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PRIMARY RESEARCH PAPER

Effects of resource pulses on nutrient availability, ecosystem productivity, and temporal variability following a stochastic disturbance in eutrophic glacial lakes

Michael J. Weber · Michael L. Brown

Abstract Hypoxia in shallow lakes represents a stochastic disturbance that may elicit a resource pulse through fish decomposition, altering nutrient availability and temporal variability of ecosystem productivity. We measured nutrient availability, primary and secondary production, and temporal variability from April through September in no, moderate, and high carrion lakes following winter 2007–2008 and used a repeated-measures ANOVA and impact trend-by-time analyses to evaluate how increasing levels of fish carrion influence recipient ecosystems. Lakes with carrion had higher nutrient concentrations, pH, turbidity, chlorophyll-*a*, and zooplankton and benthic invertebrates and less periphyton compared to no carrion lakes. Phytoplankton was positively related to carrion biomass but the association diminished through time suggesting recovery from the initial nutrient pulse. In contrast, total Kjeldahl nitrogen, turbidity, and macroinvertebrates were positively related to carrion biomass and the slope increased throughout the summer suggesting an increasing pulse effect through time. Initially, zooplankton density was negatively related to carrion biomass but then became positively related to carrion biomass. Regression slope between zooplankton and carrion biomass peaked in June before decreasing in late summer, suggesting recovery from the pulse. Combined, our results suggest that nutrients released during fish decomposition following stochastic disturbances represent an important pulse in eutrophic lakes that further enriches productivity.

M. J. Weber · M. L. Brown
Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, USA

Present Address:
M. J. Weber (✉)
Department of Natural Resource Ecology and Management, Iowa State University, 339 Science Hall II, Ames, IA 50011, USA
e-mail: mjw@iastate.edu

Introduction

Predicting the response dynamics of ecosystems to perturbation presents a major ecological challenge. Disturbance occurring through natural events may create resource pulses that can affect the dynamics, temporal variability, and flow of energy in ecosystems (Polis et al., 2004; Nowlin et al., 2007; Yang et al., 2010). Disturbance-initiated resource pulses can increase nutrient availability through increases in primary production with effects transcending to higher trophic levels that can reciprocate via lagged top-down control on primary producers (Ostfeld & Keesing,

2000; Gende et al., 2002; Yang et al., 2008; Weber & Brown, 2013). Theory suggests that resource subsidies will stabilize food webs and ecosystems but assume that subsidies are constant inputs (Huxel et al., 2002). However, many subsidies derive from stochastic pulses that may result in unpredictable ecosystem responses (Polis et al., 2004; Nowlin et al., 2008; Yang et al., 2008).

Hypoxic conditions in shallow lakes represent a stochastic disturbance that may result in partial or complete mortality of biota at multiple trophic levels, thus altering food web structure and function (Greenback, 1945; Hall & Ehlinger, 1989). This disturbance may present a large-magnitude nutrient pulse of N and P (and potentially C) to the extant ecosystem through fish carcass decomposition. Fishes are generally perceived as nutrient sinks where energy is lost from ecosystem nutrient cycles, aside from excretion, because large amounts of internal lake phosphorus and nitrogen can be bound in fish tissue (Kitchell et al., 1975; Schindler, 1977; Nakashima & Leggett, 1980). However, nutrients are released from fish tissues during decomposition that subsequently become bioavailable and alter ecosystem dynamics (Durbin et al., 1979; Gende et al., 2002; Naiman et al., 2002). For example, migrations of Pacific salmon *Oncorhynchus* spp. into freshwater tributaries in the Pacific Northwest provide an important marine-derived nutrient subsidy vital for aquatic and terrestrial ecosystem function (Gende et al., 2002; Naiman et al., 2002). However, unlike pulses derived from semelparous fishes in oligotrophic systems, hypoxic conditions in eutrophic-hypereutrophic systems may also result in the initial population collapse of grazers (Hall & Ehlinger, 1989), potentially releasing primary producers from both bottom-up and top-down controls. Thus, eutrophic ecosystems experiencing a hypoxic-induced disturbance event that eliminates portions of the biotic community at multiple trophic levels will likely respond in unpredictable ways to nutrient pulses.

An emerging paradigm in ecology is the importance of nutrient pulses in supporting ecosystem productivity (Nowlin et al., 2007; Anderson et al., 2008; Yang et al., 2008; Weber & Brown, 2013). However, nutrient pulses may have a wide range of ecosystem effects depending upon intrinsic conditions and pulse magnitude and duration (Nowlin et al., 2008; Yang et al., 2010). Nutrient availability in highly productive ecosystems is hypothesized to remain stable following nutrient pulsing due to high baseline conditions (Polis & Hurd, 1996; Stapp & Polis, 2003), but the effects of nutrient pulses in these ecosystems have received limited attention. Stochastic winterkill disturbances provide a unique opportunity to evaluate nutrient availability, productivity, temporal variability, and food web responses to resource pulses derived from fish decomposition in shallow eutrophic lakes.

Nutrient pulses can be a result of environmental or climatic events, source-sink processes, and animal population cycles (Yang et al., 2008). Nutrient pulses resulting from winterkill appear to be a resultant combination of all three mechanisms. Invasive common carp (*Cyprinus carpio*, Linnaeus) can become highly abundant in shallow productive systems (Weber et al., 2010) where they can sequester large amounts of nutrients. However, systems where common carp thrive are often shallow, environmentally unstable, and prone to hypoxic perturbation (Bajer & Sorensen, 2010), providing a triggering mechanism to release these biologically sequestered nutrients. Thus, alternating cycles of nutrient storage, release, and re-assimilation likely occur in shallow lakes where nutrients are released from fish populations following winterkill (source) but then are again stored as fishes recolonize these ecosystems (sink) and accumulate biomass.

