig. 3 Nitrogen (N; **a**, **c**, **e**) added to shallow sites from adding lake trout carcasses calculated from the wet mass of carcasses deposited. We measured ammonium concentrations (µg N l^{-1}; **b**, **d**, **f**) to assess changes in available N at the shallow sites Wolf Point (2018) and Elk Point (2019; reference; **a**, **b**), Snipe Point (**c**, **d**), and Olsen Reef (**e**, **f**) during 2018 and 2019. Week 1 is the last week of May when gillnetting began and week 20 is the end of October when gillnetting finished

pre- compared to post-treatment (emmeans, $P = 1.0$), but periphyton biomass was higher post-treatment at the reference site compared to the pre-treatment time period (emmeans, $P = 0.03$), potentially responding to autumn turnover.

Periphyton and phytoplankton NH_4^+ uptake

Adding carcasses did not alter NH_4^+ uptake by phytoplankton or periphyton. Phytoplankton demanded 32 times more NH_4^+ (2015 µg m^{-2} h^{-1};

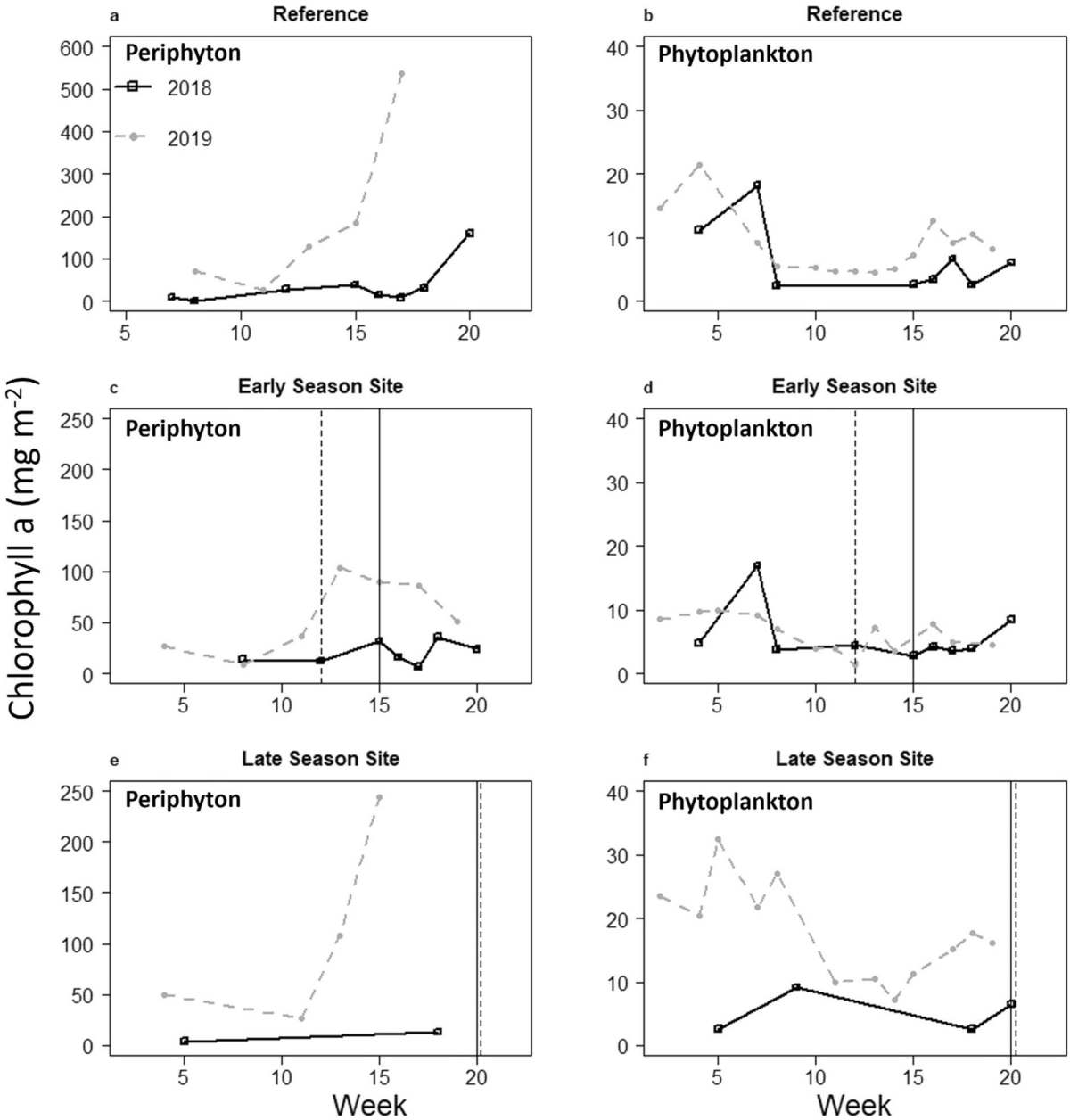

Fig. 4 Periphyton (**a**, **c**, **e**) and phytoplankton (**b**, **d**, **f**) algal biomass measured as chlorophyll *a* (mg m^{-2}) for the reference (**a**, **b**), early season site (**c**, **d**), and late season site (**e**, **f**) before and during treatments. Phytoplankton biomass was converted to areal estimates by multiplying by the site depth. Vertical lines indicated when lake trout carcasses were added to the sites in each year. Week 1 is the last week of May when gillnetting began and week 20 is the end of October when gillnetting finished

288 µg m^{-3} h^{-1}) compared to periphyton (63 µg m^{-2} h^{-1}) on average ($t = 17.2$, $P < 0.0001$). The mean residence time of an NH_4^+ molecule was 19.5 h for periphyton and 5.4 s for phytoplankton. Uptake was higher in 2019 (1400 µg m^{-2} h^{-1}) compared to 2018 (1000 µg m^{-2} h^{-1}; $t = 3.1$, $P = 0.002$). Generally, the demand for NH_4^+ by phytoplankton was highest after ice-off in June (week

