Hydrobiologia (2015) 755:107–121
DOI 10.1007/s10750-015-2220-6

PRIMARY RESEARCH PAPER

Ecological impacts of an exotic benthivorous fish, the common carp (*Cyprinus carpio* L.), on water quality, sedimentation, and submerged macrophyte biomass in wetland mesocosms

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Received: 10 August 2014 / Revised: 5 February 2015 / Accepted: 9 February 2015 / Published online: 15 February 2015

Abstract We examined the interactions of the common carp (*Cyprinus carpio* L.) and nutrient additions on water quality, sedimentation rates, and submerged macrophyte biomass in mesocosms in Delta Marsh, Manitoba, Canada. We wanted to determine if carp and nutrients interacted synergistically to increase phytoplankton biomass. A two-by-three duplicated, factorial design had the following treatments: (1) control mesocosms with no carp or nutrient additions; (2) low carp density and no nutrient additions; (3) high carp density and no nutrient additions; (4) no carp and nutrient additions; (5) low carp density and nutrient additions; and (6) high carp density and nutrient additions. The presence of carp increased ammonia concentrations, turbidity, and phytoplankton biomass as expected but did not increase total reactive phosphorus concentrations. The presence of carp did not appear to interact synergistically with nutrient additions to increase phytoplankton as has been suggested by others. In mesocosms with high carp density and receiving nutrient enrichment, phytoplankton appeared to be suppressed relative to mesocosms receiving nutrient enrichment only, and nutrient enrichment and low carp density. Overall, the presence of carp appears to mimic the effects of eutrophication. Our results demonstrate that carp can cause a shift from a clear, macrophyte-dominated state to a turbid phytoplankton-dominated state at a biomass of less than 600 kg ha^{-1}.

Keywords Common carp · Eutrophication · Wetlands · Water quality · Mesocosms · Phytoplankton · Suspended solids · Turbidity

Handling editor: Stuart Anthony Halse

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Introduction

Common carp (*Cyprinus Carpio* L.; hereafter 'carp') has a near-worldwide distribution and is one of the most introduced fish species (Badiou et al., 2011). Carp have been introduced to more than 100 countries, usually for aquaculture. Although carp can be valuable as a food and sport fish, it can cause numerous environmental changes when it invades and becomes established in freshwater ecosystems where it does not occur naturally. In particular, carp appears to reach a superabundance in regions of North America and Australia that are characterized by large spatially connected habitats and environmental instability

(Bajer & Sorensen, 2010). Over the past 60 years, carp have established permanent populations in virtually all accessible waterways in Manitoba, Canada where our study was conducted (Badiou & Goldsborough, 2006).

Carp benthivory can have profound negative effects on aquatic ecosystems by increasing turbidity via sediment resuspension (Breukelaar et al., 1994; Badiou et al., 2011; Weber & Brown, 2011; Kloskowski, 2011). Carp are known to uproot submerged macrophytes during spawning and accidentally consume them while foraging for benthic invertebrates (Lougheed et al., 1998; Zambrano & Hinojosa, 1999). Sediment resuspension and excretion by carp can increase water column nutrient concentrations, leading to phytoplankton blooms (Breukelaar et al., 1994; Khan et al., 2003; Driver et al., 2005; Matsuzaki et al., 2009). The shading effect that results from these blooms further suppresses submerged macrophytes, creating an ecological feedback mechanism that perpetuates a persistent turbid state. This results in large-scale habitat deterioration described in many aquatic ecosystems where carp occur in abundance (Scheffer, 1998; Matsuzaki et al., 2007; Bajer et al., 2009).

Delta Marsh, on the south shore of Lake Manitoba in central Canada, is one of North America's largest coastal wetlands (Watchorn et al., 2012). Over the last 50 years, the 18,500-hectare marsh has become turbid and its submerged macrophyte cover has decreased over 50% (Goldsborough & Wrubleski, 2001). It is thought that the shift from relatively clear conditions that prevailed prior to the 1960s, to the current turbid state, was caused by loss of submerged macrophyte cover that, in turn, was caused by the proliferation of carp that first arrived in the marsh in the 1950s.

Carp are tolerant of low dissolved oxygen concentrations and are extremely tolerant of high turbidity (Cooper, 1987). For this reason, carp are often the most abundant fish in degraded aquatic ecosystems where eutrophy (i.e., high turbidity, high nutrients, and low light) affords them a competitive advantage over fish species that depend on visual acuity to capture prey. Nevertheless, it is difficult to separate the effects of omnivorous fish such as carp from those associated with cultural eutrophication, as both ultimately contribute to enhanced phytoplankton biomass which is the endpoint of choice for most scientific studies of degraded aquatic ecosystems. Although the presence of carp and nutrient loading have similar negative impacts on aquatic ecosystems, they may interact synergistically to increase phytoplankton biomass (Drenner et al., 1998).

The objectives of our in situ experiment were to quantify the interactive effects of carp with inorganic nutrient additions on (1) water column nutrient concentrations, (2) turbidity and suspended solids, (3) phytoplankton biomass, and (4) submerged macrophyte biomass. We also wanted to determine if the presence of carp along with nutrient loading would trigger a shift from the clear macrophyte-dominated state to the turbid phytoplankton-dominated state (e.g., Scheffer, 1998).

Materials and methods

The study was conducted near the University of Manitoba's former Delta Marsh Field Station in Delta Marsh (Badiou & Goldsborough, 2010). The site was a flat-bottom paleochannel approximately 45 m wide where water depth ranged from 20 to 100 cm. Abundant submerged macrophytes consisted almost entirely of sago pondweed (*Stuckenia pectinata*) and coontail (*Ceratophyllum demersum*).

Twelve floating mesocosms (5 m × 5 m, open to the sediments) were installed at the study site between May 22 and May 31, 2002. The average water depth at the beginning of the experiment was 54 ± 1 cm with an average enclosed volume of about 13.6 m^3. After all mesocosms were installed, small fish were removed on 4 June using a purse seine. The mesocosms were allowed to recover from the disturbance of seining for 9 days before the experimental treatments began on 13 June. This was designated as the pre-treatment period. All subsequent results and statistical analyses presented here are based on measurements collected during the treatment period.

The experiment followed a two-by-three factorial design with duplicate mesocosms assigned randomly to each treatment. The treatments were (1) control with no fish and no nutrients (CON), (2) low carp density (600–720 $kgha^{-1}$) and no nutrient enrichment (LOW), (3) high carp density (1320–1720 $kgha^{-1}$) and no nutrient enrichment (HI), (4) no carp and nutrient enrichment (NP), (5) low carp density and nutrient enrichment (LOW-NP), and (6) high carp density and nutrient enrichment (HI-NP).

On 13 June, the LOW and LOW-NP mesocosms were each stocked with one adult carp, while the HI and HI-NP mesocosms were each stocked with two fish (Table 1). Carp stocking densities were intended to simulate those in freshwater wetlands, but there are no data available for Delta Marsh. At some sites, carp can reach values exceeding 3,000 kg ha^{-1} (Koehn, 2004) but, in systems comparable to Delta Marsh, values typically range from 450 to 800 kg ha^{-1} (Cooper, 1987; Barton et al., 2000; Colvin et al., 2012). For this experiment, we targeted carp biomasses of 600 kg ha^{-1} as representative of marsh-wide density and 1,200 kg ha^{-1} as representative of spawning density.