During the winter of 2007–2008, several South Dakota, USA eutrophic glacial lakes experienced hypoxia-induced winterkills resulting from prolonged periods of ice and snow cover. Fish assemblages inhabiting these shallow lakes are typified by abundant common carp populations (Weber et al., 2010; ~750 kg/ha, M. Weber, Iowa State University, unpublished data). Decomposition of common carp carcasses following disturbance-induced mortality may contribute to internal nutrient loading and affect ecosystem structure and function. Understanding the fate of carcass-derived nutrients in highly productive ecosystems has implications for understanding energy flux, primary production, food web interactions, and the stewardship of these systems (Wallace et al., 1999; Pace et al., 2004). Therefore, we took advantage of this large, fortuitous natural disturbance and subsequent mortality events to evaluate how decomposed fish biomass affects nutrients, primary production, invertebrate dynamics, and temporal variability. We hypothesized that nutrient availability would increase

in disturbed systems as a result of carcass decomposition. We then hypothesized that increased nutrient availability would enhance primary (phytoplankton and periphyton) and secondary (zooplankton and macroinvertebrate) production but increase temporal variation in production of all trophic levels.

Methods

Study lakes

Grass, Beaver, Henry, Whitewood, Herman, and Brant are all small, shallow lakes located in southeastern South Dakota, USA in the Prairie Pothole region (Table 1; Fig. 1). Maximum linear distance between lakes is 87 km. These lakes are morphologically similar and have predominantly soft sediment types (e.g., mud, muck, and silt). Watersheds of all lakes are dominated by row crop agriculture and all lakes are classified as eutrophic (chl *a*: 9–275 mg/m^3; Secchi depth: mean <2.5 m; Wetzel, 2001). Early ice cover and snowfall during November 2007 completely covered Northern Glaciated Plains lakes until April 2008, reducing light penetration and photosynthesis that resulted in hypoxic conditions and fish kills. Following ice off during mid-April, moderate to abundant dead fish biomass was observed in Grass, Beaver, Henry, and Whitewood. Winterkill severity was observed to be the highest in lakes with small surface area and shallow mean depth compared to larger lakes with greater mean depth.
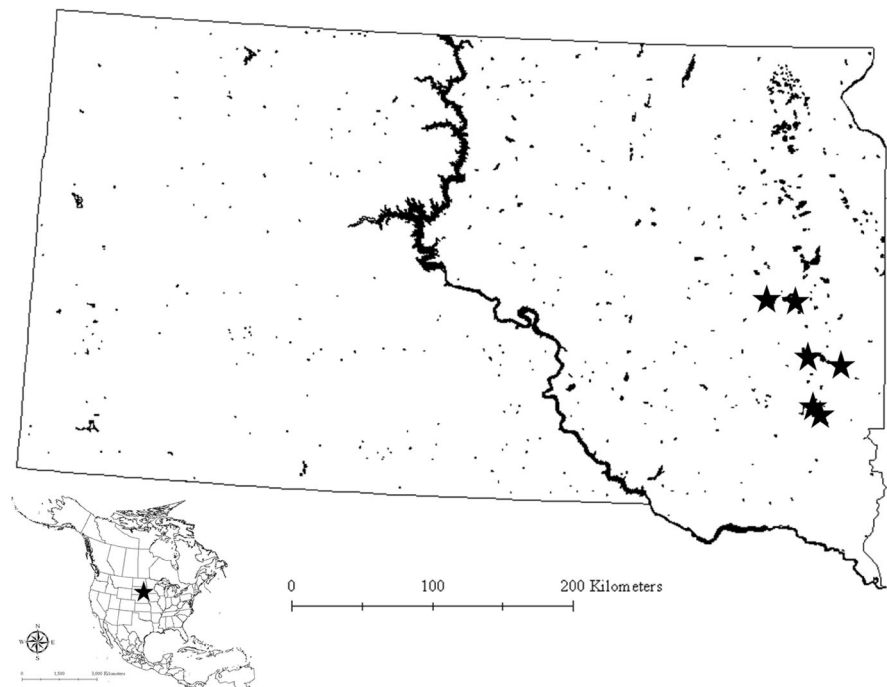
Fish biomass estimates

A random stratified sampling design with six to nine parallel shoreline transects (two to three transects at three to four locations around each lake 50–270 m long by 10 m wide, proportional to lake surface area) was employed once on lakes Grass, Beaver, Henry, and Whitewood on April 15 and 16, 2008 to estimate the abundance and biomass of fish carcasses. In contrast, lakes Herman and Brant had a deeper mean depth, no dead fish were observed following ice off, and were subsequently used as reference systems. Observers walked shoreline transects during daylight hours visually locating all fish, and identifying them to species. A random subset of 100 fish per species and transect were measured for total length (nearest

Table 1 Lake surface area and depth and mean estimated abundance and biomass of common carp carcass (±1 standard error) and total phosphorus (TP) and total Kjeldahl nitrogen (TKN) released from carcasses in no carrion lakes and lakes with moderate and high carrions biomass in eastern South Dakota during the winter of 2007–2008