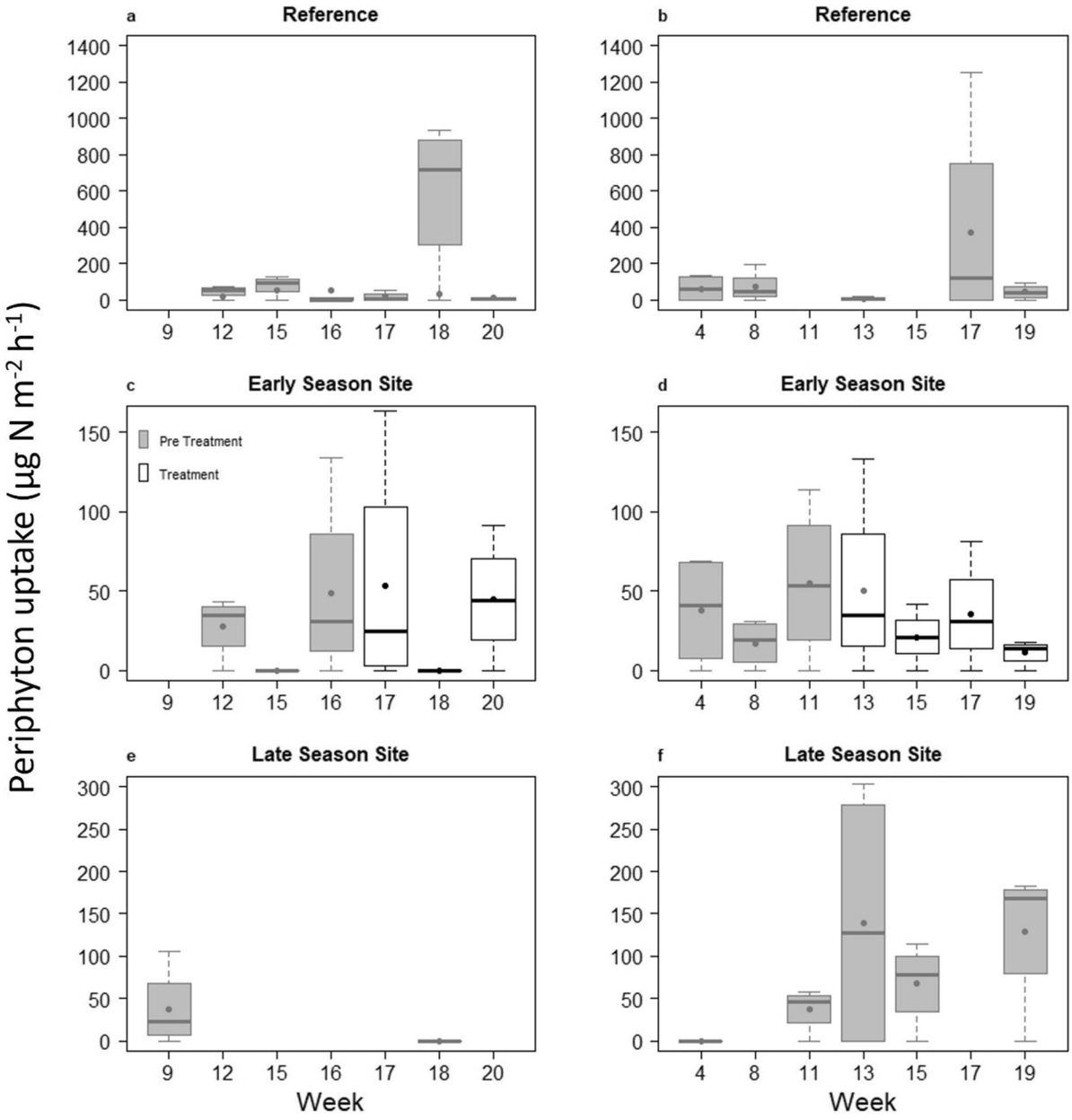

Fig. 5 Periphyton uptake in 2018 (**a**, **c**, **e**) and 2019 (**b**, **d**, **f**) at the reference (**a**, **b**), early season (**c**, **d**), and late season (**e**, **f**) spawning sites. Note differences in *x*-axis scales. Week 1 is the last week of May when gillnetting began and week 20 is the end of October when gillnetting finished. The early season site was treated prior to lake trout spawning (week 15 in 2018 and week 12 in 2019) and the late season site was treated after lake trout spawning (week 20)

9; 2278 µg m^{-2} h^{-1}) and after lake turnover in the autumn (week 18; 2899 µg m^{-2} h^{-1}), whereas demand by periphyton was generally highest in the fall (week 18; 264 µg m^{-2} h^{-1}; Figs. 5 and 6). An interaction term between site and treatment did not suggest that treatment altered uptake ($t = 0.4–1.1$,