Nutrients were added every Monday, Wednesday, and Friday from 13 June to 19 August as a liquid mixture of sodium nitrate ($NaNO_3$) and sodium phosphate dibasic dihydrate ($Na_2HPO_4 \cdot 2H_2O$). Thirty regular additions were made over 10 weeks. The nutrient loading and ratio of N to P added (8:1 by mass) are identical to that used in our other mesocosm experiments at Delta Marsh (e.g., McDougal et al., 1997) to simulate the flush of nutrients that occur when marsh sediments exposed during droughts or drawdowns are reflooded (e.g., Robinson et al., 1997). The total nutrient load for the experiment was 22.0 g m^{-2} N and 3.0 g m^{-2} P in each mesocosm. Nutrients were dissolved in 1 L of distilled deionized water and then mixed with 5 l of mesocosm water that was distributed evenly over the water surface.

Sampling and analysis

In situ profiles of photosynthetically active radiation (PAR) were measured every two weeks at 10-cm intervals through the water column using a Licor Li-1000 datalogger with a flat Li-192SA submersible quantum sensor. Light extinction coefficients (K_d) and photic zone depths (Z_d) were calculated using the linear regression equations produced from the data.

Depth-integrated water samples from each mesocosm were collected weekly using an acrylic tube. All water samples were transported immediately to the field laboratory and stored at 4°C prior to analyses. All nutrient constituents sensitive to rapid degradation were analyzed within four to six hours of collection. Unfiltered water samples were analyzed for ammonia-N (NH_3, μg l^{-1}) using the hypochlorite method (Stainton et al., 1977), nitrate/nitrite-N (NO_3/NO_2, μg l^{-1}) by UV spectrophotometry (APHA, 1992), total reactive P (TRP, μg l^{-1}) by the acid molybdate method (Stainton et al., 1977), and turbidity (NTU, Hach model 2100A). Total suspended solids (TSS, mg l^{-1}) was measured by passing a known volume of water through a pre-weighed glass microfiber filter (Whatman GF/C), which was dried for 1 h at 103°C and then weighed. The filter was fired for 1 h at 550°C to combust all organics and then reweighed to calculate the organic suspended solids (OSS, mg L^{-1}). The difference between TSS and OSS are inorganic suspended solids.

Table 1 Descriptive statistics for length and weight of all carp stocked in experimental mesocosms in Delta Marsh

Treatment	Fish 1		Fish 2		Density
	Weight (kg)	Length (cm)	Weight (kg)	Length (cm)	(kg ha^{-1})
CON	–	–	–	–	0
CON	–	–	–	–	0
NP	–	–	–	–	0
NP	–	–	–	–	0
LOW	1.5	43.0	–	–	600
LOW	1.5	45.0	–	–	600
LOW-NP	1.6	44.0	–	–	640
LOW-NP	1.8	46.0	–	–	720
HI	1.7	46.0	1.7	46.5	1360
HI	1.9	46.5	2.4	54.0	1720
HI-NP	1.9	48.0	2.2	50.0	1640
HI-NP	1.5	43.0	1.8	46.0	1320

Total chlorophyll *a* concentration (μg l^{-1}) was used as a surrogate measure of phytoplankton biomass. Intact water samples were filtered through glass microfiber filters (Whatman GF/C), neutralized with 2–3 drops of saturated $MgCO_3$, and then frozen for a minimum of 24 h to break cell membranes prior to pigment extraction. Five mL 90% methanol were added to each sample, which were kept in the dark for 24 h. Light absorbance of the raw pigment extract was measured at 665 and 750 nm using a spectrophotometer (Pharmacia Ultrospec 4000) before and after acidification with HCl, and total chlorophyll *a* concentration was calculated using the formulae of Marker et al. (1980).

Submerged macrophyte dry weight (g m^{-2}) was measured near the end of the experiment in August to avoid excessive disturbance in the mesocosms. Nine replicate samples were collected from each mesocosm using a plastic, open-ended barrel with a cross-sectional area of 0.24 m^2. All above-ground macrophyte biomass was harvested, identified to species, then dried at 105°C for 24 h, and weighed.

Sedimentation rates were estimated three times (5 July, 17 July, and 17 August) by deploying a trap at a central location in each mesocosm for a period of 7–10 days. Sediment traps consisted of a 500 mL wide-mouth plastic container (8-cm diameter, 10-cm height) held vertically by a plastic coupler attached to a wooden stake. The cross-sectional area of the trap opening was 50.3 cm^2 with a height/diameter ratio of 1.25. Cylindrical traps with height/diameter ratio greater than 5 (10 in turbulent systems) have been shown to be the most appropriate means to correctly measure the downward settling flux of particulate matter (Banas et al., 2002). The proper height/diameter ratio is important to avoid resuspension of settled particulate matter from the sediment traps. However, this would require the use of a sediment trap that would be at least 25 cm in height, given a minimum recommended diameter of 5 cm. A sediment trap this tall would ignore a substantial portion of the water column in shallow wetland environments and would be prone to disturbance by carp. Consequently, the traps we used likely allowed resuspension to occur under turbulent conditions produced by carp, so our data are used only to compare the relative impacts of carp foraging on sedimentation. Sediment collected in the traps was dried and weighed to express sedimentation on an areal basis (g m^{-2} day^{-1}).

Statistical analysis

Statistically significant ($P = 0.05$) effects of carp, nutrients, and their interactions on water quality in the mesocosms were assessed using two-factor repeated measures ANOVA. Most data were not normally distributed and were either $\log_{10}$ or $\log_{10}$ $(X + 1)$ transformed. All repeated measures ANOVAs were conducted using SAS Proc Mixed (Littell et al., 1996) and the autoregressive (order 1) covariance structure, which has the desired property of correlations increasing with decreasing time between samples. Tukey's test was used for post hoc pairwise comparisons of means for significant effects.

Results

Nutrients

Carp ($F_{2,6} = 12.87$, $P = 0.007$) and nutrient additions ($F_{1,6} = 242.93$, $P < 0.0001$) significantly increased TRP concentrations in the mesocosms (Fig. 1). The carp × nutrient interaction was also significant ($F_{2,6} = 6.41$, $P = 0.03$). *Post hoc* analysis of mesocosms not receiving nutrient additions revealed that TRP concentrations were significantly higher in the CON (68 μg l^{-1}) relative to the LOW (<25 μg l^{-1}, $P = 0.02$) and HI (<25 μg l^{-1}, $P = 0.02$) treatments, and that there was no difference in TRP between the LOW and HI treatments ($P = 1.0$; Fig. 1A). Average TRP concentrations in mesocosms receiving nutrient additions were 262, 267, and 175 μg l^{-1} in the NP, LOW-NP, and HI-NP treatments, respectively. TRP concentrations were not significantly different among any combination of mesocosms receiving nutrient additions (Fig. 1B).