Treatment	Lake	Surface area (ha)	Maximum depth (m)	Mean depth (m)	Number of dead common carp (SE)	Common carp carrion biomass (kg ± SE)	Common carp carrion biomass per surface area (kg/ha ± SE)	Mean TP released (g/ha)	Mean TKN released (g/ha)
No carrion									
	Brant	420	4.3	2.9	0 (NA)	0	0	0	0
	Herman	521	4	1.4	0 (NA)	0	0	0	0
Moderate carrion									
	Henry	940	2.4	1.2	3,089 (1,245)	21,165 (5,659)	22.52 (5.73)	101	568
	Whitewood	1,893	2	1	8,988 (3,315)	45,217 (8,231)	23.89 (7.97)	108	602
High carrion									
	Beaver	124	3	2.4	10,029 (2,934)	15,369 (6,125)	123.94 (6.84)	558	3,123
	Grass	97	1.5	<1	7,080 (17,791)	39,153 (22,121)	403.64 (122.34)	1,816	10,172

1 mm). Common carp composed the majority of fishes identified (>95 %). Thus, only common carp were used for carcass biomass and nutrient estimates. Weighted (strata) parameter estimates were calculated following procedures described by Thompson (2002) and Krebs (1999) to determine population abundance.

Common carp 50th percentile weight-length linear regression equations were used to estimate fish weight (g), and length-frequency histograms were used to estimate total biomass (kg/ha; Bister et al., 2000; Schoenebeck et al., 2012). Population biomass estimates were extrapolated to estimate the amount (g/ha) of total phosphorus (TP) and total Kjeldahl nitrogen (TKN) released from decayed common carp carcasses throughout the entire lake. Total phosphorus and TKN concentrations from common carp carcasses were unrelated to body size or sex and directly estimated as 0.45 and 2.52 % (wet weight basis), respectively (Schoenebeck et al., 2012).

Water chemistry and biological production

Lakes with high carrion (Grass and Beaver), moderate carrion (Henry and Whitewood), and no carrion (Herman and Brant) present were each sampled every 3 weeks from April 18 to September 6, 2008.

Sampling occurred at three evenly spaced fixed locations >150 m from shore in water equal to greater than mean lake depth. Due to their shallow depth and continuous wind mixing, all lakes are classified as polymictic, and the samples were assumed to be representative of the whole lake. Total phosphorus and TKN were determined by collecting sub-surface water samples (1 l) that were immediately placed on ice in the field and then frozen in the laboratory. Standard methods (U.S. EPA, 1994) were used to measure TP (Method 365.4) and TKN (Method 351.2) in the laboratory.

Turbidity (nephelometric turbidity units; NTU) was measured with a multi-parameter system (YSI 6820 data sonde, 650 data logger, Yellow Springs Instruments, Ohio, USA) and visual water transparency was measured with a 20-cm diameter Secchi disk. Limnetic chlorophyll-*a* was measured by filtering 100-ml of sub-surface water through a glass microfiber filter (47 μm porosity), extracting chlorophyll-*a* with acetone and quantifying with a fluorometer (TD700, Turner Design, California, USA). Natural rock substrates were collected to estimate periphyton production as chlorophyll-*a*. Rock surface area was determined using weight and displacement methods (Cooper & Testa, 2001); periphyton was removed

from rocks, pigments were extracted with acetone, and a fluorometer was used to measure chlorophyll-a (Stevenson & Bahls, 1999).

Zooplankton was obtained by collecting water samples throughout the water column with an integrated tube sampler (7 l), filtered through 63-µm mesh and preserved with Lugol's solution in the field. In the laboratory, zooplankton sample volumes were adjusted to 60 ml and sub-sampled with three 1-ml aliquots. Individuals were identified to suborder or family, enumerated, and counts were extrapolated to estimate total density (number/l). Macroinvertebrates were collected with a mini Ponar dredge (232 cm^2) in May, June, August, and September, washed from sediments and macrophytes into a 500-µm benthos bucket and preserved in 90 % ethanol. All macroinvertebrates were identified to family, enumerated and counts were extrapolated to densities (#/m^2).

Analysis

We used three statistical approaches to evaluate potential impacts of fish carrion decomposition on eutrophic lakes. First, response variables were compared among carrion treatments (no, moderate, and high carrion) and through time using a repeated-measures analysis of variance (ANOVA). Data were log$_{10}$ transformed to normalize the residuals. When significant differences among treatments were detected, Fisher's LSD was used to test for differences among treatments. Statistical significance was determined at $\alpha = 0.05$.

Environmental disturbances are challenging to study because researchers must statistically separate effects of the disturbance from spatiotemporal variation without the benefit of knowing when or where disturbances will occur. Because stochastic environmental disturbances are unpredictable, they typically cannot be evaluated using a replicated, balanced study design (e.g., before-after-control-impact (BACI); Eberhardt & Thomas, 1991), in the same manner that many anthropocentric environmental manipulations are done. Two of the major statistical problems with evaluating environmental disturbances are that treatment sites are not randomly located and reference sites are not true controls, making it difficult to separate spatiotemporal variation in response variables from effects of the environmental disturbance (Wiens & Parker, 1995). However, several study designs have been developed and compared in

their capacities to deal with these analytical pitfalls. These methods allow evaluation of environmental disturbances based on the premise that ecological responses will change commensurate with the level of disturbance (Wiens & Parker, 1995). Using this framework, temporally repeated sampling events across multiple levels of disturbance can be used to evaluate potential impacts and recovery time (Wiens & Parker, 1995). The most powerful of these approaches is the impact trend-by-time interaction, where impacts are measured as a continuous variable across multiple study sites temporally while allowing response variables (e.g., nutrient availability) to naturally vary among sites (Wiens & Parkerm, 1995). For example, Wiens et al. (2004) used this approach to evaluate the relationship between Horned Grebes (*Podiceps auritus*, Lawrence) and an oiling index among the bays of Prince William Sound over several years.

