2-2013

Continuous, Pulsed and Disrupted Nutrient Subsidy Effects on Ecosystem Productivity, Stability, and Energy Flow

Michael J. Weber
South Dakota State University

Michael L. Brown
South Dakota State University

Recommended Citation

Weber, Michael J. and Brown, Michael L., "Continuous, Pulsed and Disrupted Nutrient Subsidy Effects on Ecosystem Productivity, Stability, and Energy Flow" (2013). *Natural Resource Management Faculty Publications*. 107.
http://openprairie.sdstate.edu/nrm_pubs/107

esa ECOSPHERE

Continuous, pulsed and disrupted nutrient subsidy effects on ecosystem productivity, stability, and energy flow

MICHAEL J. WEBER[1],† AND MICHAEL L. BROWN

Department of Natural Resource Management, South Dakota State University, Brookings, South Dakota 57007 USA

Citation: Weber, M. J., and M. L. Brown. 2013. Continuous, pulsed and disrupted nutrient subsidy effects on ecosystem productivity, stability, and energy flow. Ecosphere 4(2):27. http://dx.doi.org/10.1890/ES12-00354.1

Abstract. Resource pulses and subsidies can supply ecosystems with an important source of nutrients that supports additional productivity at multiple trophic levels. Common carp *Cyprinus carpio* provide ecosystems with a continuous nutrient subsidy through bioturbation and excretion but may also initiate a nutrient pulse through carcass decomposition. We examined how continuous (common carp foraging and excretion), pulsed (carcass decomposition) and disrupted (carp introduced and then removed) nutrient subsidies differed in their ability to alter nutrient availability, ecosystem productivity and stability and energy flow. Nitrogen and phosphorus availability and primary production were highest in pulsed, intermediate in continuous and lowest for disrupted and control systems. Continuous, and to a lesser extent pulsed, systems were associated with decreased water clarity and macrophyte coverage. Nutrient pulses ascended to higher trophic levels and supported greater densities of consumers (i.e., zooplankton and macroinvertebrates). Biotic and abiotic responses in disrupted systems quickly returned to control levels and water quality improved. Light penetration and *Daphnia* spp. dynamics were more stable in systems with pulses whereas stability of other variables was similar across treatments. Biotic materials collected from pulsed and continuous subsidy systems were typically enriched in δ^{15}N suggesting common carp-derived nutrients supported increased productivity whereas δ^{13}C signatures were depleted suggesting a transition to more pelagic energy pathways, likely due to enhanced phytoplankton production. Our results suggest that continuous and pulsed nutrient subsidies vary in their ability to support and sustain ecosystem productivity with resulting variation in food web structure and ecosystem stability.

Key words: alternative stable states; common carp; *Cyprinus carpio*; decomposition; disturbance; eutrophication; food webs; Midwest; nutrients; pulse; shallow lake; subsidy.

Received 12 November 2012; revised and accepted 3 January 2013; **published** 26 February 2013. Corresponding Editor: E. García-Berthou.

[1] Present address: Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa 50011 USA.

† **E-mail:** mjw@iastate.edu

INTRODUCTION

Nutrient subsidies represent an important ecological concept because they provide a critical energy source for recipient ecosystems that can elevate productivity (Polis et al. 1997, 2004). Animals are one important vector that can provide a continuous subsidy within ecosystems (Vanni 2002, Vanni et al. 2006). For example, common carp *Cyprinus carpio* increase nutrient availability and ecosystem instability in shallow lake ecosystems through benthic foraging behaviors and excretion that transfer nutrients from sediments to pelagic habitats (Weber and Brown

2009). This nutrient subsidy, in addition to increased sediment re-suspension and reductions in aquatic macrophyte coverage and invertebrate densities, can enhance the frequency and duration of phytoplankton blooms, resulting in the transformation of shallow aquatic ecosystems from a clear- to turbid-water state (Scheffer et al. 1993, Weber and Brown 2009).

In contrast to continuous nutrient subsidies, ecosystems may also be supplied by resource pulses that are infrequent events of short duration and large magnitude (Yang et al. 2008). Natural stochastic disturbances often promote nutrient pulses in ecosystems (Yang et al. 2010) and may reduce common carp populations in lakes, thereby altering nutrient availability, food web structure, energy flow and ecosystem stability (Weber 2011). Across the upper northern hemisphere, prolonged periods of ice and snow cover on shallow lakes periodically result in hypoxic conditions (i.e., winterkill), disrupting ecosystem structure, function and community assemblages (Tonn et al. 2004, Weber 2011). Although winterkill disturbances may reduce effects of mechanical common carp foraging disturbances (Weber and Brown 2009), bottom-up processes derived from carcass decomposition resource pulses may still have important effects on aquatic communities.

A large portion of a lake's nutrients can be stored in fish tissue (Kitchell et al. 1975, Nakashima and Leggett 1980, Andersson et al. 1988) and this nutrient sink may become a pulse of newly available nutrients following hypoxic conditions as nutrients are released from decomposing carcasses (Gende et al. 2002, Nowlin et al. 2008, Yang et al. 2010). Resource pulses can represent a substantial proportion of total nutrient availability in some systems, affecting a wide range of communities and taxa (Ostfeld and Keesing 2000, Nowlin et al. 2008, Yang et al. 2010). Although the release of nutrients from carcasses is useful in nutrient-limited systems (Gende et al. 2002, Naiman et al. 2002), nutrient pulses in eutrophic and hypereutrophic systems where common carp thrive may supplement algal bloom magnitude, duration and frequency and enhance eutrophication processes (Weber 2011, Schoenebeck et al. 2012). Thus, understanding how fish-derived nutrient additions from alternative pathways (continuous subsidy versus brief pulse) affect nutrient availability, ecosystem productivity, energy flow and community dynamics has broad ecological and management applications.

Ecologists are becoming increasingly aware of the importance of continuous and pulsed nutrient subsidies within ecosystems (Polis et al. 2004, Nowlin et al. 2008, Yang et al. 2010). Although common carp nutrient subsidies from benthic foraging are well understood (Weber and Brown 2009), the effect of a resource pulse associated with common carp decomposition following disturbance has received limited attention. Quantitative measures and comparisons of producer and consumer responses to resource subsidies and pulses are needed to improve ecologists' understanding of nutrient influxes and their influence on food web structure and ecosystem stability (Yang et al. 2010). In this study, we compared the effects of common carp bioturbation (continuous), decomposition (pulse) and removal (disrupted) on aquatic food webs and ecosystem productivity. This study represents one of the first controlled experimental assessments comparing ecologically relevant differences of continuous, pulsed and removed subsidies in view of ecosystem productivity, stability and energy flow. First, we hypothesized that pulsed subsidies would briefly increase ecosystem productivity whereas continuous subsidies would increase and sustain production. Second, as a result of differences in the sustainability of increased productivity between continuous and pulsed treatments, we hypothesized continuous subsidies would increase stability whereas pulsed subsidies would decrease stability. Third, we hypothesized both continuous and pulsed treatments would result in food web shifts as consumers become more reliant upon increased pelagic resources produced from the subsidies. Finally, in contrast to continuous and pulsed subsidies, we hypothesized that productivity in disrupted subsidy treatments would decline and eventually mimic conditions in control systems.