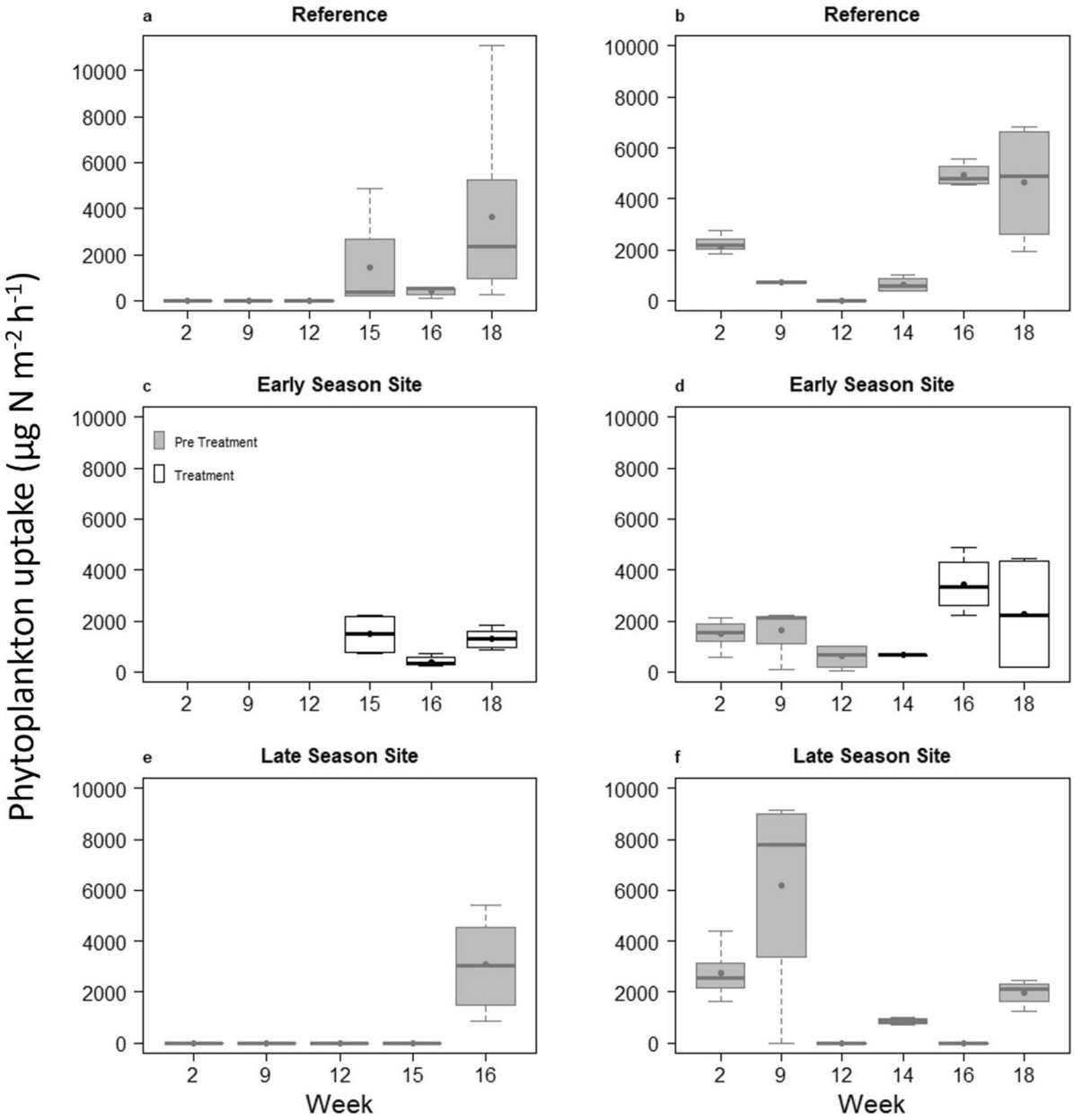

Fig. 6 Phytoplankton uptake in 2018 (**a**, **c**, **e**) and 2019 (**b**, **d**, **f**) at the reference (**a**, **b**), early season (**c**, **d**), and late season (**e**, **f**) spawning sites. Week 1 is the last week of May when gillnetting began and week 20 is the end of October when gillnetting finished. The early season site was treated prior to lake trout spawning (week 15 in 2018 and week 12 in 2019) and the late season site was treated after lake trout spawning (week 20)

$P = 0.29$–0.71); however, differences may be attributed to autumn turnover because adding carcasses to shallow sites occurred at about the same time as stratification ended. One piece of evidence to support our turnover hypothesis is that the reference site had higher demand in autumn compared to earlier measurements (emmeans, $P = 0.03$). Additionally, fluxes did not differ pre- versus post-treatment

at the early (emmeans, $P = 0.12$) or late season sites (emmeans, $P = 0.77$).

Discussion

Nutrients from lake trout carcasses deposited in deep areas of Yellowstone Lake appeared to have a larger effect on algal biomass and nutrient cycling than carcasses deposited at shallow spawning sites by causing a second algal bloom lake-wide in autumn, but the magnitude of these effects compared to other ecosystem inputs needs further investigation. Ammonium concentrations at deep sites varied little during the open water season, but we observed an increase in NH_4^+concentrations after carcasses were added to shallow sites. We did not measure increases in algal biomass or NH_4^+ uptake after adding carcasses to spawning sites, but we did measure increases at all sites in the autumn. Phytoplankton may not have responded to carcass treatments because of the large volume of the lake and strong currents that move plankton (Benson, 1961). Conversely, we predicted carcasses would cause bottom-up effects by fertilizing periphyton increasing their biomass and uptake as suggested by nutrient diffusing substrata (Lujan et al., 2022); however, we did not detect changes in periphyton biomass and uptake. Uptake by periphyton was far less than phytoplankton and contributed little to N cycling. We measured increased uptake at the reference site, suggesting that the phenomenon was occurring beyond the treatment sites. We suggest that the higher algal biomass and uptake was due to autumn turnover rather than adding carcasses to spawning sites. Autumn turnover brought mineralized nutrients from carcasses at deep sites to surface waters.