NH_3-N concentrations were significantly affected by carp ($F_{2,6} = 12.85$, $P = 0.007$) and nutrient additions ($F_{1,6} = 82.81$, $p < 0.0001$), and the carp x nutrient interaction was also significant ($F_{2,6} = 5.28$, $P = 0.05$; Fig. 2). Concentrations in the LOW (50 μg l^{-1}, $P = 0.03$) and HI (59 μg l^{-1}, $P = 0.01$) treatments were significantly higher than the CON treatment (<25 μg l^{-1}) but did not differ from one another ($P = 0.9$; Fig. 2A). In mesocosms receiving nutrient additions, NH_3-N concentrations generally increased throughout the treatment period

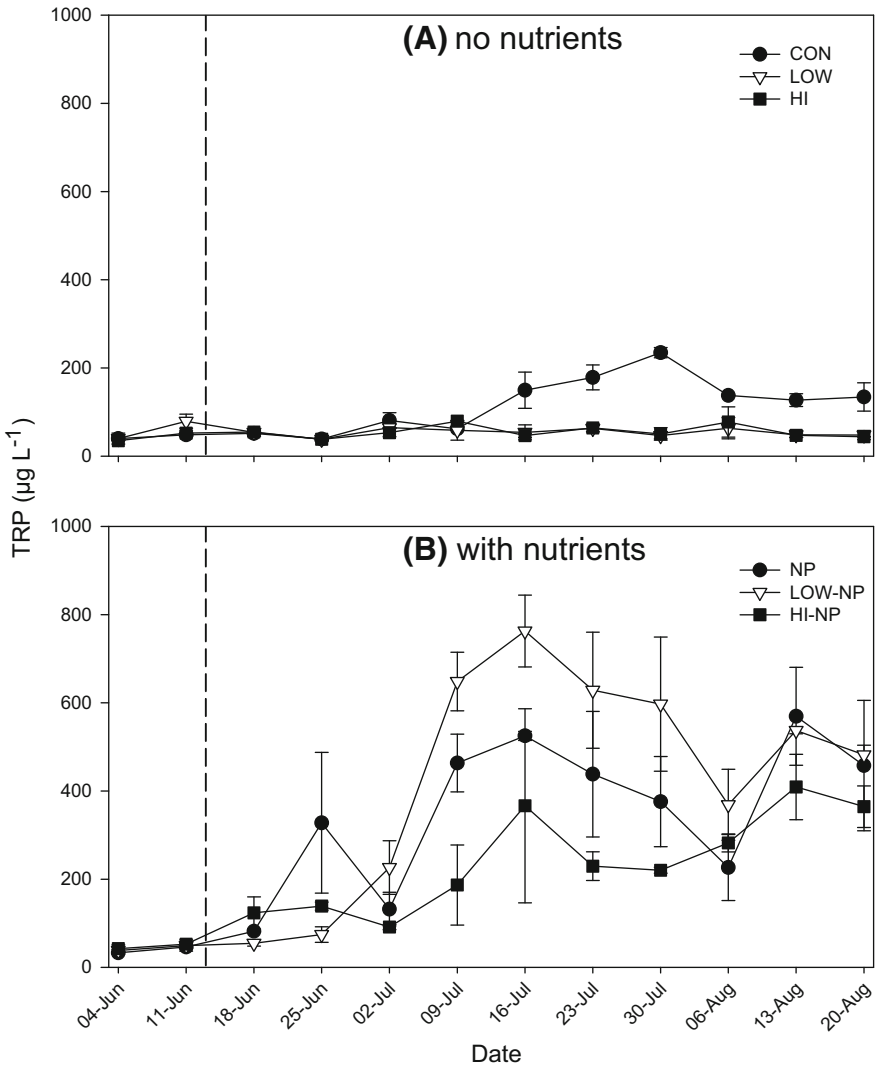

Fig. 1 Total reactive P concentrations (µg l^{-1}; ± SE; $n = 2$) in mesocosms without nutrient additions (**A**) and mesocosms receiving nutrient additions (**B**) stocked with no carp, low carp, and high carp biomass. *Vertical dashed line* indicates the start of nutrient additions and carp stocking on 13 June

(Fig. 2B). Average NH_3-N concentrations in mesocosms receiving nutrient additions were 91, 131, and 105 µg l^{-1} in the NP, LOW-NP, and HI-NP treatments, respectively. However, as was the case for TRP, differences were not statistically significant among any combination of mesocosms receiving nutrient additions.

Unlike NH_3-N and TRP, NO_3-N concentrations were not significantly affected by carp ($F_{2,6} = 1.66$, $P = 0.3$), and no significant carp x nutrient interaction was detected ($F_{2,6} = 0.41$, $P = 0.6826$). Conversely, nutrient additions significantly increased NO_3-N concentrations ($F_{1,6} = 34.53$, $P = 0.001$).

Turbidity, suspended solids, and phytoplankton chlorophyll *a*

Carp treatments ($F_{2,6} = 9.82$, $P = 0.01$) and nutrient additions ($F_{1,6} = 12.76$, $P = 0.01$) both significantly increased turbidity in the mesocosms (Fig. 3). No significant carp x nutrient interaction was detected ($F_{2,6} = 3.24$, $P = 0.1$). Mean turbidity in mesocosms not receiving nutrient additions was highest in HI (41 NTU), lowest in CON (14 NTU), and intermediate in LOW (25) treatments (Fig. 3A). The HI treatment was significantly higher than the CON treatment ($P = 0.0325$) but was not significantly different from

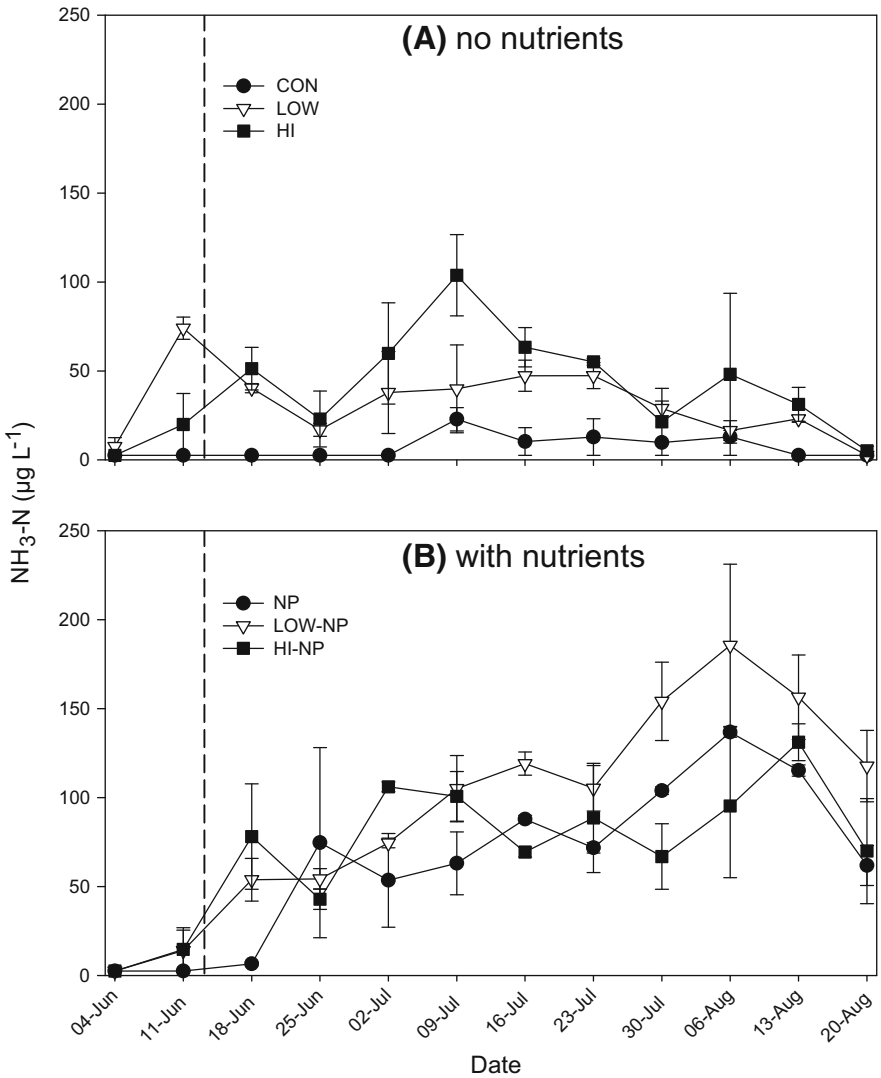

Fig. 2 Ammonia-N concentrations (µg l^{-1}; ±SE; $n = 2$) in mesocosms without nutrient additions (**A**) and mesocosms receiving nutrient additions (**B**) stocked with no carp, low carp, and high carp biomass. *Vertical dashed line* indicates the start of nutrient additions and carp stocking on 13 June

