Received: 30 August 2018 | Revised: 28 February 2019 | Accepted: 27 May 2019

DOI: 10.1002/aqc.3185

RESEARCH ARTICLE

WILEY

Invasive silver carp may compete with unionid mussels for algae: First experimental evidence

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Abstract

1. Unionid mussels are imperilled throughout the US, where their global diversity is highest. Silver carp (*Hypophthalmichthys molitrix* Valenciennes in Cuvier & Valenciennes, 1844), an invasive planktivorous fish, has spread throughout Midwestern rivers and currently threatens the Great Lakes. Because silver carp remove plankton and other particles from the water column, they may compete with mussels for food resources. This would be among the first examples of a direct competitive interaction between fish and mussels.
2. To examine the potential for competition, a 30 day tank experiment was performed with 2 year old fatmucket mussels (*Lampsilis siliquoidea* Barnes, 1823) and age-1 silver carp in three treatments: fatmucket only, silver carp only and fatmucket + silver carp. All tanks were given a commercial algal-based diet daily and dry mass of suspended particles (an estimate of available food) and NH_4, NO_3 and NO_2 concentrations were quantified every 5 days to track food availability and changes in nutrients. Initial and final silver carp total length (mm) and mass (g), and fatmucket length (mm), height (mm) and surface area (cm^2) were measured.
3. Survival was 100% over the test duration for both species. Fatmucket grew less in the fatmucket + silver carp treatment, whereas silver carp growth was undetectable regardless of treatment. Fatmucket also exhibited increased movement in the presence of silver carp. Suspended particles did not differ among treatments. Dissolved nitrogen concentrations were higher in the silver carp treatments, suggesting that silver carp increase nutrient availability in aquatic systems.
4. Overall, the slower growth rates observed in the fatmucket + silver carp treatment compared with the mussel-only treatment suggest exploitative competition between invasive planktivorous silver carp and fatmucket, and this competition may contribute to additional stress on already imperilled mussels.

KEYWORDS

alien species, competition, fish, introduction, invertebrates, river

1 | INTRODUCTION

Unionid mussels (hereafter mussels) are particularly sensitive to environmental changes and have declined substantially in recent decades (Haag & Williams, 2014; Lydeard et al., 2004). In the US, 37 of the 300 identified species are extinct, and 189 species are on the International Union for Conservation of Nature Red List (Lydeard et al., 2004). These declines are often attributed to commercial harvest, river flow alteration by channelization and impoundments, and water pollution (Haag & Williams, 2014). Declines in mussel abundance may greatly alter freshwater systems, as these species perform important ecosystem functions, including serving as a food source, stabilizing sediment, and transforming and transporting nutrients by filter feeding on plankton and dissolved organic matter from the benthos (Vaughn, 2017; Vaughn & Hakenkamp, 2001; Vaughn, Nichols, & Spooner, 2008). Mussels are the dominant filter-feeders in many freshwater systems (Strayer, Caraco, Cole, Findlay, & Pace, 1999) and thus may be susceptible to changes in the quality or quantity of suspended particles. Conservation efforts and reintroductions of mussel species are now occurring throughout North America (Haag & Williams, 2014), but new threats to mussel diversity are emerging that may hinder conservation efforts. One such threat to freshwater diversity is the introduction of invasive species (Dudgeon et al., 2006).

Invasive species adversely affect mussels in many ways, including consumption (Klocker & Strayer, 2004), fouling (Haag, Berg, Garton, & Farris, 1993), competition for food (Strayer & Smith, 1996) and displacement of fish hosts (Salonen, Marjomäki, & Taskinen, 2016). Invasive bivalves, such as *Corbicula* spp. and zebra mussels (*Dreissena polymorpha* Pallas, 1771) reduce phytoplankton abundance (Cohen, Dresler, Phillips, & Cory, 1984; Welker & Walz, 1998) and rapidly deplete suspended particles, which could limit resources available to mussels (Ricciardi, Neves, & Rasmussen, 1998) and lead to competition for food (Cherry, Scheller, Cooper, & Bidwell, 2005; Pigneur et al., 2014; Ferreira-Rodriguez, Sousa, & Pardo, 2018). Invasive zebra mussels have already been linked to local extinction of mussel populations (Strayer et al., 1999), and invasive *Corbicula* spp. may lower the growth and condition of native mussels (Ferreira-Rodriguez et al., 2018). Additional invasions by other planktivore species may further stress remaining mussel populations in habitats where they are already threatened by previous invasions and human impacts, in the Laurentian Great Lakes, the Mississippi River Basin and worldwide.