Changes in nutrient cycling due to decomposing carcasses

Depositing carcasses on the bottom of Yellowstone Lake appeared to alter the ecosystem. Whale carcasses that sink to the depths of the ocean (e.g., 1000 m) enrich sediments and decompose slowly mineralizing nutrients over several years (Smith & Baco, 2003). A winter fish kill supplied up to 4.3 kg N h^{-1} and 0.5 kg P ha^{-1} increasing phytoplankton biomass the following summer in a prairie lake (Schoenebeck et al., 2012). Due to the number of lake trout added to the depths of Yellowstone Lake, carcasses supplied available nutrients that were locked in the hypolimnion until turnover. Wildebeest carcasses from mass drowning events in the Serengeti provided 6–78% of total N and 31–451% total P into the Mara River (Subalusky et al., 2017a, b); however, inputs from wildebeests are new nutrients to the ecosystem and lake trout nutrients are recycled within the lake. More information is needed to estimate the contribution of N and P from carcasses to the Yellowstone Lake ecosystem. The large size of the lake suggests a modest increase in N concentrations (0.01 µg N l^{-1} in 2018) from carcasses alone; however, the shortened residence time of nutrients in the lake trout pool makes these nutrients available ~ 12 times sooner compared to an uncontrolled population. Models exploring how shortened residence time of lake trout may alter the ecosystem alongside other potential factors are needed to estimate changes.

Nitrogen is probably mineralized more quickly than P (Parmenter & Lamarra, 1991; Nobre et al., 2019, Subalusky et al., 2020) and is available as NH_4^+ or dissolved organic N. The soft tissue of vertebrates contains a higher percentage of N (11%) compared to P (0.4%) and the soft tissues of wildebeest carcasses decomposed in < 70 days in the Mara River, Kenya (Subalusky et al., 2017a, b). Fish carcasses released 95% of N within the first 60 days in a wetland (Parmenter & Lamarra, 1991) indicating that N may quickly mineralize in Yellowstone Lake after carcasses are deposited. Our results support the rapid mineralization of soft tissue in fish carcasses as we observed higher NH_4^+ concentrations after carcasses were deposited at shallow sites similar to what Subalusky et al. (2017a, b) observed. Conversely, P likely becomes available after longer periods. Vertebrate bones contain 95% of the P in their bodies and only 5% of the N (Subalusky et al., 2017a, b). Ten times more N leached from bones compared to P within the initial 80–120 days after death and 15% of the dry mass of bones was labile (Subalusky et al., 2020). The remaining 85% of the dry mass of wildebeest bones leached higher amounts of P and took > 80 years to decompose. Almost 99% of P from gizzard shad carcasses, mostly bone, were re-mineralized into the water column over 20 years in a eutrophic lake in Ohio (Nobre et al., 2019).

Decomposition of lake trout carcasses was mostly due to bacteria and fungi in Yellowstone Lake, and

occurred more slowly in the hypolimnion. Whole carcasses decomposed more slowly in the depths of the lake ($k = 0.0075$ day^{-1}) compared to ground carcasses the littoral zone ($k = 0.0679$ day^{-1}) of Yellowstone Lake partially due to cooler temperatures and less surface area of carcasses in the hypolimnion (Glassic et al., in press). Scavengers and consumers can consume 60% of carcasses in some ecosystems (Subalusky et al., 2017a, b), but scavenging in the depths of Yellowstone Lake appeared limited with the exception of oligochaetes (Glassic et al., in press). Our observations suggest that bacteria and fungi are the main organisms breaking down deposited lake trout. We observed that the muscle decomposed rapidly while skin and bone remained in our decomposition experiments (Glassic et al., 2023). Together, the number of carcasses and rapid mineralization of N in soft tissue was a readily available source of N. We suggest investigating the stoichiometry of Yellowstone Lake in future projects. We predict that the differential mineralization of N and P in Yellowstone Lake may shift the ratio of these nutrients in space and time, but we need more information to assess how this may affect the ecosystem.