the LOW treatment ($P = 0.8$). In the mesocosms receiving nutrient additions, mean turbidity levels were 32, 58, and 41 NTU in the NP, LOW-NP, and HI-NP treatments, respectively. In general, turbidity increased throughout the treatment period (Fig. 3B) and was not statistically different for any combination of the mesocosms receiving nutrient additions.

Total suspended solids increased significantly in response to carp ($F_{2,6} = 18.96$, $P = 0.003$) and nutrient treatments ($F_{1,6} = 27.66$, $P = 0.002$; Fig. 4). Statistical analyses also revealed a significant carp x nutrient interaction ($F_{2,6} = 5.52$, $P = 0.04$). In the mesocosms not receiving nutrient additions, TSS concentrations were significantly higher in the LOW (mean = 54.7 mg L^{-1}; $P = 0.02$) and HI (mean = 91.2 mg L^{-1}; $P = 0.005$) treatments relative to the CON treatment (mean = 18.0 mg L^{-1}) (Fig. 4A). In the HI treatment, TSS increased rapidly during the first four weeks of the experiment to a maximum of 153.9 mg L^{-1}, a concentration more than 2.5 times greater than the concentration for the same date in the LOW treatment (Fig. 4A). Unlike the rapid increase observed in HI treatment mesocosms, TSS concentrations in the LOW treatments increased at a slower rate but over a longer period of time, reaching a maximum of 85.5 mg L^{-1} six weeks into the experiment (Fig. 4A). TSS was higher in mesocosms receiving nutrient additions ($P = 0.002$) compared to

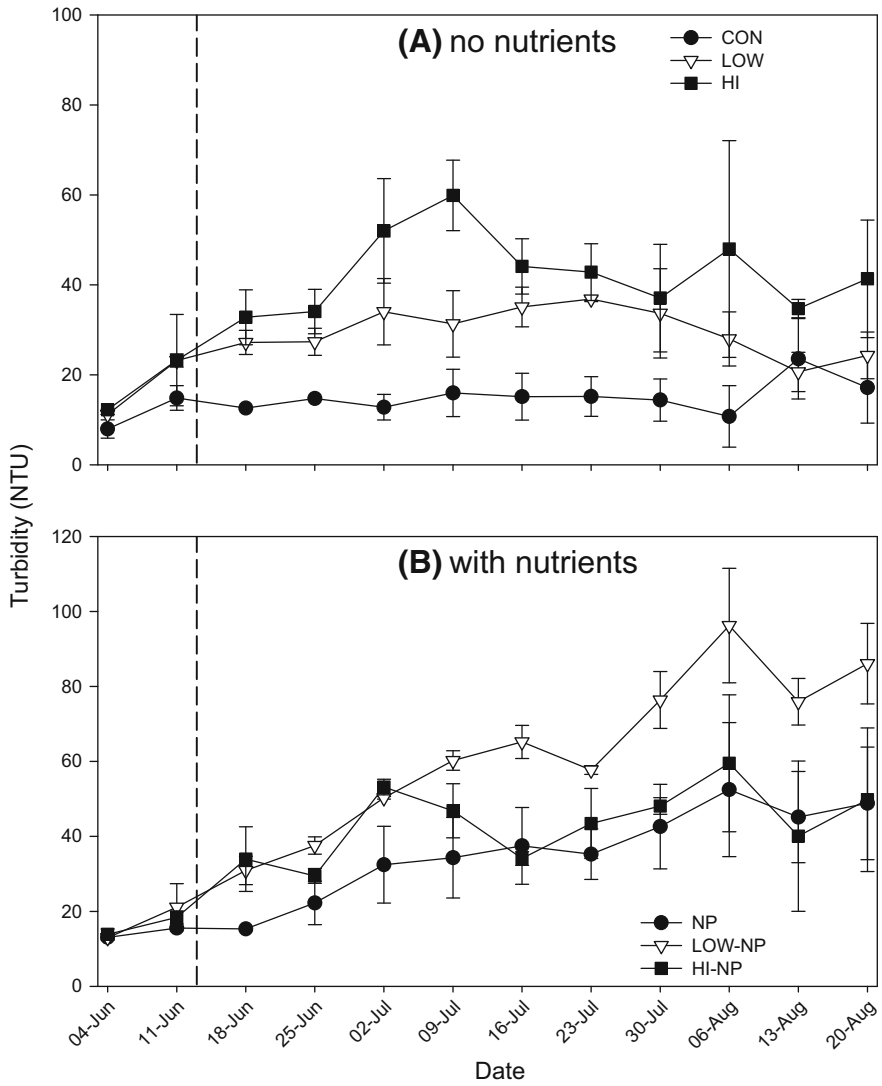

Fig. 3 Turbidity (NTU; ±SE; $n = 2$) in mesocosms without nutrient additions (**A**) and mesocosms receiving nutrient additions (**B**) stocked with no carp, low carp, and high carp biomass. *Vertical dashed line* indicates the start of nutrient additions and carp stocking on 13 June

those not receiving nutrient additions, with mean TSS values in mesocosms measuring 72.6, 108.0, and 109.9 mg L^{-1} in the NP, LOW-NP, and HI-NP treatments, respectively (Fig. 4B). Although TSS in the LOW-NP and HI-NP treatments appears to be similar, and higher than the NP treatment, there were no statistical differences among any combination of the mesocosms receiving nutrient additions. In general, TSS followed a similar trend in mesocosms receiving nutrient additions, regardless of carp treatment, with concentrations increasing initially for the first 3 weeks after which values were fairly stable for the remainder of the experiment (Fig. 4B).