METHODS

Sixteen opaque 4,543-L mesocosms (2.4 m diameter, 1.3 m height) each containing 5 cm of homogenized lake sediment were filled with groundwater (total Kjeldahl nitrogen, 1.5 mg/L;

total phosphorus, <0.001 mg/L) to a depth of 1 m and seeded with equivalent densities of aquatic macrophytes (sago pondweed *Potamogeton pectinatus*), zooplankton and macroinvertebrates (chironomids and gastropods). Approximately 60% of the mesocosm surface area was shaded with an opaque cover to reduce direct sunlight and evaporation. Following a three-week developmental period, common carp were obtained by electrofishing and placed into twelve randomly selected mesocosms (four remained as fishless controls) at 1,000 kg/ha (one common carp [453 ± 8 g] per mesocosm), representative of high density populations (Panek 1987). Mesocosms were allowed to develop for an additional 14 d after which one of three treatments (four replicates per treatment) was applied: carp were euthanized and returned to the mesocosm (pulsed subsidy), carp were left within the mesocosms alive (continuous subsidy), or carp were removed from the mesocosm (disrupted subsidy) and monitored for an additional eight weeks.

Productivity measurements

Water quality measurements were obtained weekly beginning May 16, 2010 (week 1) and monitored for eight weeks through July 12, 2010 (week 9). Ammonium and turbidity (nephelometric turbidity units; NTU) were measured with a multi-parameter system (6820 data sonde, 650 data logger; Yellow Springs Instruments, Ohio, USA). Visual water transparency was measured with a 20-cm diameter Secchi disk and solar irradiance was measured at the sediment-water interface with a photometer (LI-193; LI-COR, Nebraska, USA). Total phosphorus (TP; Method 365.4), soluble reactive phosphorus (SRP; Method 365.2), total Kjeldahl nitrogen (TKN; Method 351.2) and nitrate (Method 417F) were determined from a water sample (1 L) that was placed on ice in the field, frozen in the laboratory and later analyzed using methods described by the U.S. EPA (1994).

Limnetic chlorophyll *a* was measured by filtering 100 mL of water through a glass microfibre filter (47 μm porosity), extracting chlorophyll with acetone and quantifying with a fluorometer (TD700, Turner Design, California, USA). Periphyton chlorophyll *a* was obtained by placing a ceramic tile (210 cm^2) in each mesocosm for 3 weeks which was retrieved, placed on ice in the field and frozen in the laboratory. In the laboratory, periphyton was scraped from the tile, pigments were extracted with acetone and a fluorometer was used to determine chlorophyll *a* content (Stevenson and Bahls 1999). Sago pondweed coverage was visually estimated as percent surface area.

Zooplankton was sampled at three locations within each mesocosm with an integrated column sampler (5 cm diameter, 100 cm length), filtered through 63-μm mesh and preserved with Lugol's solution in the field. Macroinvertebrates were collected with a mini Ponar dredge (240 cm^2), washed from sediments and macrophytes into a 500-μm benthos bucket and preserved in 90% ethanol. In the laboratory, zooplankton were identified and enumerated to suborder or family and total density (number/L) was estimated. All macroinvertebrates and aquatic insects were identified to family and enumerated to estimate total density (number/m^2).

Stable isotopes

Biotic samples listed previously were collected at the conclusion of the experiment (July 12, 2010) for stable isotope analysis to evaluate possible changes in energy utilization ($\delta^{13}C$) and trophic position ($\delta^{15}N$) of primary producers and consumers due to the presence of nutrient subsidies or pulses from common carp. Zooplankton and invertebrates were allowed to soak in aerated de-chlorinated water for 8 h to allow for gut evacuation and frozen. Other biological material collected was placed on ice in the field and frozen in the laboratory.

Aquatic macrophytes were prepared with a dilute HCl (1 mol/L) soak solution to remove carbonate carbon and rinsed with deionized water prior to drying. All other samples were rinsed with deionized water. Samples were dried in scintillation vials at 60°C for 72 h in a drying oven, cooled in a dessicater, ground to a fine powder with a mortar and pestle and packed in to 4 × 6 mm tin capsules for mass spectrometer analysis.

Mass balance spectrometry was performed on all samples to determine $\delta^{13}C$ and $\delta^{15}N$ ratios using a continuous-flow isotope ratio mass spectrometer (Europa Scientific Ltd, United Kingdom) equipped with a dual-ion collection

Table 1. Repeated measures ANOVA results for parameters measured in mesocosms examining the effects of continuous, pulsed and disrupted common carp nutrient subsidies during a nine-week experiment.

	Treatment			Time			Treatment × Time		
Variable	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Nitrate	3, 108	139.27	<0.01	8, 108	30.34	<0.01	24, 108	5.79	<0.01
Ammonium	3, 108	95.75	<0.01	8, 108	36.99	<0.01	24, 108	23.77	<0.01
Total Kjeldahl nitrogen	3, 108	40.91	<0.01	8, 108	1.63	0.17	24, 108	18.89	<0.01
Soluble reactive phosphorus	3, 108	33.57	<0.01	8, 108	3.19	<0.01	24, 108	2.35	<0.01
Total phosphorus	3, 108	12.70	<0.01	8, 108	0.73	0.67	24, 108	5.67	0.02
Turbidity	3, 108	78.35	<0.01	8, 108	3.84	<0.01	24, 108	2.18	<0.01
Secchi depth	3, 108	48.12	<0.01	8, 108	1.15	0.34	24, 108	1.92	0.01
Luminance	3, 108	24.45	<0.01	8, 108	9.68	<0.01	24, 108	3.09	<0.01
Phytoplankton chl *a*	3, 108	44.84	<0.01	8, 108	5.54	<0.01	24, 108	1.63	0.06
Periphyton chl *a*	3, 39	12.37	<0.01	3, 39	29.96	<0.01	9, 39	3.77	<0.01
Sago pondweed coverage	3, 108	39.39	<0.01	8, 108	5.64	<0.01	24, 108	2.02	<0.01
Daphnia spp. density	3, 108	15.07	<0.01	8, 108	5.93	<0.01	24, 108	2.16	<0.01
Rotifer density	3, 108	1.29	0.28	8, 108	5.82	<0.01	24, 108	0.57	0.93
Total zooplankton density	3, 108	13.74	<0.01	8, 108	4.41	<0.01	24, 108	1.93	0.02
Chironomid density	3, 108	2.98	0.03	8, 108	1.84	0.08	24, 108	0.78	0.76
Gastropod density	3, 108	3.15	0.03	8, 108	3.48	<0.01	24, 108	4.82	<0.01

beam for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratio measurements. Stable isotope ratios were reported in parts per thousand (‰) of delta units (δ) relative to the international standard for the particular isotope

$$\delta^{13}C \text{ or } \delta^{15}N = \Big((R_{\text{sample}} - R_{\text{standard}}) - 1\Big) \times 1000 \tag{1}$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The carbon standard was Pee-Dee Belemnite limestone (PDB, $\delta^{13}C = 0‰$) and nitrogen values were compared to atmospheric nitrogen ($\delta^{15}N = 7.7‰$).