Changes in periphyton and phytoplankton biomass, and NH_4^+ demand

The role of periphyton in nutrient cycling of lakes is vastly understudied compared to phytoplankton. Most lake studies focused on the accessible and more easily sampled phytoplankton (Lowe, 1996), whereas the benthos is difficult to sample in large, deep lakes. Investigating benthic processes in lakes requires equipment such as SCUBA divers, likely contributing to the lack of lentic studies. Few studies measured nutrient uptake in both the pelagic and benthic zones of lakes. An exception is Vadeboncoeur & Steinman (2002), who found that uptake by phytoplankton was much higher than periphyton in Lake Tahoe and Castle Lake, California. Results from Yellowstone Lake further support that phytoplankton dominate nutrient cycling in large lakes. Deep lakes are probably always dominated by phytoplankton, but the role of periphyton in the littoral zone remains largely unstudied. Phytoplankton took up 99.9% of NH_4^+ lake-wide in Yellowstone Lake, which can be at least partially explained by the large area of the pelagic zone (341 km^2 and 20 m depth) compared to the littoral zone (~ 78.4 km^2, < 20 m).

The contribution of periphyton to nutrient cycling in lakes can depend on several factors including morphometry and light (Vadeboncoeur & Steinman, 2002). An experiment that fertilized an entire lake with N and P revealed that phytoplankton production was stimulated while benthic production decreased (Vadeboncoeur et al., 2001). Phytoplankton and other suspended solids reduce light that reaches periphyton (Lowe, 1996) such as observed in Swedish and Antarctic lakes (Hansson, 1992), and Lake Okeechobee, Florida (Havens et al., 1996). Additionally, abiotic and biotic factors associated with depth can alter periphyton in lakes, including temperature, turbulence, substrate, and grazers (Hill, 1996); however, depth did not appear to explain differences in uptake in our study or in nutrient diffusing substrata in Yellowstone Lake (Lujan et al., 2022). In deep, steep-sided lakes, such as Lake Tahoe, less habitat was available for periphyton leading to less primary productivity by periphyton compared to phytoplankton (Wetzel, 1964; Loeb et al., 1983). Yellowstone Lake has a well-developed littoral zone where 23% of the lake is < 20 m deep. Periphyton biomass was nine times higher than phytoplankton, but pelagic uptake was 4.5 times higher than periphyton. Perhaps these differences are at least partially explained by the higher nutrient concentrations near the sediment–water interface and because nutrient demand is inversely related to nutrient concentration (Tronstad et al., 2015). Our study showed that measuring phytoplankton nutrient dynamics captured most of the nitrogen uptake in Yellowstone Lake and this may be true for most deep, large lakes; however, periphyton may play a larger role in clear, shallow lakes (e.g., Axler & Reuter, 1996). Periphyton's susceptibility to many factors beyond nutrients presents a continued challenge to estimate the contribution of pelagic and benthic algae in lentic ecosystems (Meerhoff & Jeppesen, 2009).

Autumn turnover delivered mineralized nutrients from carcasses to surface waters

Ammonium concentrations, phytoplankton biomass and phytoplankton uptake increased in Yellowstone Lake each autumn. The increase occurred several weeks after carcasses were added to the early season

site and we observed increases at all sites, including the reference site. In 2018, we thought the proximity of the reference site to the early season site was cause for concern because we observed that NH_4^+ concentrations increased simultaneously. We moved our reference site across the lake in 2019 and observed the same increase. Therefore, we do not attribute the increased NH_4^+ concentrations, algal biomass or uptake in the autumn to depositing carcasses at spawning sites, but to a lake-wide event instead. Additionally, we observed higher ^{15}N signatures of phytoplankton after autumn turnover suggesting that N from carcasses is being taken up by phytoplankton (L. Tronstad, unpublished data). Autumn turnover occurs in mid-September (week 18) annually and was likely responsible for higher NH_4^+ concentrations and phytoplankton biomass in surface waters. Higher concentrations of NH_4^+, phytoplankton biomass or phytoplankton uptake in autumn were not previously observed in Yellowstone Lake in 1972 (Knight, 1975) or 2005 (Tronstad et al., 2015); however, phytoplankton biomass increased during autumn in recent monitoring (Koel et al., 2019).