Like total suspended solids, OSS increased significantly in response to carp ($F_{2,6} = 7.73$, $P = 0.02$) and nutrient ($F_{1,6} = 48.74$, $P = 0.0004$) treatments. Statistical analyses did not reveal any significant carp x nutrient interaction ($F_{2,6} = 4.26$, $P = 0.07$). In mesocosms not receiving nutrient additions, OSS in the LOW and HI treatments generally increased over the first 5 weeks of the experiment and then declined over the remaining 5 weeks. OSS in the CON treatment remained fairly consistent throughout the experiment. In mesocosms receiving nutrient additions, OSS in the NP and HI-NP treatments increased over the first 3 weeks at which point they leveled off

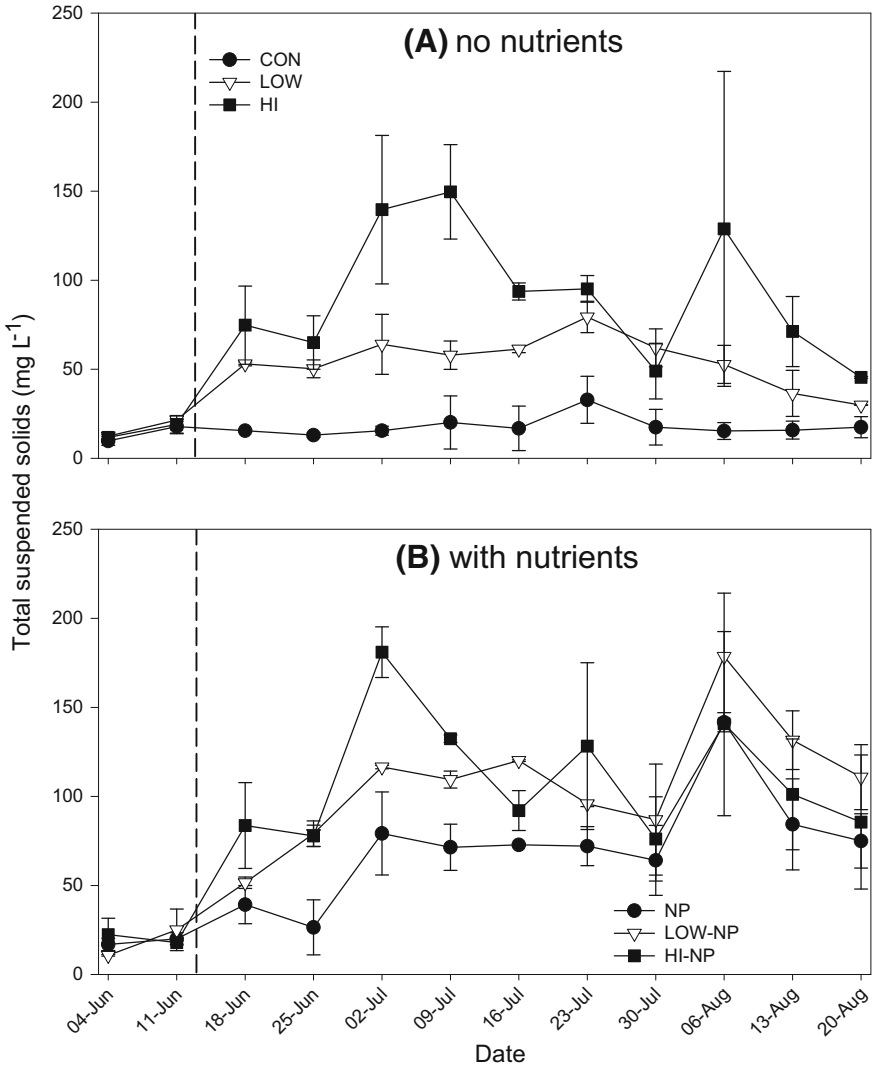

Fig. 4 Total suspended solids (mg l^{-1}; ±SE; $n = 2$) in mesocosms without nutrient additions (**A**) and mesocosms receiving nutrient additions (**B**) stocked with no carp, low carp, and high carp biomass. *Vertical dashed line* indicates the start of nutrient additions and carp stocking on 13 June

and remained consistent until the end of the experiment. Conversely, OSS in the LOW-NP treatment appeared to increase steadily throughout the entire study period. Mean OSS values in mesocosms not receiving nutrient additions were 15.4, 32.7, and 42.3 mg l^{-1} in the CON, LOW, and HI treatments, respectively. OSS was significantly higher in the HI treatment relative to the CON treatment ($P = 0.03$). In mesocosms receiving nutrient additions, mean OSS measured 65.5, 91.9, and 67.7 mg l^{-1} in the NP, LOW-NP, and HI-NP treatments, respectively. Although OSS in the LOW-NP treatment appeared to be higher than those in the NP and HI-NP treatments, there was no statistical difference among any combination of the mesocosms receiving nutrient additions.

Similar to OSS, phytoplankton chlorophyll concentration increased significantly in response to carp ($F_{2,6} = 5.51$, $P < 0.04$) and nutrient treatments ($F_{1,6} = 53.82$, $P = 0.0003$; Fig. 5). Statistical analyses did not reveal any significant carp x nutrient interaction ($F_{2,6} = 3.70$, $P = 0.09$). Trends in chlorophyll were similar to those observed for OSS. Mean chlorophyll *a* values in mesocosms not receiving nutrient additions were 50, 92, and 127 µg l^{-1} in the CON, LOW, and HI treatments, respectively. Chlorophyll concentration was significantly higher in the HI ($P = 0.01$) and LOW ($P = 0.02$) treatments relative

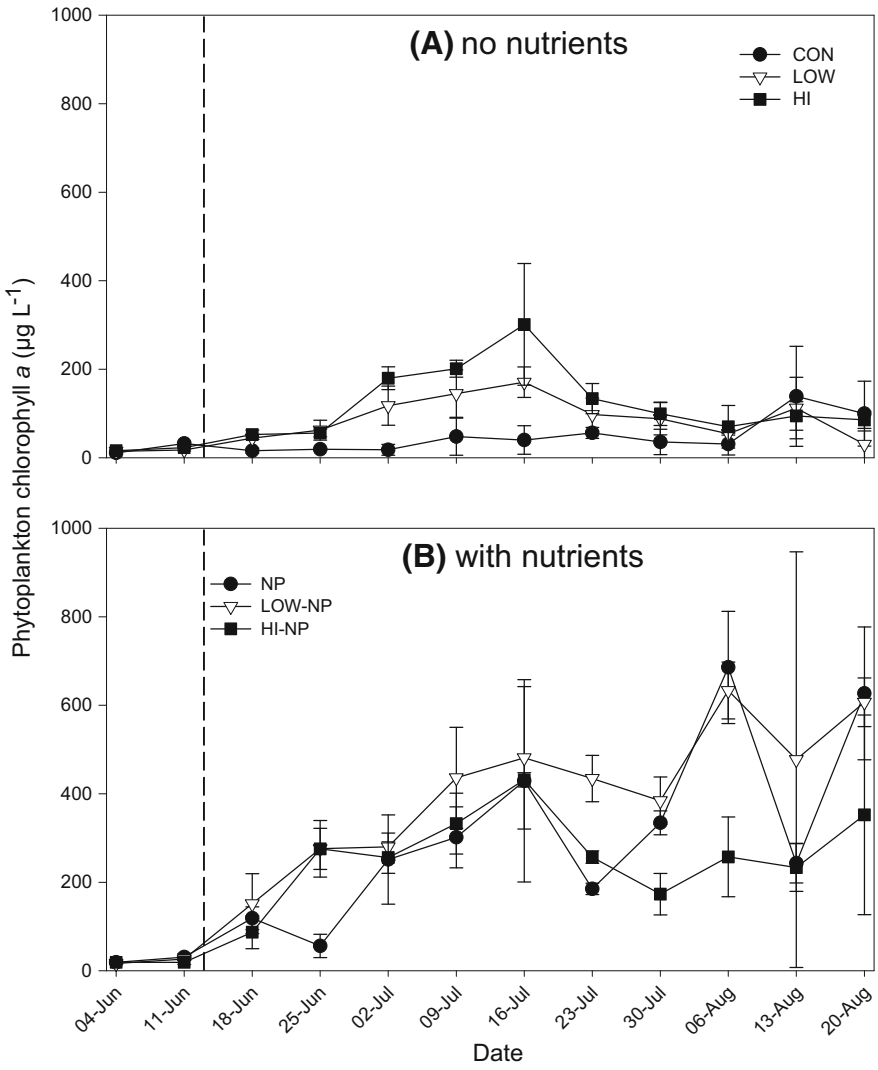

Fig. 5 Phytoplankton total chlorophyll (µg l^{-1}; ±SE; $n = 2$) in mesocosms without nutrient additions (**A**) and mesocosms receiving nutrient additions (**B**) stocked with no carp, low carp, and high carp biomass. *Vertical dashed line* indicates the start of nutrient additions and carp stocking on 13 June

to the CON treatment. In mesocosms receiving nutrient additions, mean chlorophyll *a* concentrations measured 323, 416, and 266 µg l^{-1} in the NP, LOW-NP, and HI-NP treatments, respectively. As for OSS, although chlorophyll in the LOW-NP treatment appeared to be higher than those in the NP and HI-NP treatments, there was no statistical difference among any combination of the mesocosms receiving nutrient additions.