Our second approach was to use an impact trend-by-time interaction study design to evaluate the effects of hypoxia-induced winterkill on shallow lake productivity. Regression analyses were used to evaluate the effect of time (intercept) which would indicate changes in the response variable temporally unrelated to winterkill treatment, common carp carrion density (slope) which would indicate differences in response parameters among lakes, and their interaction which would indicate treatment disturbance level effects that vary through time on nutrient concentrations, turbidity, water clarity, and primary and secondary productivity. Increasing positive slope estimates through time indicate an increasing effect from the carrion, whereas decreasing slope values indicate a reduced carrion effect or the system is recovering from the disturbance (Wiens & Parker, 1995). Following recommendations of Day et al., (1997), we included lake surface area and mean depth in models to reduce variation in response variables associated with intrinsic lake characteristics. However, the inclusion of these variables in the model did not change the results. Thus, these extraneous parameters were removed from analyses for simplicity. A type I error rate of 0.10 was used to increase statistical power to detect interactions and to guard against making Type II errors (i.e., failing to identify winterkill effects; Wiens & Parker, 1995; Day et al., 1997).

Finally, nutrient pulses can either increase or decrease temporal variability of ecosystems (Huxel et al., 2002; Nowlin et al., 2007). We compared

temporal variability of each previously mentioned response variable among treatments to understand how resource pulses would affect temporal variability in eutrophic systems. Temporal variability was estimated with the coefficient of variation (CV) where CV is equal to 100 times the sample standard deviation divided by the mean of all sampling dates ($n = 7$; Nowlin et al., 2007); higher CV values correspond to greater variability in temporal parameter estimates. Differences in CVs among treatments were compared with a one-way ANOVA with each lake serving as a replicate. Statistical significance was determined at $\alpha = 0.05$, and differences among treatments were tested post hoc with Fisher's LSD test.

Results

Carp biomass, water chemistry, and biological production

All lakes became ice-free between April 10–14, 2008 and high fish carcass biomass was observed in lakes Beaver and Grass and moderate fish carcass biomass was observed in Henry and Whitewood. Fish decomposition in these lakes released high and moderate estimated amounts of TP and TKN (Table 1). Water chemistry varied among lakes with high, moderate, or no carrion conditions. High and moderate carrion lakes had similar TP levels ($t = 0.15$, $P = 0.88$) that were two and a half times higher compared to no carrion lakes ($t = 3.69$, $P = 0.001$; $t = 3.54$, $P = 0.002$, respectively; Table 2; Fig. 2A). High carrion lakes also had TKN concentrations two times higher than moderate carrion lakes ($t = 7.53$, $P < 0.0001$) and two and a half times higher than no carrion lakes ($t = 10.93$, $P < 0.001$). TKN concentrations in moderate carrion lakes were higher than no carrion lakes ($t = 3.40$, $P = 0.002$; Table 2; Fig. 2B).

High and moderate carrion lakes also had reduced water transparency compared to no carrion systems. Turbidity varied temporally and among treatments (Table 2; Fig. 2E). Moderate carrion lakes initially had higher turbidity compared to no carrion or high carrion lakes ($t = 4.42$–5.24, $P = 0.04$–0.05), but all lake types had similar turbidity on May 8 ($t = 0.09$–1.02, $P = 0.40$–0.93). Turbidity was marginally higher on June 23 in high carrion compared to

no carrion lakes ($t = 2.45$, $P = 0.08$) with significant differences detected by August 12 ($t = 3.25$, $P = 0.03$). Similar to turbidity, Secchi depth also varied as a function of lake type but did not vary significantly temporally (Table 2). No carrion lakes had greater Secchi depth than high carrion lakes ($t = 3.36$, $P = 0.01$) and marginally greater Secchi depth than moderate carrion lakes ($t = 2.19$, $P = 0.07$). Secchi depth was similar in moderate and high carrion lakes ($t = 1.17$, $P = 0.28$) (Table 2).

The presence of fish carrion affected pelagic productivity. Phytoplankton chlorophyll-*a* varied among treatments but not through time (Table 2; Fig. 2C). High carrion lakes had approximately ten times higher phytoplankton chlorophyll-*a* than no carrion lakes ($t = 3.21$, $P = 0.04$) but similar phytoplankton production as moderate carrion lakes ($t = 1.02$, $P = 0.29$). Total zooplankton and *Daphnia* spp. density varied across the interaction of lake type and time (Table 2; Fig. 2F). High carrion lakes initially had lower zooplankton densities than both moderate carrion ($t = 4.05$, $P = 0.03$) and no carrion lakes ($t = 4.92$, $P = 0.02$). Zooplankton density increased rapidly in high carrion lakes and all three lake types had similar zooplankton densities on May 8 ($t = 1.34$–2.68, $P = 0.08$–0.27) with high carrion lakes having approximately ten times greater zooplankton densities compared to no carrion systems by May 30 ($t = 3.81$–4.74, $P = 0.02$–0.03). *Daphnia* spp. density in high carrion lakes was reduced compared to other lake types in April ($t = 4.97$, $P = 0.02$) and May ($t = 3.43$, $P = 0.03$), more abundant than no carrion lakes in June ($t = 4.75$, $P = 0.02$) and similar among lake types the remainder of the sampling period (t = 1.31–2.21, $P = 0.09$–0.33). In contrast to pelagic production, benthic primary productivity was lower in high carrion lakes compared to moderate and no carrion lakes. Periphyton chlorophyll-*a* varied among treatments and time (Table 2; Fig. 2D). Periphyton chlorophyll-*a* was four times higher in no carrion lakes than high ($t = 2.70$, $P = 0.01$) or moderate ($t = 4.85$, $P < 0.0001$) carrion lakes.