Nutrient cycling in Yellowstone Lake appeared to change during the previous 15 years. We observed two peaks in algal blooms, higher NH_4^+ concentrations and shallower Secchi disk depths in 2018 and 2019 compared to earlier measurements. We previously observed phytoplankton blooming after ice-off (Tronstad et al., 2010), but we observed blooms after spring and autumn turnover in this study. In a literature review investigating 125 time series of phytoplankton biomass, 20% of lakes experienced spring and autumn blooms (Winder & Cloern, 2010). Concentrations of NH_4^+ during the open water season were higher in our study compared to 2004 and 2005 (Tronstad et al., 2010). We used the same method and instrument to measure concentrations; therefore, N inputs may have increased over that time. Monitoring suggests that Secchi disk depths, which are driven by algal biomass (Tronstad et al., 2010), are becoming shallower over time (L.M. Tronstad, unpublished data). Nitrogen may come from various sources, but the two most likely possibilities are atmospheric deposition and depositing lake trout carcass. Atmospheric deposition represents new nutrients to the lake ecosystem, and N deposition increased between 2005 and 2019 by 0.19 mg m^{-2} day^{-1} (Yellowstone National Park, Tower Falls, National Atmospheric Deposition Program; http://nadp.slh.wisc.edu/). In the years of our study (2018–2019), 0.43 mg N m^{-2} day^{-1} were added to the lake from atmospheric deposition which is a small flux compared to the flux of N from zooplankton excretion (101 mg N m^{-2} day^{-1}; Tronstad et al., 2015); however, atmospheric deposition transports new N to the lake. We assumed that zooplankton excretion was similar because the biomass of zooplankton has not changed appreciably since 2004 (Tronstad et al., 2010; Koel et al., 2019). The degree to which atmospheric deposition contributes to the N cycling in Yellowstone Lake should be investigated; however, we do not attribute the pulse of nutrients at autumn turnover to atmospheric deposition because nutrients are added to the lake continuously through dry and wet deposition.

Changes in pelagic nutrient cycling may be due to more lake trout being deposited and mineralized in Yellowstone Lake. We estimate that ~ 9583 kg N and ~ 2091 kg P are deposited in the depths of Yellowstone Lake each summer from carcasses resulting in ~ 28 mg N m^{-2} day^{-1} and ~ 6.1 mg P m^{-2} day^{-1} being transported to surface waters when the lake turns over in the autumn. We calculated this number based on 330,000 lake trout harvested annually with an average dry mass of 264 g (500 mm total length; Tronstad et al., 2015), 11% N, and 2.4% P by dry mass (Griffiths, 2006). We assumed that the lake was well mixed vertically and horizontally, and all P was decomposed in carcasses. Nutrients from carcasses are recycled within the lake ecosystem; however, the residence time of nutrients stored in these fish is much shorter under suppression. Seventy percent of lake trout captured in gillnets during 2019 were 2 years old compared to 25 years for populations that are not controlled (Koel et al., 2020a). The combination of ~ 300,000 carcasses deposited in the lake annually and the rapid mineralization of muscle may contribute to the N pulses we observed in autumn. Tronstad et al. (2015) discovered that the highest flux of NH_4^+ uptake by phytoplankton in 2005 was in July, and pelagic uptake was less in June and October. We measured greater than six times higher demand by phytoplankton in autumn compared to Tronstad et al. (2015). The higher uptake rate we measured may be due to more nutrients being available at autumn turnover and the increase in demand stimulated by nutrients (Thomas & Bebrian, 2008). Yellowstone National Park predicts the number of harvested lake

trout will decrease after implementing the new carcass management strategy because lake trout embryos will be reduced, and nutrient dynamics are predicted to return to what was historically observed.

Adding lake trout carcasses to Yellowstone Lake during the open water season likely increased the available nutrients, and these nutrients were transported to surface waters when the lake turned over in autumn. Similarly, total N and P concentrations increased after turnover when rainbow trout and waterfowl carcasses were added to a freshwater marsh in Wyoming (Parmenter & Lamarra, 1991). Previous nutrient concentrations were measured when ~ 35,000 lake trout carcasses were returned to the lake annually (Tronstad et al., 2015; Koel et al., 2020a). Increased lake trout abundance and efforts to gillnet them led to an average of > 330,000 lake trout carcasses returned to the lake annually between 2015 and 2019, increasing available N in the lake. Based on the amount of N added to Yellowstone Lake from carcasses in 2018 and 2019 (mean = 3276 kg annually), periphyton would take up the N in 757 centuries and phytoplankton could assimilate the added N in 1.7 h using lake-wide estimates and assuming no other N inputs. We surmised that returning far more carcasses to the lake during the open water season may drive algal blooms after autumn turnover; however, removing carcasses from the ecosystem could also have far reaching negative consequences by decreasing lake productivity over time. More information is needed to estimate the degree to which carcasses alter nutrient dynamics. We hypothesize that the autumn algal bloom will diminish when fewer carcasses are deposited into the lake during summer.