Sedimentation rates

Sedimentation rates were increased by carp treatment during all three sampling periods (5–12 July, $F_{2,6} = 41.68$, $P = 0.0003$; 16–23 July, $F_{2,6} = 34.63$, $P = 0.0005$; and 13–20 August, $F_{2,6} = 9.83$, $P = 0.01$). Different from TSS, which was mostly comprised of organic material in all treatments, the sediments that accumulated in sediment traps were largely inorganic (range 64.1–82.3%). Sedimentation rates in mesocosms not receiving nutrient additions ranged from 0.9 to 3.6, 44.7 to 84.6, and 86.5 to 207.9 g m^{-2} day^{-1} in the CON, LOW, and HI treatments, respectively. During all the three sampling periods, sedimentation rates in the HI treatment were significantly higher than those in the CON treatment (5–12 July, $P = 0.002$; 16–23 July, $P = 0.01$; and 13–20 August, $P = 0.04$). Sedimentation rates in the

LOW treatment mesocosms were significantly higher than those in the CON treatment mesocosms for two of the three sampling periods (5–12 July, $P = 0.01$; and 16–23 July, $P = 0.008$). In mesocosms receiving nutrient additions, sedimentation rates ranged from 3.1 to 11.1, 5.0 to 136.4, and 50.6 to 286.5 $gm^{-2}\,d^{-1}$ in the NP, LOW-NP, and HI-NP treatments, respectively. With the exception of sedimentation rates in the LOW-NP treatment from the 13–20 August sampling period, rates were higher in the LOW-NP and HI-NP treatments relative to the NP treatment. Sedimentation rates in the HI-NP treatment mesocosms were significantly higher than those in the NP treatments for the 5–12 July ($P = 0.02$) and 16–23 July sampling periods ($P = 0.01$) but not for the 13–20 August sampling period ($P = 0.5$). Sedimentation rates in the LOW-NP treatment mesocosms were only significantly higher than those in the NP treatments for one of the three sampling periods (5–12 July, $P = 0.04$). As was the case for the no nutrient treatments, sedimentation rates between the LOW-NP and HI-NP treatments were never significantly different from one another for any sampling period. Although ANOVAs did not always yield significant differences between the low and high carp treatments relative to no carp treatments, linear regression analysis yielded a significant positive relationship ($F_{1,5} = 90.50$, $P = 0.0007$) between carp biomass and sedimentation rates averaged over the entire study period, explaining 95% of the variance.

Submerged macrophytes and light penetration

Submerged macrophyte biomass was significantly decreased by carp ($F_{2,6} = 15.16$, $P = 0.005$) and nutrient treatments ($F_{1,6} = 17.18$, $P = 0.006$; Fig. 6). There was also a significant carp x nutrient treatment interaction ($F_{2,6} = 14.10$, $P = 0.005$). Submerged macrophyte dry weight measured at the end of the treatment period in mesocosms not receiving nutrient additions was 78.7, 9.2, and 0.8 g m^{-2} in the CON, LOW, and HI treatments, respectively. Biomass was significantly lower in the HI ($P = 0.003$) and the LOW ($P = 0.006$) treatments relative to the CON treatment. In mesocosms receiving nutrient additions, submerged macrophyte biomass measured 3.6, 3.7, and 1.1 g m^{-2} in the NP, LOW-NP, and HI-NP treatments, respectively. There were no statistical differences in submerged macrophyte biomass among any combination of the mesocosms receiving nutrient additions.

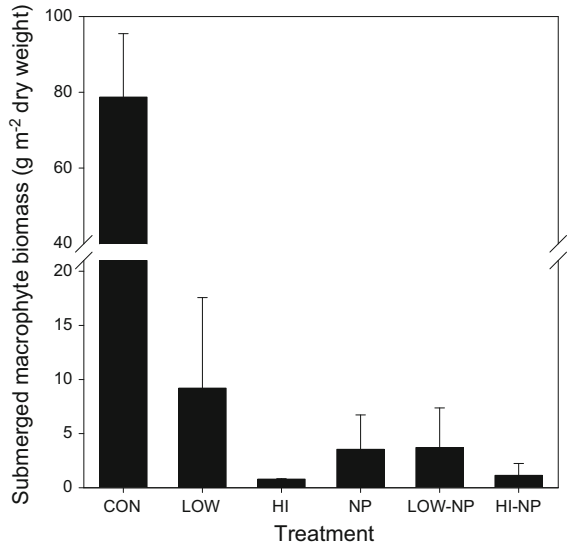

Fig. 6 Submerged macrophyte biomass (g m^{-2} dry weight; ±SE; $n = 2$) in mesocosms without nutrient additions and mesocosms receiving nutrient additions (N + P) stocked with no carp, low carp, and high carp biomass. Macrophytes were harvested at the end of the experiment on 20 August

Light penetration, which was measured as the percent of surface irradiance reaching the sediment–water interface, was significantly reduced by carp ($F_{2,6} = 10.53$, $P = 0.01$; Fig. 7) and nutrient treatments ($F_{1,6} = 41.87$, $P = 0.0006$) but was unaffected by carp x nutrient treatment interactions ($F_{2,6} = 2.28$, $P = 0.2$). In general, light penetration decreased over time throughout all treatments. Mean percent surface irradiance at the sediment–water interface in mesocosms not receiving nutrient additions was 18.8, 5.1, and 3.1% in the CON, LOW, and HI treatments, respectively (Fig. 7A). Light penetration was significantly greater in the CON treatment relative to the HI treatment ($P = 0.03$). In mesocosms receiving nutrient additions, mean % surface irradiance at the sediment–water interface was 3.7, 0.9, and 0.8% in the NP, LOW-NP, and HI-NP treatments, respectively (Fig. 7B). There were no statistical differences in light penetration among any combination of the mesocosms receiving nutrient additions.