Analysis

Measurements of biotic and abiotic parameters across sampling dates were not independent of one another. Water quality and invertebrate data were $\log_{10}$ transformed to normalize the residuals and compared among treatments and through time with univariate repeated measures analysis of variance (ANOVA). Mauchly's test was used to evaluate the assumptions of equality and compound-symmetry (sphericity) of the between-group covariance matrices. Tests of sphericity were not significant ($P = 0.13$) and thus test statistics were not adjusted. In addition to mean values, temporal variability of nutrients, phytoplankton, periphyton, macrophytes, zooplankton and macroinvertebrates were estimated with the temporal coefficient of variation (CV; Nowlin et al. 2007) where CV is equal to 100 times the standard deviation of all post-treatment sampling dates divided by the mean of all post-treatment sampling dates. Treatment effects on CVs were compared with a one-way ANOVA with each mesocosm providing a replicate. Lastly, stable isotope values were $\log_{10}$ transformed and differences in $\delta^{13}C$ and $\delta^{15}N$ values of biological material were compared among treatments using ANOVA. Statistical significance was determined at $\alpha = 0.05$ and post hoc Tukey's LSD tests were used to distinguish differences for all comparisons. All analyses were conducted using SAS software Version 9.1.

RESULTS

Nutrient dynamics

Nutrient concentrations in pulsed treatments initially increased then declined throughout the experiment whereas those in continuous, disrupted and control systems were more temporally stable, resulting in significant treatment by time interactions (Table 1). Nitrate concentrations declined temporally in all treatments and were lowest in pulsed, intermediate in continuous and highest in disrupted systems (Fig. 1A). In contrast, ammonium, TKN, SRP and TP concentrations generally increased for the first three to four weeks before declining and were greatest in pulsed, intermediate in continuous, and lowest in disrupted and control systems. Ammonium and TKN had similar responses to the subsidies. Ammonium and TKN increased in pulsed

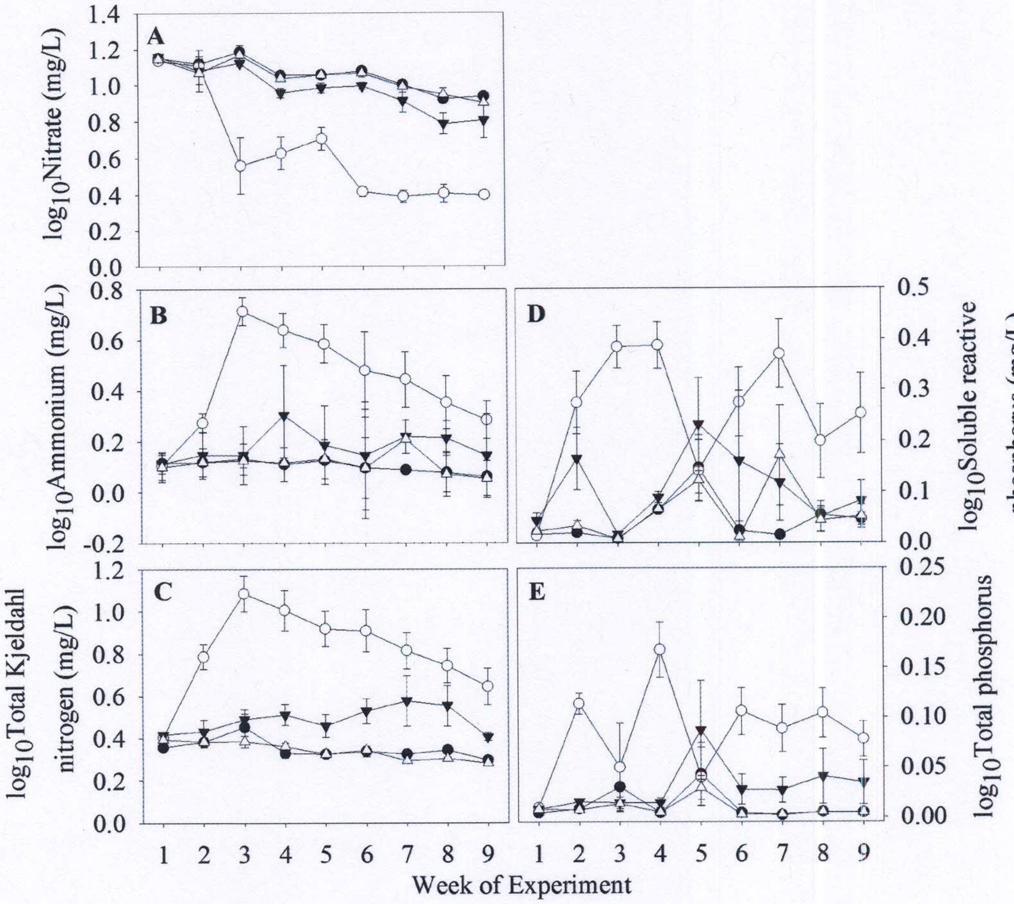

Fig. 1. Mean nitrate (A), ammonium (B), total Kjeldahl nitrogen (C), soluble reactive phosphorus (D) and total phosphorus (E; ±1 SE) among control (black circle), pulsed (open circle), continuous (black triangle) and disrupted (open triangle) treatments during the nine-week experiment.

systems during the first three weeks when these nutrients were up to twenty times higher in pulsed compared to other treatments before gradually declining but remained higher than the other treatments (Fig. 1B, C). Ammonium and TKN concentrations in continuous subsidy systems gradually increased and were sustained at higher levels compared to disrupted and control systems which were similar to one another following week four. Pulsed systems also had up to ten times higher SRP values compared to other treatments, continuous subsidy systems had intermediate SRP values following week six, and disrupted and control systems had similar low levels of SRP throughout the experiment (Fig. 1D). Finally, total phosphorus concentrations increased the first four weeks and remained up to 45 times greater in pulsed compared to the other three treatments (Fig. 1E).