Benthic macroinvertebrates collected were primarily chironomids and gastropods (>95 %). Gastropod and chironomid densities were both affected by the interaction of lake type and time (Table 2). Gastropod density was six times higher in high carrion lakes in May ($P < 0.05$) but then declined and was similar

Table 2 Repeated-measures ANOVA results for total phosphorus (mg/l), total Kjeldahl nitrogen (mg/l), turbidity (NTU), Secchi depth (cm), phytoplankton chlorophyll-a (μg/l), periphyton chlorophyll-a (μg/cm^2), and zooplankton (number/l^3), *Daphnia* spp. (number/l^3), benthic invertebrate (number/m^2), gastropod (number/m^2), and chironomid (number/m^2) density in lakes following no, moderate, or high carrion (Lake type) from April 18 through September 9 (time) and their interaction

Variable	Lake type			Time			Lake type x Time		
	DF	F	P	DF	F	P	DF	F	P
Total phosphorus	2, 27	8.72	0.001	6, 27	4.33	0.02	12, 27	0.26	0.98
Total Kjeldahl nitrogen	2, 27	62.53	<0.0001	6, 27	2.64	0.03	12, 27	1.08	0.42
Turbidity (NTU)	2, 27	3.33	0.16	6, 27	8.04	0.04	12, 27	12.36	0.01
Secchi depth	2, 27	5.81	0.03	6, 27	12.56	0.21	12, 27	4.29	0.36
Phytoplankton chl a	2, 27	5.07	0.04	6, 27	11.93	0.14	12, 27	5.98	0.24
Periphyton chl a	2, 27	11.8	0.0001	6, 27	5.07	0.01	12, 27	0.54	0.82
Total zooplankton density	2, 27	6.79	0.02	6, 27	3.75	0.03	12, 27	4.7	0.05
Daphnia spp. density	2, 27	5.09	0.04	6, 27	8.03	0.04	12, 27	4.6	0.04
Benthic invertebrate density	2, 9	18.15	0.001	3, 9	4.47	0.57	6, 9	1.39	0.38
Gastropod density	2, 9	3.08	0.04	3, 9	2.25	0.09	6, 9	5.04	0.03
Chironomid density	2, 9	15.06	0.01	3, 9	7.08	0.04	6, 9	5.83	0.04

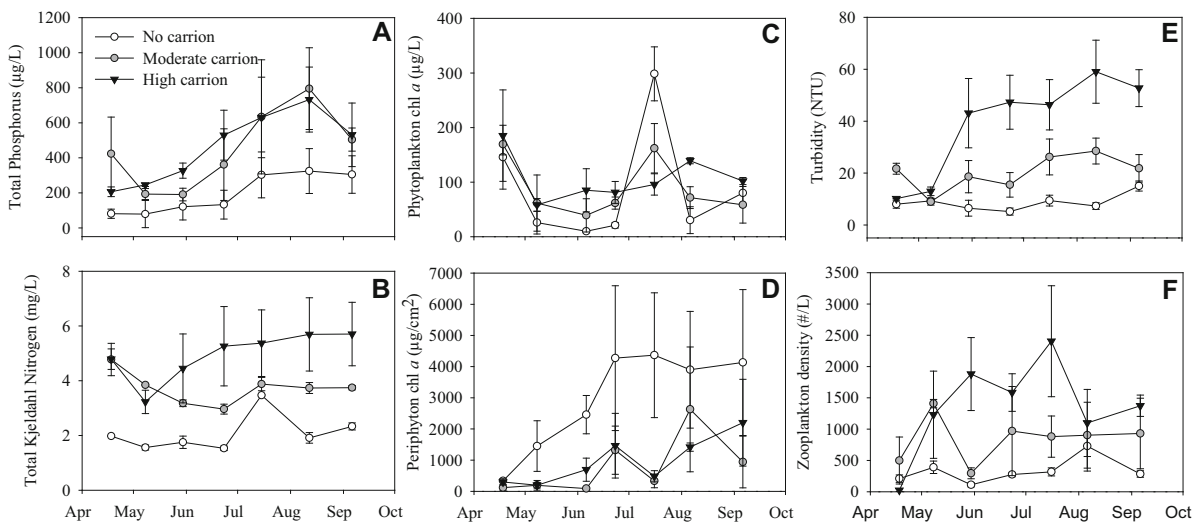Degrees of freedom (DF), F statistics, and P values are presented for each variable

Fig. 2 Mean (±1 standard error) total phosphorus (**A**), total Kjeldahl nitrogen (**B**), phytoplankton (**C**), periphyton (**D**), turbidity (**E**), and zooplankton values (**F**) for no carrion lakes and lakes with moderate and high carrion from April 18–September 6, 2008

among lake types in June, August and September (Fig. 3A). All three lake types had similar chironomid densities on May 8 ($t = 0.21–0.97$, $P = 0.40–0.85$) but high carrion lakes had higher chironomid densities than no carrion lakes by June 23 ($t = 3.23$, $P = 0.05$) and 10 times higher chironomid densities than moderate carrion lakes by August 12 ($t = 4.42$, $P = 0.02$;