Discussion

Our experiment demonstrates that carp have significant negative implications for water quality. Carp effects in

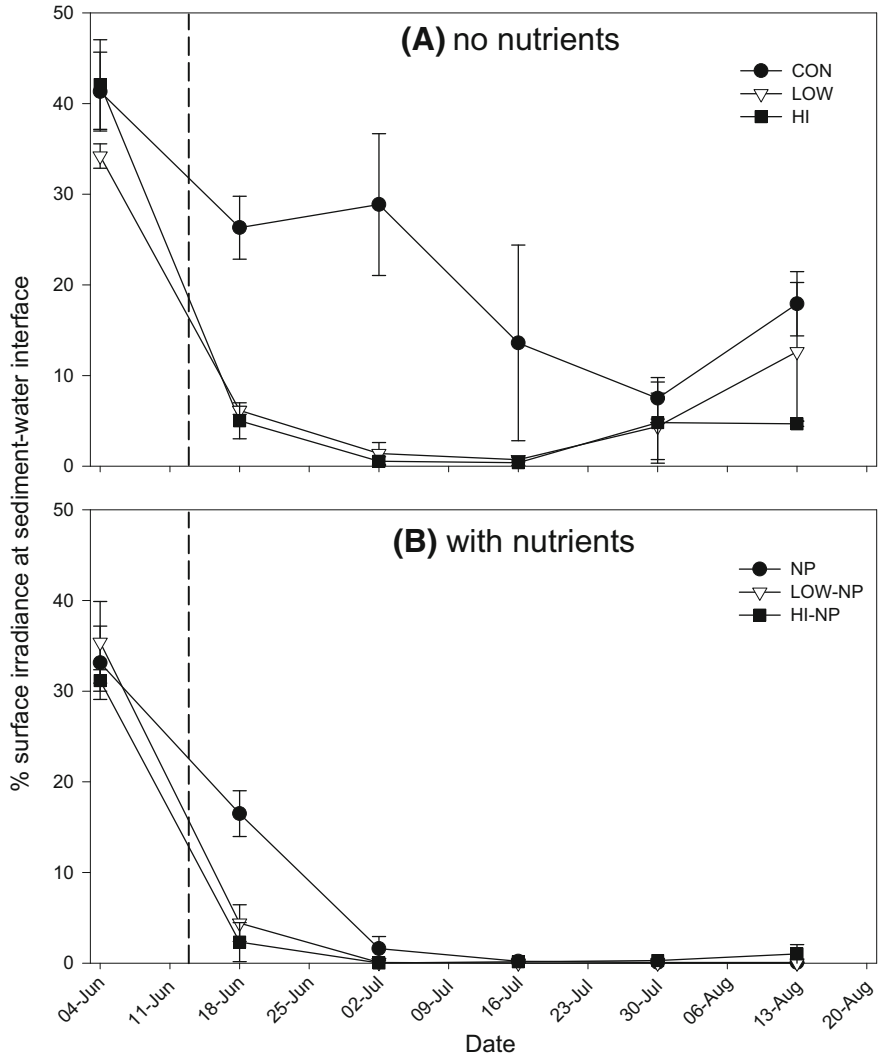

Fig. 7 Percent surface irradiance reaching the sediment–water interface (%; ±SE; $n = 2$) in mesocosms without nutrient additions (**A**) and mesocosms receiving nutrient additions (**B**) stocked with no carp, low carp, and high carp biomass. *Vertical dashed line* indicates the start of nutrient additions and carp stocking on 13 June

mesocosms not receiving nutrient additions were similar to those without carp but receiving nutrients, indicating that the presence of carp can mimic the effects of eutrophication (Andersson et al., 1978), at least in shallow wetland environments such as these. The experimental treatments resulted in a dramatic increase in turbidity, relative to control mesocosms, indicating that the presence of carp can trigger a switch from the clear macrophyte-dominated state to the turbid phytoplankton-dominated state. Although one of our goals was to determine if carp interact synergistically with nutrient loading to increase dissolved nutrient concentrations in the water column, exacerbating the effects of eutrophication, we found that nutrient additions appeared to saturate the experimental systems, making it difficult to differentiate carp effects from those of nutrient additions. However, there were significant carp x nutrient treatment interaction effects with concentrations of TRP, NH_3, and TSS.

Effects of carp and nutrients on water chemistry

We hypothesized that TRP and NH_3 concentrations would increase in the presence of carp because benthivorous fish such as carp are known to release nutrient-rich sediment pore water through their feeding activities, by resuspending nutrient-rich sediments, and by excreting nutrients acquired from benthic prey items (Chumchal & Drenner, 2004; Driver et al., 2005; Glaholt & Vanni, 2005; Matsuzaki et al., 2009; Wahl

et al., 2011). Contrary to our expectation, TRP was significantly higher in the CON treatment relative to the LOW and HI treatments indicating that carp did not increase water column TRP concentrations in the unfertilized mesocosms. Other studies on the effects of benthivorous fish on dissolved P concentration have reported similar findings (Keen & Gagliardi, 1981; Breukelaar et al., 1994; Shormann & Cotner, 1997; Matsuzaki et al., 2007, 2009; Nieoczym & Kloskowski, 2014). Keen & Gagliardi (1981) suggest that benthivorous brown bullheads release dissolved P through excretion and disturbance of the sediment–water interface, but this soluble fraction is sorbed quickly to suspended sediments generated through benthivore activity and removed through sedimentation. Lougheed et al. (1998) also found that TP concentrations increased in the presence of carp but SRP did not, indicating that dissolved P was sorbed to suspended sediments. In the oxic conditions of the water column, phosphates have a high affinity for suspended sediments containing iron oxides and are subsequently transported to the sediments (Almroth, 2002), possibly explaining why TP increases in the presence of carp but not SRP or TRP.

The lower water column TRP levels in the presence of carp in the unfertilized mesocosms, relative to controls, can be explained by a combination of two mechanisms. First, any P released due to carp activity, whether through resuspension or excretion, is rapidly consumed and converted into particulate P within algal cells (Matsuzaki et al., 2009). Secondly, any remaining dissolved P is likely sorbed to the sediments resuspended by carp. The fact that TRP remained constant throughout the treatment period in the LOW and HI treatments, while OSS and chlorophyll *a* (representing algal biomass) increased, supports the possibility that the P released in the unfertilized mesocosms as a result of carp activities was sequestered rapidly by phytoplankton. As expected, water column TRP concentrations in fertilized mesocosms generally increased throughout the experiment. However, given the amount of P added, water column concentrations remained low at all three carp densities for the first 3 weeks after the start of additions. This time lag is likely due to P limitation of phytoplankton. Over this same time period, phytoplankton chlorophyll *a* increased dramatically at all carp densities to concentrations in excess of 200 μg l^{-1}, levels typical of hypertrophy.

Carp increased, albeit not significantly, the water column concentrations of TRP in the LOW-NP and decreased TRP in the HI-NP treatments, relative to mesocosms receiving only nutrient additions (NP). This contradicted our hypothesis that water column nutrient concentrations would increase with increasing densities of carp. Perhaps by resuspending a greater volume of sediment, more P in the HI-NP treatments was being bound and therefore was not included in the TRP fraction. Furthermore, due to increased sedimentation rates, larger quantities of P were being transferred from the water column to the sediment–water interface in the HI-NP treatment. This is supported by the fact that, in fertilized mesocosms, sediment P concentrations (data not shown) in the NP and HI-NP treatments were similar to one another and higher than the LOW-NP treatment, indicating that more P was being transferred to the sediment–water interface. As was the case for unfertilized mesocosms, the higher TRP concentrations observed in the NP treatment relative to the HI-NP treatment was due to the fact that a larger fraction of dissolved P was sorbed to suspended sediments in the HI-NP treatment, which subsequently lowered the TRP concentration.