Water clarity

Water clarity parameters varied temporally among the subsidies resulting in significant treatment by time interactions (Table 1). Pulsed and continuous subsidies both resulted in decreased water clarity. Turbidity was ten times lower in control systems during week one (pre-treatment initiation) compared to all other systems with live common carp. After treatments were initiated, turbidity was up to 30 times higher in the continuous subsidy, fifteen times higher in pulsed systems and lowest in the

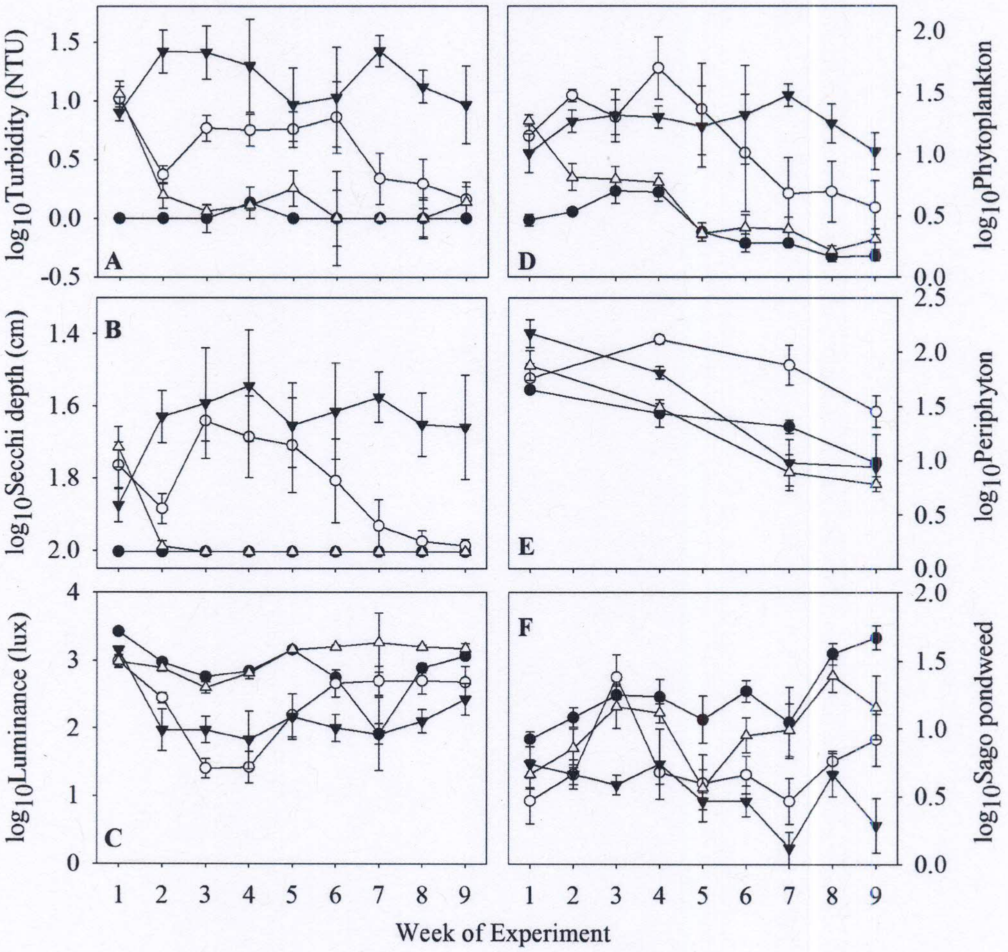

Fig. 2. Mean turbidity (A), Secchi depth (B), luminance (C), phytoplankton chlorophyll *a* (D), periphyton chlorophyll *a* (E) and sago pondweed coverage (F; ±1 SE) among control (black circle), pulsed (open circle), continuous (black triangle) and disrupted (open triangle) treatments during the nine week experiment. Note the inverted Secchi depth y-axis and that a log$_{10}$Secchi depth = 2 represents the bottom of the mesocosm.

disrupted and control systems (Fig. 2A). Similarly, Secchi depth also was deepest in control and disrupted systems (Fig. 2B). Secchi depth increased for one week in pulsed systems, declined the next three weeks and then increased during the final four weeks. In contrast, Secchi depth in continuous subsidy systems immediately decreased and was stable throughout the experiment. Temporal changes in light penetration were similar to Secchi depth and declined in pulsed systems for four weeks before increasing back to similar levels as disrupted systems. Light penetration in continuous systems remained suppressed throughout the experiment (Fig. 1C).

Biological production

Phytoplankton chlorophyll *a* peaked during week four and was highest in pulsed and continuous, intermediate in disrupted and lowest in control systems (Table 1, Fig. 2D). After week four, phytoplankton production declined in pulsed systems but was more stable in continuous, disrupted and control systems. Temporal variation in the production of periphyton and sago pondweed among subsidies resulted in a significant treatment and time interaction (Table