Fig. 3B). Total benthic macroinvertebrate density was affected by lake type but not by time or their interaction (Table 2; Fig. 3C). High carrion lakes had higher total macroinvertebrate densities than no carrion ($t = 5.66$, $P = 0.0006$) and moderate carrion ($t = 4.63$, $P = 0.002$) lakes which had similar total benthic macroinvertebrate densities ($t = 1.03$, $P = 0.33$).
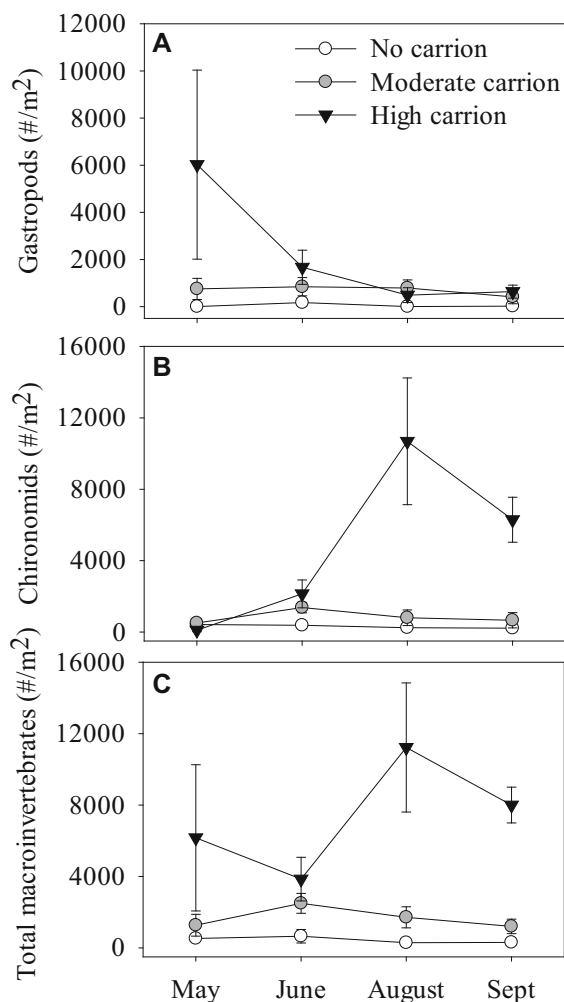
Fig. 3 Mean (±1 standard error) gastropod (**A**), chironomid (**B**) and total macroinvertebrate (**C**) density from May 8–September 6, 2008 in no carrion, moderate, and high carrion lakes

Impact-by-time

Interaction effects between common carp carrion and time were significant for seven of the eleven variables evaluated, suggesting an effect of carrion decomposition (Table 3). The slopes between carrion biomass and TKN, turbidity, total macroinvertebrates, and chironomids increased through time, suggesting that they increased more rapidly as carrion biomass increased and increased at a faster rate later in the summer (Fig. 4). In contrast, the slope of phytoplankton was the highest following ice off and became smaller throughout summer, suggesting that it was

recovering from the initial pulse (Fig. 4). Initially, zooplankton densities were negatively related to carrion biomass in April and May, likely due to wintertime hypoxia. However, zooplankton was positively related to carrion densities by May. A quadratic relationship best described the slope between carrion biomass and total zooplankton and *Daphnia* spp. densities, suggesting carrion had an increasing effect on zooplankton until June and after which zooplankton started recovering from the nutrient pulse. Total phosphorus, Secchi depth, and periphyton were also significantly affected by carrion biomass, but lacked a significant interaction effect (Table 3), suggesting winterkill effects could not be separated from spatial variation in parameters among lakes.

Ecosystem temporal variability

Carrion-derived nutrient pulses affected the temporal variation of nutrient availability and production of a primary producer and consumer. The CV of TKN ($F_{2,3} = 9.07$, $P = 0.03$), phytoplankton ($F_{2,3} = 8.07$, $P = 0.05$), and total zooplankton ($F_{2,3} = 8.06$, $P = 0.05$) were 2–3 times higher in no carrion systems compared to moderate and high carrion systems ($P < 0.05$). In contrast, the CV of turbidity ($F_{2,3} = 0.11$, $P = 0.90$), Secchi depth ($F_{2,3} = 0.41$, $P = 0.70$), total phosphorus ($F_{2,3} = 1.22$, $P = 0.41$), periphyton ($F_{2,3} = 0.96$, $P = 0.48$), *Daphnia* spp. ($F_{2,3} = 0.17$, $P = 0.85$), chironomid ($F_{2,3} = 0.87$, $P = 0.50$), and total macroinvertebrates ($F_{2,3} = 0.09$, $P = 0.92$) were similar among treatments.

Discussion

The effects of nutrient pulses in productive environments are thought to be minimal (Polis & Hurd, 1996; Stapp & Polis, 2003). Yet, common carp carcass pulses delivered substantial quantities of P and N that influenced nutrient concentrations, even in these highly eutrophic ecosystems. The importance of aquatic organism decomposition for ecosystem productivity is not a new phenomenon and examples can be found on ocean floors (Smith et al., 1989), in the Pacific Northwest (Gende et al., 2002; Naiman et al., 2002) and along the Atlantic seaboard (Durbin et al., 1979; West et al., 2010) where carcass decomposition increases nutrient availability and stimulates primary

Table 3 Regression results for total phosphorus (mg/l), total Kjeldahl nitrogen (mg/l), turbidity (NTU), Secchi depth (cm), phytoplankton chlorophyll-*a* (μg/l), periphyton chlorophyll-*a* (μg/cm^2) and zooplankton (number/l^3), *Daphnia* spp. (number/l^3), benthic invertebrate (number/m^2), gastropod (number/m^2), and chironomid (number/m^2) density with increasing common carp carrion biomass from April 18 through September 9 (time) and their interaction