As expected, NH_3 concentrations increased in the presence of carp in unfertilized mesocosms, probably as a result of excretion by carp and the release of nutrient-rich interstitial water. However, the increase was not proportional to carp biomass. This may be explained by rapid uptake of NH_3 by phytoplankton (Matsuzaki et al., 2009). Shormann & Cotner (1997) found that carp enhance NH_3 mineralization and suggested this was the result of larger numbers of bacteria associated with resuspended sediments. Similarly, Wainright (1987) found that remineralization rates were stimulated by sediment resuspension due to the fact that suspended sediments became more densely packed with bacteria relative to those at the sediment–water interface. Once resuspended through the foraging activities of carp, organic matter may degrade more rapidly due to the well-mixed and oxic conditions in the water column relative to the sediments (Wainright & Hopkinson, 1997). In our fertilized mesocosms, NH_3 generally increased in a linear fashion over the course of the experiment and was unaffected by the presence of carp.

Effects of carp on water clarity

Carp increased turbidity, suspended solids, and phytoplankton chlorophyll *a* in our unfertilized mesocosms, and, as predicted, these increases were

proportional to carp biomass. Mean TSS concentrations increased by approximately 37 and 73 mg l^{-1} in the LOW and HI treatments, respectively. We calculated that TSS increased at a rate of 6.1 and 4.8 mg l^{-1} for every 100 kg ha^{-1} of carp stocked in the LOW and HI treatments, respectively. These rates compare favorably with those of Breukelaar et al. (1994), who calculated rates of increase in TSS of 3.8 and 6.3 mg l^{-1} for every 100 kg ha^{-1} of carp stocked, respectively. The lower rate of increase in TSS calculated for the HI treatment is likely the result of light limitation induced by the high inorganic suspended solids which, in turn, prevented increases in the organic fraction of TSS by reducing phytoplankton productivity. This is supported by the rates of increase calculated for chlorophyll concentrations, which were higher in the LOW treatment (7 μg l^{-1} for every 100 kg ha^{-1} of carp stocked), relative to the HI treatment (5 μg l^{-1} for every 100 kg ha^{-1} of carp stocked). These rates are similar to, but slightly lower than, the rate calculated by Breukelaar et al. (1994) where chlorophyll increased by 9 μg l^{-1} for every 100 kg ha^{-1} of bream (*Abramis brama*) stocked. Similar findings of carp impacts on clarity have been reported by many others (Lougheed et al., 1998; Angeler et al., 2002; Parkos et al., 2003; Matsuzaki et al., 2007, 2009) and phytoplankton chlorophyll *a* (Breukelaar et al., 1994; Angeler et al, 2002; Khan et al., 2003; Chumchal & Drenner, 2004; Driver et al., 2005; Matsuzaki et al., 2007, 2009; Kloskowski, 2011). Conversely, Parkos et al. (2003) found that carp significantly increased suspended solids and turbidity but did not increase chlorophyll concentrations and Wahl et al. (2011) found that chlorophyll *a* was decreased in the presence of carp.

In our fertilized mesocosms, suspended solids concentrations increased with carp biomass in much the same way as unfertilized mesocosms. However, while not significant statistically, OSS and phytoplankton chlorophyll *a* concentrations were noticeably higher in the LOW-NP treatment relative to the NP and HI-NP treatment. This contradicts our hypothesis that carp and nutrients would interact synergistically to increase phytoplankton productivity, and that these increases would be proportional to carp stocking density. Kyeongsik et al. (1999) found that algal biomass was enhanced by mixing and nutrient additions but impaired by increased suspended sediments. It is likely that phytoplankton chlorophyll and OSS in our experiment were enhanced as a result of carp keeping the added nutrients in suspension. This effect was particularly pronounced in the LOW-NP treatment where mixing maintained nutrients in the water column but did not generate enough suspended sediment to limit light. Conversely, most of the added nutrients in the NP and HI-NP treatments did not remain in the water column, but for different reasons. In the NP treatment, the absence of carp allowed most of the nutrients added to the mesocosms to be transferred to the sediment–water interface and therefore was not available to phytoplankton. Conversely, the high concentration of inorganic suspended solids generated by carp in the HI-NP treatment likely limited light and scavenged dissolved nutrients from the water column at a greater rate compared to the LOW-NP treatment, thereby reducing phytoplankton biomass.

Effects of carp on submerged macrophytes and light penetration

As we hypothesized, submerged macrophytes were reduced in the presence of carp. Macrophyte biomass measured at the end of the experiment was positively correlated ($P = 0.0005$) to the mean percent surface irradiance reaching the sediment–water interface, which explained approximately 95% of the variation in submerged plants. This correlation suggests that carp do not reduce submerged macrophyte biomass through physical damage or consumption, but by limiting light availability. Further evidence comes from the fact that the addition of nutrients also significantly reduced submerged macrophyte biomass to levels between those of low and high carp densities (in the absence of fertilization). However, we did not quantify the direct physical impacts of carp on submerged macrophytes (uprooting) and therefore cannot assess the contribution of direct physical disturbance relative to indirect disturbance resulting from light limitation.

Lougheed et al. (1998) found that the species richness of submerged macrophytes declines significantly above a critical threshold of 20 NTU. Our results suggest the same is true for macrophyte biomass. In the control mesocosms where the mean turbidity was 15 NTU, biomass measured at the end of the experiment was about 79 g m^{-2} (dry weight). However, doubling the mean turbidity measured in the control, as was the case in the LOW treatment, resulted

in biomass more than eight times lower than those measured in the control mesocosms.

Conclusions

Our results demonstrate that carp generally impact aquatic ecosystems in much the same way as eutrophication. They also showed that carp can trigger a shift from the clear, macrophyte-dominated state to a turbid, phytoplankton-dominated state, and this switch likely occurs at a carp biomass less than 600 kg ha^{-1}. Similar findings in mesocosm and whole ecosystem studies have been reported at carp densities between 100 and 600 kg ha^{-1} (Matsuzaki et al., 2007; Bajer et al., 2009; Kloskowski, 2011). We found that the switch to a turbid state occurred rapidly after the introduction of carp, generally within 2–4 weeks. This has important ramifications for how shallow lakes and wetlands are managed because carp densities during the spawning season are often greater than those that were used here. Also, the average size of spawning carp in Delta Marsh is typically much larger (Wrubleski, unpublished data) than the carp stocked in this study, suggesting that their physical impacts directly related to sediment disturbance may be even greater. In contrast, Badiou & Goldsborough (2010) did not find that carp caused a shift to a turbid state when introduced to large experimental wetland cells at a similar range of densities. However, a shift to turbid state in this case was likely avoided due to the buffering capacity afforded the experimental wetlands as a result of their abundant and dense submerged macrophyte beds as well as the high levels of colored humic substances in the water column that likely limited phytoplankton growth.

Our results suggest that a model proposed by Drenner et al. (1996, 1998), predicting that carp interact synergistically with nutrient loading to increase phytoplankton biomass, needs to be modified to incorporate the effects of severe light-limiting conditions that occurs at high carp biomass as well as some of the altered water column nutrient dynamics that appear to be affected by high levels of suspended sediments. Understanding these mechanisms will be important for setting biomanipulation targets to achieve water clarity objectives and ecosystem restoration goals for shallow lakes and wetlands impacted by eutrophication in the presence of large benthivorous fish.

Acknowledgments Financial support for this project was provided by Institute of Wetland and Waterfowl Research of Ducks Unlimited Canada and the Natural Sciences and Engineering Research Council of Canada. We gratefully acknowledge the facilities and staff of the former Delta Marsh Field Station (University of Manitoba) and assistance with field sampling provided by Birte Gerdes, Andrea Patenaude, Kevin Jacobs, Andrea Andruschak, and Dan Leitch.

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