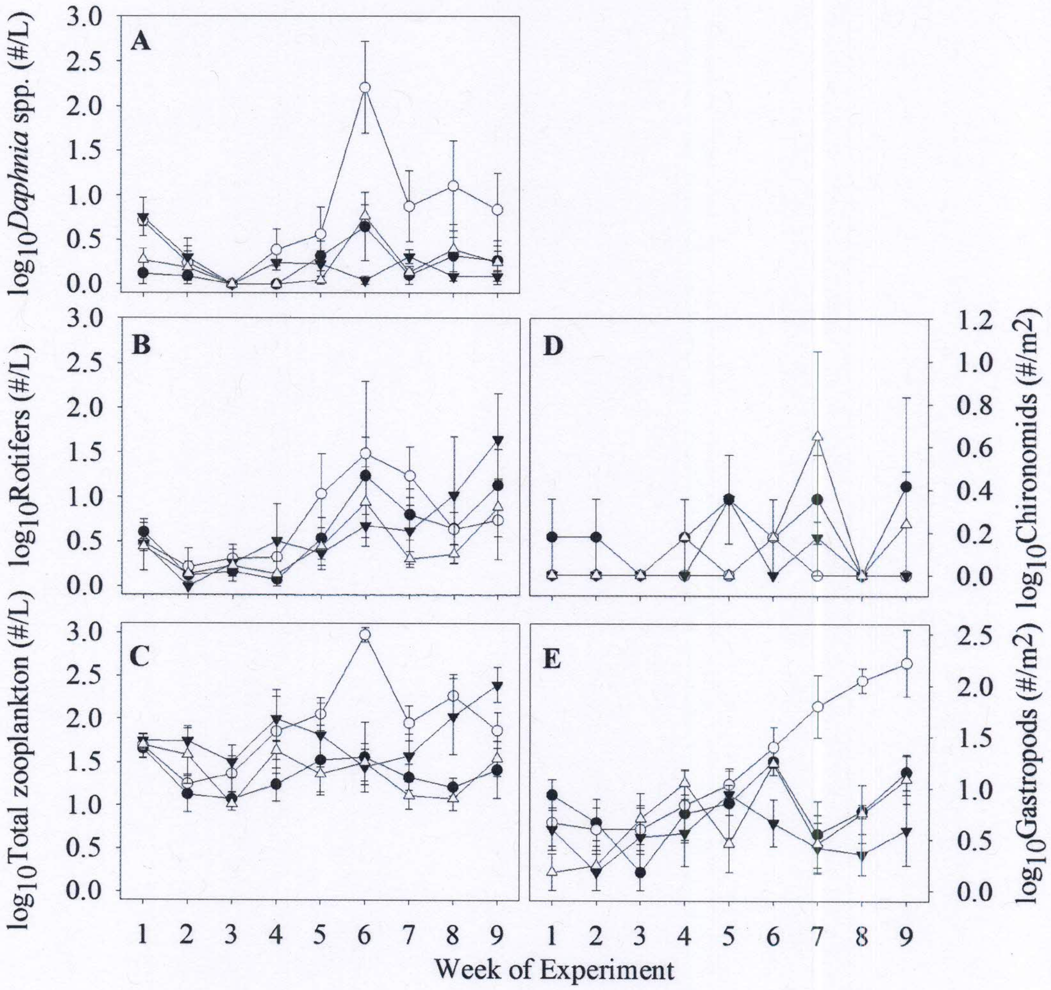

Fig. 3. Mean *Daphnia* spp. (A), rotifer (B), total zooplankton (C), chironomid (D) and gastropod density (E; ±1 SE) among control (black circle), pulsed (open circle), continuous (black triangle) and disrupted (open triangle) treatments during the nine-week experiment.

1). Periphyton chlorophyll *a* was greater in continuous subsidy compared to pulsed or control systems on week one but by week four, pulsed systems had greater periphyton production than any other treatment and it remained higher through the end of the experiment (Fig. 2E). Sago pondweed coverage was highest in control systems and lowest in continuous and pulsed subsidy systems throughout the experiment (Fig. 2F). However, sago pondweed coverage in disrupted systems increased throughout the experiment and had similar coverage as control systems during three of the nine weeks.

Daphnia spp. and total zooplankton density were low for the first five weeks of the experiment but peaked on week six resulting in a significant treatment and time interaction (Table 1). *Daphnia* spp. and total zooplankton densities were >10 times higher in pulsed treatments on week six than the other three treatments with differences among pulsed, control and disrupted treatments persisting through week nine (Fig. 3A, C). Additionally, total zooplankton densities were higher in continuous subsidy systems compared to disrupted and control systems the final two weeks due to an

Table 2. Analysis of variance results for coefficient of variation (CV), δ^{15}N, and δ^{13}C responses in mesocosms examining the effects of continuous, pulsed and disrupted common carp nutrient subsidies during a nine-week experiment. An ellipsis (...) indicates that data were not available for stable isotope analysis.

	CV			δ^{15}N			δ^{13}C		
Variable	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Nitrate	3, 12	0.81	0.51	...	...	...	...	...	...
Ammonium	3, 12	0.61	0.62	...	...	...	...	...	...
Total Kjeldahl nitrogen	3, 12	1.87	0.19	...	...	...	...	...	...
Soluble reactive phosphorus	3, 12	0.58	0.65	...	...	...	...	...	...
Total phosphorus	3, 12	0.84	0.50	...	...	...	...	...	...
Turbidity	3, 12	0.78	0.53	...	...	...	...	...	...
Secchi depth	3, 12	15.24	<0.01	...	...	...	...	...	...
Luminance	3, 12	3.67	0.04	...	...	...	...	...	...
Phytoplankton	3, 12	0.56	0.65	3, 12	11.41	<0.01	3, 12	8.59	<0.01
Periphyton	3, 12	0.56	0.65	3, 12	17.31	<0.01	3, 12	9.05	<0.01
Sago pondweed coverage	3, 12	1.49	0.27	3, 12	0.53	0.67	3, 12	9.16	<0.01
Daphnia spp.	3, 12	3.67	0.04	...	...	...	...	...	...
Rotifer	3, 12	2.11	0.15	...	...	...	...	...	...
Total zooplankton	3, 12	0.90	0.47	3, 12	17.01	<0.01	3, 12	7.89	<0.01
Chironomid	3, 12	0.08	0.98	...	...	...	...	...	...
Gastropod	3, 12	0.07	0.98	3, 12	97.29	<0.01	3, 12	0.70	0.57

increase in rotifer density. Rotifer density was similar among treatments but increased throughout the experiment (Table 1, Fig. 3B).

Chironomid density was highest in control and disrupted systems and lowest in continuous and pulsed subsidy systems (Table 1, Fig. 1D). In contrast, gastropod density was lowest in continuous subsidy systems and highest in pulsed systems where it increased throughout the experiment (Table 1, Fig. 3E). By week nine, pulsed systems contained twice the density of gastropods compared to the other treatments.

Ecosystem stability

Pulsed, continuous and disrupted treatments affected the temporal variability of water clarity, light penetration and the production of a primary consumer. The CV of Secchi depth was >10 times higher in continuous and pulsed treatments compared to disrupted and control treatments whereas CV of light penetration was more than two times greater in pulsed and disrupted treatments compared to control treatments (Table 2). The CV of *Daphnia* spp. density was also more than two times higher in the pulsed than continuous subsidy treatment. In contrast, the CV of nitrate, ammonium, TKN, SRP, TP, turbidity, phytoplankton, periphyton, sago pondweed, rotifers, total zooplankton, chironomids and gastropods were similar among treatments.

Trophic position and energy flow

Stable isotope δ^{15}N signatures of biological materials generally increased with resource pulses and subsidies. Periphyton, phytoplankton, gastropod and zooplankton δ^{15}N signatures collected in continuous and pulsed nutrient subsidy treatments had higher δ^{15}N values (6–14‰; 1.8–4.1 increase in trophic level) than those derived from control or disrupted treatments (Table 2, Fig. 4). Sago pondweed had similar δ^{15}N values among treatments but mean values followed the same trend in δ^{15}N values observed in other biota. δ^{13}C signatures were also generally more negative in systems receiving resource pulsed and continuous subsidies, suggesting a shift from benthic to pelagic energy pathways. Sago pondweed, periphyton, phytoplankton and zooplankton δ^{13}C signatures were 6–10‰ more negative in continuous or pulsed subsidy treatments compared to removed and control treatments (Table 2, Fig. 4). In contrast, gastropod δ^{13}C values were similar among treatments.