Variable	Carrion biomass			Time			Carrion × Time		
	DF	*F*	*P*	DF	*F*	*P*	DF	*F*	*P*
Total phosphorus	1, 28	9.01	0.006	6, 28	1.98	0.10	6, 28	0.59	0.74
Total Kjeldahl nitrogen	1, 28	62.53	<0.0001	6, 28	1.38	0.26	6, 28	2.31	0.06
Turbidity (NTU)	1, 28	107.14	<0.0001	6, 28	0.71	0.65	6, 28	7.08	0.0001
Secchi depth	1, 28	9.53	0.005	6, 28	1.31	0.29	6, 28	0.41	0.86
Phytoplankton chl *a*	1, 28	3.17	0.09	6, 28	7.64	<0.0001	6, 28	2.15	0.08
Periphyton chl *a*	1, 28	4.11	0.05	6, 28	1.65	0.17	6, 28	0.21	0.97
Total zooplankton density	1, 28	43.72	<0.0001	6, 28	0.83	0.55	6, 28	3.86	0.006
Daphnia spp. density	1, 28	6.12	0.02	6, 28	1.34	0.27	6, 28	5.99	0.0004
Benthic invertebrate density	1, 16	40.08	<0.0001	3, 16	0.20	0.90	3, 16	4.99	0.01
Gastropod density	1, 16	3.09	0.10	3, 16	0.43	0.73	3, 16	0.43	0.74
Chironomid density	1, 16	137.77	<0.0001	3, 16	0.20	0.90	3, 16	44.68	<0.0001

Degrees of freedom (DF), *F* statistics and *P* values are presented for each variable

and secondary production (but see Nedzarek et al. 2015). However, little is known about the role of nutrient pulses in highly productive freshwater ecosystems. Common carp carcass biomass following hypoxia was variable across systems supplying moderate and large nutrient pulses. Biomass of common carp carcass and its contribution to nutrient availability in this study should be viewed as conservative, as many carcasses were likely not located near the shore and thus not accounted for in biomass estimates. Nonetheless, the conservative estimate of P and N released from common carp carcass decomposition exceeded contributions from allochthonous cicadas (Nowlin et al., 2007) and anadromous fishes (Moore & Schindler, 2004; Walters et al., 2009), each of which have profound food web effects.

Shallow lakes across the Midwest where common carp dominate fish community biomass are often N limited with low N:P ratios (Weber et al., 2010). Because common carp carcasses are N rich (Schoenebeck et al., 2012), they may release primary producers from N limitations. Although rarely evaluated, resource pulses may also provide additional carbon that could also result in increased productivity (Polis et al., 2004). Although dissolved organic carbon levels are relatively homogenous across lakes evaluated here (10–40 mg/l; South Dakota Department of Environment and Natural Resources), the effects of

carbon pulses on ecosystem productivity warrant future investigation. Nutrient availability and pelagic primary productivity increased with common carp resource pulses and effects increased from moderate to high carcass availability. Effects of pulses on nutrient availability and pelagic production occurred rapidly and persisted throughout the summer. Although pelagic primary production increased with nutrient pulses, benthic primary production decreased. Systems with moderate and high carrion experienced higher turbidity and reduced water clarity due to greater pelagic primary productivity, likely limiting light availability for benthic primary production in these systems. A shift from benthic to pelagic production is indicative of eutrophication processes and can have resounding effects on energy flow and food web structure (Vadeboncoeur et al., 2003; Weber & Brown, 2013).

Effects of nutrient pulses on primary production may ascend to consumers and regulate their life histories and population dynamics with resulting ecosystem consequences (Ostfeld & Keesing, 2000; Polis et al., 2004; Nowlin et al., 2007; Yang et al., 2008). High carrion systems with the largest pulse of nutrients supported greater pelagic and benthic invertebrate densities compared to moderate carrion and no carrion systems. Increased secondary production may have been a product of bottom-up processes resulting