Conclusion

With the increasing threat of invasive species to aquatic ecosystems, exploring management options and estimating how management strategies may affect non-target species and other trophic levels within the ecosystem is crucial. Using carcasses to suppress lake trout embryos appeared to have small effects on nutrient concentrations, algal biomass, and nitrogen uptake in the benthic and pelagic zones—a welcome conclusion considering the novel suppression method is highly effective at reducing lake trout embryos at spawning sites (Thomas et al., 2019; Poole et al., 2020; Koel et al., 2020b). We were initially concerned that adding carcasses to shallow spawning sites could cause bottom-up effects; however, the effects on periphyton were mainly localized and minuscule. Phytoplankton had higher N demand, but we did not observe an algae bloom from depositing carcasses at shallow sites, likely due to the large volume of water and strong currents in Yellowstone Lake. In contrast, depositing ≥ 300,000 lake trout carcasses in the depths of Yellowstone Lake may have caused a phytoplankton bloom in autumn. Nitrogen is quickly mineralized and these nutrients are brought to the surface waters all at once during autumn turnover. Our observations support the continued exploration of these methods on the lake ecosystem; however, the degree to which algal blooms depend on the mass of carcasses deposited in the depths of Yellowstone Lake and the frequency at which carcasses are added needs further investigation. Returning lake trout to the depths of the lake returned nutrients to the ecosystem that were previously stored for long periods (lake trout live 25 years or more), and these actions appeared to alter the timing and magnitude of algal blooms. Monitoring algal blooms in lakes where an invasive fish is being controlled or eliminated may suggest the degree to which primary producers are altered by the management actions.

Millions to billions of dollars are spent each year to prevent or control invasive species in the US alone (Lovell & Stone, 2005) and the suppression program in Yellowstone Lake is no exception (~ $2.75 million USD in 2019; Koel et al., 2020a). Understanding how these actions alter ecosystems is critical to make measures more efficient and economical, as we are measuring in Yellowstone Lake. Non-target organisms can negatively respond to management actions (Homans & Smith, 2013) such as when an invasive cordgrass was removed that the rare California clapper rail (*Rallus obsoletus* Ridgway, 1874) used for habitat (Buckley & Han, 2014). These birds declined partially because the native grass was slow to recolonize. In Yellowstone Lake, cutthroat trout are responding positively to the removal of the invasive apex predator. Restoring native ecosystems after invasion requires long-term commitment and a willingness to adapt to the unique characteristics of each ecosystem (Norton, 2009). The public is willing to invest in managing invasive species (Levers &

Pradhananga, 2021), but many challenges lie ahead (Havel et al., 2015). Having a clearer understanding of how controlling or eradicating an invasive species affects ecosystem processes and other trophic levels can help ensure that our investments have the most effective outcomes.

Acknowledgements Thank you to Samantha Poratti, Jeff Kasowski, Dan Geldolf, Phil Doepke, Patricia Bigelow, Ana Holley, Drew MacDonald, Nate Thomas, David Swisher, Nathan Mansor and the Yellowstone National Park seasonal fisheries crews of 2018 and 2019 for logistical help and assistance in the field and laboratory. Robert O. Hall, Sarah Collins, Catherine Wagner, Katrina Cook, Isabella Sadler, Madison Crawford and 4 anonymous reviewers provided comments that improved the manuscript. Robert O. Hall assisted with uptake calculations. Yellowstone National Park and Yellowstone Forever funded this research. The Montana Cooperative Fishery Research Unit is jointly sponsored by the U.S. Geological Survey, Montana Fish, Wildlife & Parks, Montana State University, and the U.S. Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. An earlier version of this manuscript was submitted to the University of Wyoming to partially fulfil D.R. Lujan's MS degree.

Funding This project was funded by the US National Park Service.

Data availability All data generated during this study are included in the supplemental material.

Declarations

Competing interests The authors have no competing interests to declare.

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