DISCUSSION

Ecosystems are often sustained by continuous nutrient subsidies or large magnitude stochastic nutrient pulses. Determining how continuous and pulsed resources permeate into food webs and the magnitude of their effects on ecosystems presents a substantial challenge to ecology

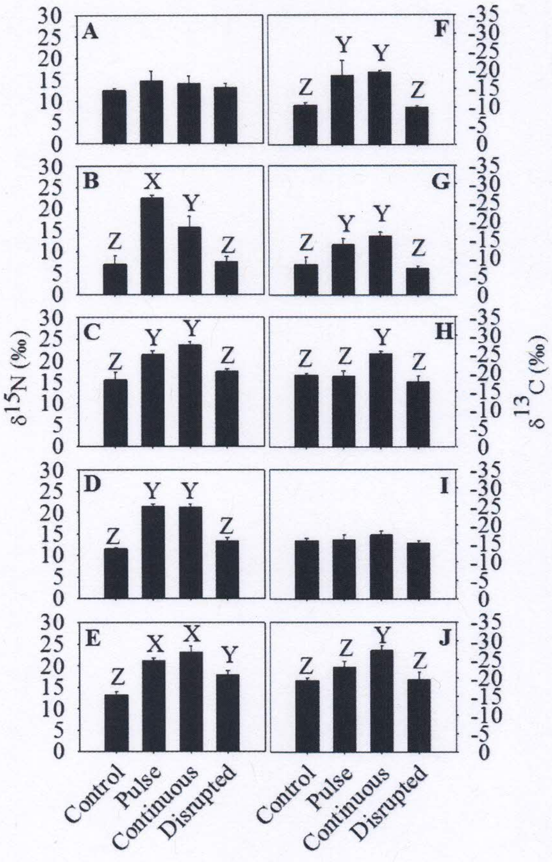

Fig. 4. Mean $\delta^{15}N$ values (left panels; ±1 SE) for sago pondweed (A), periphyton (B), gastropods (C), phytoplankton (D) and zooplankton (E) and $\delta^{13}C$ values (right panels; ±1 SE) for sago pondweed (F), periphyton (G), gastropods (H), phytoplankton (I) and zooplankton (J) collected from control, pulsed, continuous and disrupted treatments. Different letters within a panel indicate significant differences ($P < 0.05$).

(Ostfeld and Keesing 2000). This study represents the first controlled experiment comparing ecosystem productivity, stability and energy flow in systems receiving continuous, pulsed and disrupted nutrient subsidies under ecologically relevant conditions (i.e., similar biomass of common carp in all treatments). Ecosystems rapidly responded to each treatment. As hypothesized, decomposing common carp provided an important nutrient pulse that stimulated algal production which subsequently competed with macrophytes for light and nutrients, shifting energy flow from benthic to pelagic pathways. One of the most striking differences was observed between continuous and pulsed treatments. Despite the ability of common carp to increase nutrient availability and phytoplankton production as a result of bioturbation (Weber and Brown 2009), the magnitude of nutrient availability and primary and secondary production was typically greater in pulsed than continuous subsidy treatments. In contrast, disrupted systems where common carp were removed quickly returned to an 'undisturbed' state and mimicked control system conditions that were more reliant on benthic production.

Fishes are often considered nutrient conveyors as they move nutrients across ecosystem boundaries (Vanni 2002, Vanni et al. 2006) but also as nutrient sinks where ecosystem productivity is lost (Andersson et al. 1988, Griffiths 2006). For instance, semelparous Pacific salmon populations are widely recognized as nutrient conveyors as they acquire a vast amount of nutrients in the marine environment but translocate these nutrients to freshwater streams during spawning migrations where carcass-derived nutrients enhance primary and secondary production in aquatic and terrestrial ecosystems (Gende et al. 2002, Naiman et al. 2002). However, bioturbation by salmon during redd fanning can result in the loss of nutrients downstream (Moore et al. 2007) and declines in benthic primary and secondary production, potentially offsetting some of the local benefits provided by carcass-derived nutrients (Tiegs et al. 2009). Common carp carcass decomposition also provided a large nutrient pulse that enhanced primary and secondary productivity. However, in contrast to salmon, bioturbation by common carp prior to disturbances increases pelagic nutrient availability and primary production through sediment nutrient release (Weber and Brown 2009). Thus, instead of offsetting physical disturbances, ecological effects of carcass-derived nutrients released during decomposition may act in an additive or synergistic manner with those released by live common carp prior to catastrophic disturbance. Nutrient availability in pulsed systems peaked 2–3 weeks post-mortem and was initially 3–5 fold greater than those in continuous subsidy systems. Increases in nutrient availability through subsidies or pulses may release primary producers from nutrient limitations and stimulate biological production at multiple trophic levels.

Primary producers often respond rapidly to nutrient pulses and subsidies due to short generation times (Yang et al. 2010). While carrion-derived nutrients are generally considered beneficial due to the accompanying increased productivity in oligotrophic ecosystems (Gende et al. 2002, Naiman et al. 2002), there is also potential to exacerbate eutrophication processes in more productive ecosystems (West et al. 2010, Weber 2011). System productivity often switches from benthic to pelagic dominance as eutrophication progresses because phytoplankton competes with periphyton and submergent macrophytes for available light and nutrients (Sand-Jensen and Borum 1991, Vadeboncoeur et al. 2003). Concurrent increases in phytoplankton and periphyton with elevated nutrient levels in systems with common carp indicates that even though light availability was lower compared to control and disrupted systems, periphyton was not light-limited, perhaps due to light penetration through opaque mesocosm walls. Instead, both phytoplankton and periphyton production increased in systems with pulsed and continuous nutrient subsidies, suggesting primary producers were initially nutrient limited. Increased primary production has previously been associated with common carp bioturbation and associated nutrient cycling (Weber and Brown 2009) and marine-derived nutrients from anadromous fish decomposition (Gende et al. 2002, Naiman et al. 2002). However, the relative importance of these two ecologically relevant pathways has not been compared. Response of primary producers to nutrient pulses is often rapid but will lag behind nutrient availability and is eventually reduced below pre-pulsed levels as primary consumer abundance increases and exert top-down control (Nowlin et al. 2008, Yang et al. 2010). Phytoplankton production was higher in pulsed compared to continuous subsidy treatments but eventually declined to below continuous treatment levels following reduced nutrient availability. As hypothesized, nutrient pulses from decomposing common carp carcasses appear to provide brief increase in nutrient availability that increases productivity and promotes instability whereas continuous subsidies increase nutrient availability and primary production at a lower but more sustainable level.

Aquatic macrophytes are an integral component affecting alternative stable states of shallow lakes (Scheffer et al. 1993). Although common carp were eliminated early on in disrupted treatments, sago pondweed did not respond as quickly as water quality parameters (i.e., nutrient availability, turbidity). Continuous and pulsed treatments had the lowest sago pondweed coverage, likely due to uprooting (former) and competition for light and nutrients with phytoplankton (former and latter). Reduced macrophyte coverage in winterkill systems may increase return time of shallow lakes to a clear-water state. Although systems with nutrient pulses rapidly returned to a clear-water state in this study (eight weeks), natural lakes have longer fetches that, exposed to wind and wave action, would promote re-suspension of sediment and phytoplankton particles without the stabilizing properties of aquatic macrophytes (Scheffer and Jeppesen 2007). Thus, natural systems may require longer durations to return to a clear-water state following winterkill than those observed here (Weber 2011).