Fig. 4 Slope of the relationship between common carp carrion biomass across six lakes and total Kjeldahl nitrogen (**A**), turbidity (**B**), phytoplankton (**C**), total zooplankton (**D**), Daphnia (**E**), total macroinvertebrate (**F**), and chironomid values on each of the sampling dates (*points*). Linear or quadratic relationships are fit and *r* values are presented
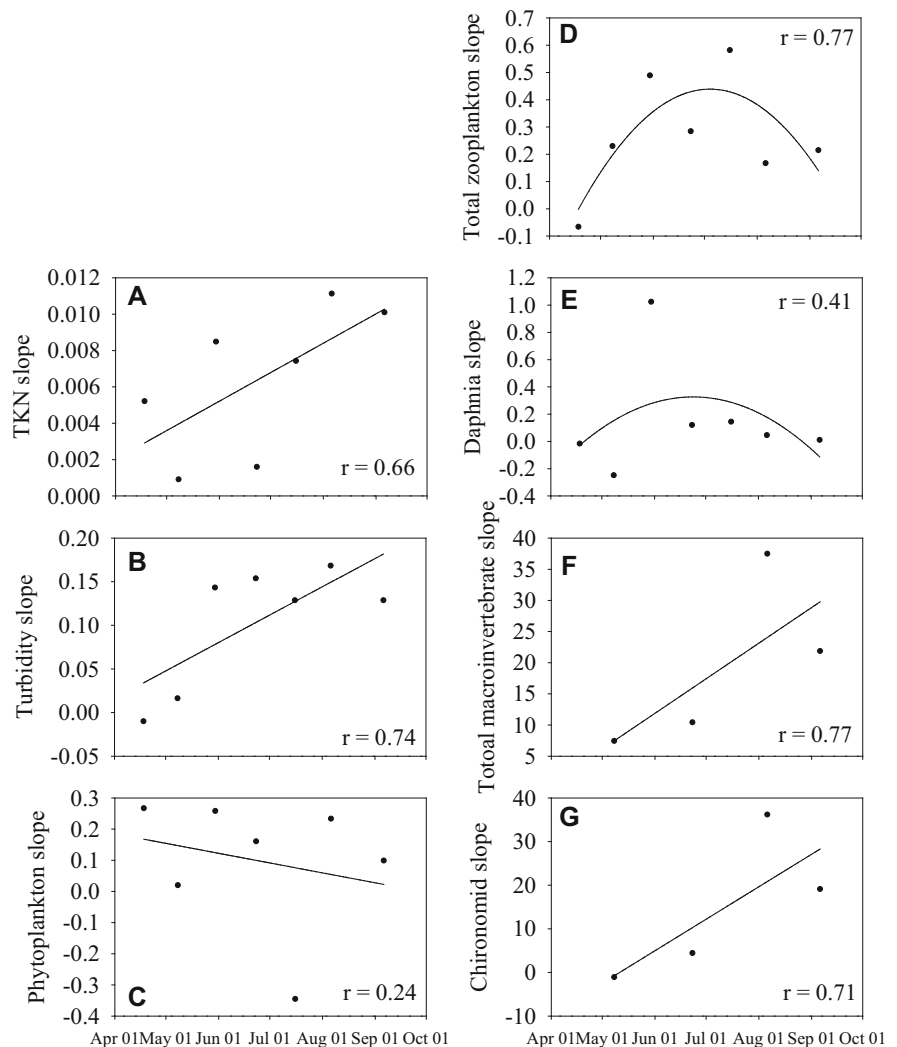
from the nutrient pulse. Alternatively, the trophic cascade hypothesis predicts that the elimination of planktivorous fishes will release primary consumers from top-down control (Carpenter et al., 1985). Deleterious effects of common carp foraging and bioturbation on invertebrate populations are well documented (review by Weber & Brown, 2009) and reductions or eliminations of common carp populations following wintertime hypoxia may have released invertebrates from predation. Zooplankton densities in high carrion systems were initially lower than no carrion lakes likely due to the effects of winterkill disturbance (Isermann et al., 2004). However, zooplankton density rapidly increased, was higher in carrion systems by mid-May and was predicted to

control algal biomass, promoting the clear-water phase (Carpenter et al., 1985; Hall & Ehlinger, 1989; Rudstam et al., 1993). Yet, phytoplankton density remained high throughout the growing season and did not experience a precipitous decline with increasing grazing pressure, suggesting bottom-up subsidies were more important than top-down control. Benthic invertebrate consumers took longer to respond to resource pulses than did pelagic consumers, with population increases in moderate and high carrion systems not observed until June or August, likely due to longer generation times of these organisms (Nowlin et al., 2008; Yang et al., 2010).

Little experimental information is available concerning the effects of nutrient pulses on temporal

variation of shallow lake production. Theoretical models suggest that small nutrient pulses will stabilize food webs, whereas large nutrient pulses will reduce ecosystem variability (Huxel et al., 2002). Evidence from terrestrial experiments supports this theory and suggests that producers and consumers on islands receiving nutrient pulses from seabird guano are more variable than islands that are not subsidized (Anderson & Polis, 2004). Allochthonous nutrient pulses resulting from terrestrial transfer to aquatic ecosystems can also affect the variability of nutrient availability and biological organisms with variability fluctuating according to the magnitude of the pulse and extant productivity conditions (Nowlin et al., 2007). Results presented here are consistent with these findings and suggest that nutrient pulses in eutrophic ecosystems can subsidize these environments. Nitrogen, phytoplankton, and total zooplankton were less temporally variable in systems receiving common carp carcass pulses suggesting these short-term pulsed events can stabilize and sustain increased levels of pelagic production for prolonged durations. In contrast, turbidity, Secchi depth, P, *Daphnia* spp., chironomid, and total macroinvertebrate variability were similar among treatments suggesting that these parameters are either temporally more stable and less influenced by nutrient pulses or alternatively that our sampling design was not sensitive enough to detect differences among treatments.

Unlike predictable nutrient pulses derived from anadromous fish migrations or insect emergence, winterkill events are extremely difficult to predict (Greenbank, 1945). Randomness of winterkill events makes it difficult to collect multi-parameter data on these systems prior to the winterkill disturbance (i.e., before-after-control-impact design) and other factors related to hypoxia (i.e., redox nutrient release from the sediment) may have contributed to the observed biotic and abiotic differences found in this study. While rigorous statistical techniques are available to analyze these types of unpredictable environmental events, they do have some pitfalls (Wiens & Parker, 1995). Future efforts should be extended toward long-term productivity monitoring of systems prone to winterkill to better understand their influence on nutrient cycling. However, lake communities (cyprinid and percid based) and watersheds (predominantly agriculture) that were evaluated are similar to one another, making it unlikely that system-specific differences were

responsible for the magnitude of observed patterns. Schoenebeck et al. (2012) provided historical evidence that long-term nutrient dynamics and plankton production were enhanced the year following winterkill disturbance. Additionally, Weber & Brown (2013) found fish decomposition had a more pronounced effect on nutrient availability, primary and secondary production, and energy flow than did bioturbation and excretion by live common carp. Thus, winterkill disturbances do appear to provide an important nutrient pulse effect in shallow eutrophic lakes through fish decomposition-derived nutrients, with implications for ecosystem productivity, temporal variability, and food web dynamics.

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