An emerging paradigm suggests water chemistry exhibits a greater immediate response to nutrient subsidies than primary and secondary consumers and responses to subsidies become dampened and response time increases at higher trophic levels (Chaloner et al. 2007). However, in the absence of fish predation, nutrient pulses supported higher *Daphnia* spp., total zooplankton and gastropod densities compared to other treatments. Common carp often shift zooplankton assemblages from large- to small-bodied taxa and reduce the abundance of macroinvertebrates through direct and indirect processes (Weber and Brown 2009). Common carp removal resulted in invertebrate densities similar to controls whereas gastropods were more abundant in systems with nutrient pulses, suggesting their populations were enhanced through nutrient and primary producer enrichment. Nutrient pulses often elicit a series of direct and indirect bottom-up effects followed by top-down control (Ostfeld and Keesing 2000, Yang et al. 2008) with consumer response times lagging behind nutrient availability and primary production (Yang et al. 2010). Phytoplankton and periphyton production decreased with reduced nutrient availability (bottom-up) and increased grazer density (*Daphnia* spp. and gastropod; top-down) in systems with pulsed nutrients. Higher invertebrate densities associated with the pulsed treatment did occur towards the end of the experiment, suggesting that invertebrate response time to nutrient pulses is slower due to longer generation times.

In addition to increases in ecosystem production, nutrient subsidies and pulses may influence food web structure (Vanni et al. 2005, Nowlin et al. 2007, Yang et al. 2010). Yet, the effects of nutrient subsidies and pulses on energy flow and ecosystem stability have received limited attention. Enriched $\delta^{15}N$ signatures of biological material in systems receiving nutrient subsidies and pulses provided evidence that common carp derived nitrogen was assimilated at multiple trophic levels, resulting in the observed increased productivity. We hypothesized that significant food web shifts would occur as a result of increased productivity. Stable isotope signatures revealed shifts in energy flow throughout the food web in support of our hypothesis. Continuous and pulsed subsidy treatments experienced dense phytoplankton blooms, high levels of organic turbidity and contained biota with more negative $\delta^{13}C$ signatures, suggesting they were more reliant on pelagic energy pathways. In comparison, biota in control and disrupted systems had less negative $\delta^{13}C$ signatures indicating a stronger link with benthic production, suggesting that food webs in restored ecosystems where common carp are removed may function similar to 'undisturbed' systems. Shallow lakes in the clear-water state are generally supported by benthic productivity whereas shallow lakes in the turbid water state are more reliant on pelagic productivity (Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2002). Thus, eutrophication can be characterized not only by increased algal production but also by diverting energy flow from benthic to pelagic pathways (Vadeboncoeur et al. 2002, 2003). Several studies have noted decreased benthic production due to common carp predation (Weber and Brown 2009) but results presented here provide the first evidence that consumers switch to pelagic energy pathways as a result of common carp perturbation. Pelagic energy pathways are less efficient than benthic pathways and a reliance on pelagic production may result in decreased production at higher trophic levels even when primary productivity is increased (Vadeboncoeur et al. 2001, 2002, Vander Zanden et al. 2006).

Experiments evaluating and comparing the effects of continuous and pulsed nutrient subsidies on aquatic ecosystem stability are lacking. Predictive models are contradictory and suggest that continuous resource subsidies can either stabilize or destabilize food webs by affecting the variability or minimum size of recipient populations and ecosystem components (Huxel and McCann 1998, Huxel 1999). Continuous and pulsed nutrient subsidies had opposing effects on ecosystem stability in this study. As hypothesized, secchi depth, light penetration, and *Daphnia* spp. tended to be less stable in systems receiving a nutrient pulse but more stable in systems receiving a continuous nutrient subsidy. Nutrient dynamics, primary producers, primary consumers and secondary consumers receiving nutrient pulses tend to be less stable than populations that do not receive nutrient pulses (Polis et al. 2004) and stability may decline with pulse size (Nowlin et al. 2007). Systems receiving continuous nutrient subsidies from live common carp are typically in the turbid-water state (Weber and Brown 2009) which is extremely stable (Scheffer and Jeppesen 2007). Continuous subsidies may stabilize ecosystems by providing a sustainable energy source and thereby decreasing temporal variability of nutrients cascading up to higher trophic levels (Takimoto et al. 2002, Polis et al. 2004).

Understanding the sources of and ecosystem responses to nutrient subsidies and pulses represents an important ecological challenge because they can influence the distribution, abundance and growth of consumers at multiple trophic levels (Polis et al. 2004, Nowlin et al. 2007, Yang et al. 2008, 2010). Annual pulses of marine-derived nutrients stimulate production in oligotrophic aquatic and terrestrial ecosystems in the Pacific Northwest and are a vital for ecosystem health (Gende et al. 2002, Naiman et al. 2002). However, nutrient subsidies are not beneficial in all ecotones. Excessive nutrient loading and ensuing eutrophication resulting in increased phytoplankton blooms, decreased water transparency, hypoxic conditions and fish kills, representing one of the greatest threats to shallow lakes throughout the world (Smith 1998).

Additionally, many ecosystems experience infrequent, large magnitude nutrient pulses that increase resource availability and alter population dynamics at multiple trophic levels (Nowlin et al. 2008). While infrequent and erratic nutrient pulses in terrestrial systems have garnered the attention of ecologists (Ostfeld and Keesing 2000, Yang et al. 2008, 2010), less is known about similar pulses in freshwater environments outside of anadromous fish migrations. Results presented here provide key insights into the effects of a freshwater fish and natural disturbance on nutrient availability and ecosystem productivity, stability and energy flow through alternative pathways (bioturbation versus carcass decomposition) and how remedial management efforts (i.e., carp removal) may mitigate these effects. Regardless of nutrient source (excretion, bioturbation, decomposition), nutrients released by common carp were derived from benthic food sources and were translocated to the pelagia, providing a 'new' source for nutrients for primary production (Vanni 2002). This transition from benthic to pelagic pathways can affect community structure, stability of pelagic food webs and energy pathways. Often, eutrophication cannot be reversed by reducing nutrient inputs (Scheffer et al. 1993). Instead, alternative remediation, including reducing nutrient recycling or nutrient removal, advances restoration efforts (Cooke et al. 1993). These results demonstrate that common carp disturbance can increase ecosystem production, shift energy pathways and alter ecosystem stability, influencing food web and ecosystem dynamics.

ACKNOWLEDGMENTS

We thank the technicians who participated with data collection and processing for this project. K. Bertrand, E. García-Berthou and two anonymous reviewers provided useful comments on a previous version of this manuscript. Partial funding for this project was provided through the Federal Aid in Sport Fish Restoration Act Study 1513 (Project F-15-R-42) administered through South Dakota Department of Game, Fish and Parks and the South Dakota Agricultural Experiment Station.

LITERATURE CITED

Andersson, G., W. Graneli, and J. Stenson. 1988. The influence of animals on phosphorus cycling in lake ecosystems. Hydrobiologia 170:267–284.

Chaloner, D. T., G. A. Lamberti, A. D. Cak, N. L. Blair, and R. T. Edwards. 2007. Inter-annual variation in responses of water chemistry and epilithon to Pacific salmon spawners in an Alaskan stream. Freshwater Biology 52:478–490.

Cooke, G. D., E. B. Welch, S. A. Peterson, and P. R. Newroth. 1993. Restoration and management of lakes and reservoirs. Lewis Publishers, Boca Raton, Florida, USA.

Gende, S. M., R. T. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917–928.

Griffiths, D. 2006. The direct contribution of fish to lake phosphorus cycles. Ecology of Freshwater Fish 15:86–95.

Huxel, G. R. 1999. On the influence of food quality in consumer-resource interactions. Ecology Letters 2:256–261.

Huxel, G. R., and K. McCann. 1998. Food web stability: the influence of trophic flows across habitats. American Naturalist 152:460–469.

Kitchell, J. F., J. F. Koonce, and P. S. Tennis. 1975. Phosphorus flux through fishes. Verhandlungen des Internationalen Verein Limnologie 19:2478–2484.

Moore, J. W., D. E. Schindler, J. L. Carter, J. Fox, J. Griffiths, and G. W. Holtgrieve. 2007. Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. Ecology 88:1278–1291.

Naiman, R. J., R. E. Bilby, D. E. Schindler, and J. M. Helfield. 2002. Pacific salmon, nutrients and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.

Nakashima, B. S., and W. C. Leggett. 1980. The role of fishes in the regulation of phosphorus availability in lakes. Canadian Journal of Fisheries and Aquatic Sciences 37:1540–1549.

Nowlin, W. H., M. J. Gonzalez, M. J. Vanni, M. H. H. Stevens, M. W. Fields, and J. J. Valentei. 2007. Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. Ecology 88:2174–2186.

Nowlin, W. H., M. J. Vanni, and L. H. Yang. 2008. Comparing resource pulses in aquatic and terrestrial ecosystems. Ecology 89:647–659.

Ostfeld, R. S. and F. Keesing. 2000. Pulsed resources and community dynamics in terrestrial ecosystems. Trends in Ecology and Evolution 15:232–237.

Panek, F. M. 1987. Biology and ecology of carp. Pages 1–15 *in* E. L. Cooper, editor. Carp in North America. American Fisheries Society, Bethesda, Maryland, USA.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics

28:289–316.

Polis, G. A., M. E. Power, and G. Huxel. 2004. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois, USA.

Sand-Jensen, K., and J. Borum. 1991. Interactions among phytoplankton, periphyton and macrophytes in temperate fresh-waters and estuaries. Aquatic Botany 41:137–175.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8:275–279.

Scheffer, M., and E. Jeppesen. 2007. Regime shifts in shallow lakes. Ecosystems 10:1–3.

Schoenebeck, C. W., M. L. Brown, S. R. Chipps, and D. R. German. 2012. Nutrient and algal responses to fish-derived nutrient subsidies in eutrophic lakes prone to winterkill. Lake and Reservoir Management 28:189–199.

Smith, V. H. 1998. Cultural eutrophication of inland, estuarine and coastal waters. Pages 7–49 *in* M. L. Pace and P. M. Groffman, editors. Successes, limitations and frontiers of ecosystem science. Springer-Verlag, New York, New York, USA.

Stevenson, R. J., and L. L. Bahls. 1999. Periphyton protocols. Pages 6.1–6.23 *in* Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish. Second edition. U.S. EPA 841-B-99-002. U.S. EPA, Office of Water, Washington, D.C., USA.

Takimoto, G., T. Iwata, and M. Murakami. 2002. Seasonal subsidy stabilizes food web dynamics: balance in a heterogeneous landscape. Ecological Research 17:433–439.

Tiegs, S. D., E. Y. Campbell, P. S. Levi, J. Rüegg, M. E. Benbow, D. T. Chaloner, R. W. Merritt, J. L. Tank, and G. A. Lamberti. 2009. Separating physical disturbance and nutrient enrichment caused by Pacific salmon in stream ecosystems. Freshwater Biology 54:1864–1875.

Tonn, W. M., P. W. Langlois, E. E. Prepas, A. J. Danylchuk, and S. M. Boss. 2004. Winterkill cascade: indirect effects of a natural disturbance on littoral macroinvertebrates in boreal lakes. Journal of the North American Benthological Society 23:237–250.

U.S. EPA (Environmental Protection Agency). 1994. Methods for chemical analysis of water and wastes. U.S. EPA 600/4-79-020. U.S. EPA, National Environmental Research Center, Cincinnati, Ohio, USA.

Vadeboncoeur, Y., E. Jeppeson, M. J. Vander Zanden, H. Schierup, K. Chistoffersen, and D. M. Lodge. 2003. Cultural eutrophication and the loss of benthic energy pathways in lakes. Limnology and Oceanography 48:1408–1418.

Vadeboncoeur, Y., D. M. Lodge, and S. R. Carpenter. 2001. Whole-lake fertilization effects on distribution of primary production between benthic and pelagic habitats. Ecology 82:1065–1077.

Vadeboncoeur, Y., M. J. Vander Zanden, and D. M. Lodge. 2002. Putting the lake back together: Reintegrating benthic pathways into lake food web models. BioScience 52:44–54.

Vander Zanden, M. J., S. Chandra, S. K. Park, Y. Vadeboncoeur, and C. R. Goldman. 2006. Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. Canadian Journal of Fisheries and Aquatic Sciences 63:2608–2620.

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152–2161.

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics 33:341–370.

Vanni, M. J., K. K. Arend, M. T. Bremigan, D. B. Bunnell, J. E. Garvey, M. J. Gonzales, W. H. Renwick, P. A. Soranno, and R. A. Stein. 2005. Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems. BioScience 55:155–167.

Vanni, M. J., A. M. Bowling, E. M. Dickman, R. S. Hale, K. A. Higgins, M. J. Horgan, L. B. Knoll, W. H. Renwick, and R. A. Stein. 2006. Nutrient cycling by fish supports relatively more primary production as lake productivity increases. Ecology 87:1696–1709.

Weber, M. J. 2011. Influence of resource pulses following stochastic disturbances on aquatic food webs. Dissertation. South Dakota State University, Brookings, South Dakota, USA.

Weber, M. J., and M. L. Brown. 2009. Effects of common carp on aquatic ecosystems 80 years after 'Carp as a dominant': Ecological insights for fisheries management. Reviews in Fisheries Science 17:524–537.

West, D. C., A. W. Walters, S. Gephard, and D. M. Post. 2010. Nutrient loading by anadromous alewife (*Alosa pseudoharengus*): contemporary patterns and predictions for restoration efforts. Canadian Journal of Fisheries and Aquatic Sciences 67:1211–1220.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse-consumer interactions. Ecological Monographs 80:125–151.