One such invasive planktivore, silver carp (*Hypothalmichthys molitrix*), can deplete plankton resources, which may contribute to reduced food availability, leading to population declines in mussels. Silver carp were introduced into the US as an algal control agent in aquaculture (Chick & Pegg, 2001). They are large-bodied and have been observed to consume zooplankton, phytoplankton and particles between 5 and 450 μm (Smith, 1989), although the sizes of particles consumed by silver carp may vary with total length owing to changes in the pore size of their gill rakers (Walleser, Sandheinrich, Howard, Gaikowski, & Amberg, 2014). Silver carp have spread to more than 80 countries worldwide (Kolar et al., 2007), possibly competing with native species throughout their invaded range (Gophen & Snovsky, 2015; Lübcker et al., 2016). Moreover, range expansion of silver carp throughout the Mississippi River Basin, which has the largest number of endemic mussels in the world (Ricciardi et al., 1998), has posed a threat to local aquatic communities. For example, evidence from rivers with invasive silver carp suggests declines in native planktivorous fish species, such as gizzard shad (*Dorosoma cepedianum*; Irons, Sass, McClelland, & Stafford, 2007; Pendleton, Schwinghamer, Solomon, & Casper, 2017) and zooplankton (DeBoer, Anderson, & Casper, 2018; Sass et al., 2014). Phytoplanktivory by silver carp has also been observed (Calkins, Tripp, & Garvey, 2012; Tristano, 2018; Williamson & Garvey, 2005), but their impact on algal availability in freshwater systems is less certain. Although the particle sizes consumed by silver carp and mussels (<25 μm; Baker & Levinton, 2003) suggest that these species may compete for food resources, little is known about their degree of dietary overlap or their potential competitive interactions. Some examples of silver carp and mussel interactions suggest that low densities of silver carp may positively affect mussel growth, and that size-selective filter feeding by these potential competitors results in low dietary overlap (Mueller, Eversole, Turker, & Brune, 2004; Yan, Zhang, Liu, & Li, 2009). Mussels have flexible feeding strategies and can complement filter feeding of suspended particles in the water column with feeding on organic matter from sediments (Nichols & Garling, 2005), which may make mussels less dependent on suspended plankton as a food source under certain conditions, reducing potential overlap with silver carp.

Given that mussels are declining precipitously worldwide, concerted efforts towards their conservation are urgently needed. Recently, the Freshwater Mollusk Conservation Society (FMCS) stated that addressing the impacts of past, ongoing and newly emerging stressors, including invasive fishes, is one of the top 10 goals of native mussel conservation (FMCS, 2016). The purpose of this experiment was to examine the effects of silver carp on a native freshwater mussel (fatmucket, *Lampsilis siliquoidea*), which overlaps in range with silver carp within the Mississippi River Basin, and to evaluate the impacts of each species on the growth and survival of the other. It was hypothesized that interspecific competition would produce resource limitations for one or both species, which would reduce growth or survival.

2 | METHODS

To evaluate potential competition between age-1 silver carp and 2 year old fatmucket, a 30 day replicated tank experiment was conducted at the Southern Illinois University–Carbondale (SIUC) Saluki Aquarium wetlab (Carbondale, IL, USA). Housing and husbandry protocols used in this experiment were approved by the SIUC Institutional Animal Care and Use Committee (protocol no. 16–011). Three treatments (silver carp only [one silver carp], fatmucket only [five mussels] and fatmucket + silver carp [one silver carp and five mussels]) were each replicated four times with each replicate housed in an independent recirculating system. An additive experimental design was used in this study to mimic the invasion of silver carp into new ecosystems, before the potential displacement or reduction of native species that may occur after silver carp invasion. Moreover, additive experiments are an accepted approach to evaluate interspecific interactions (Snaydon, 1991).

Two-year-old fatmucket (60 individuals) were obtained from Genoa National Fish Hatchery (US Fish and Wildlife Service, Genoa, WI, USA) in September 2016. Mussels were spawned from three females collected from Navigation Pool 10 in the Upper Mississippi River in 2014. After arrival at SIUC, mussels were held in an 11 L recirculating tank and fed daily with a commercial algal diet mix (detailed below) for 1 month prior to the experiment. Age-0 silver carp were obtained from the US Geological Survey, Columbia Environmental Research Center (Columbia, MO, USA) and were held in outdoor ponds for about 1 year before being moved inside and fed daily with a commercial diet mix (detailed below) for 1 month before the experiment began. Total length (mm) and wet mass (g) of each silver carp were recorded at the start of the experiment and the total length and mass were measured again at the end of 30 days. Initial silver carp total length and mass (mean ± SE) were 336.4 ± 3.5 mm and 333.4 ± 8.7 g, respectively. Mussels were photographed at the beginning and end of the 30 day experiment to estimate growth. ImageJ (Rasband, 1997) was used to measure each mussel from digital photographs for length (mm; longest axis), height (mm; second longest axis, Figure 1), and surface area (cm^2; Figure 1). Surface area was measured using the threshold tool in ImageJ to delineate the edge of the dark mussel shell in each photograph from the light background. The area enclosed by the polygon was called the surface area. Mussels were marked with coloured nail polish to distinguish among individuals. At the beginning of the experiment, mussels were (mean ± SE) 21 ± 0.3 mm in length, 12 ± 0.2 mm in height and 23 ± 6 cm^2 in surface area.

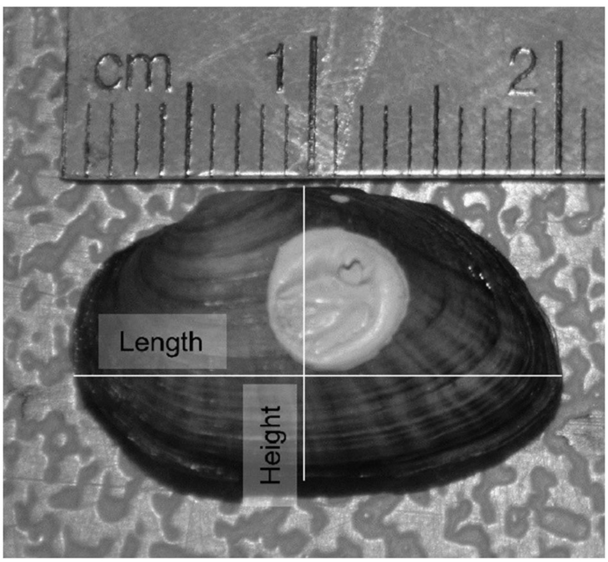

FIGURE 1 Growth metrics of individual fatmucket mussels (*Lampsilis siliquoidea*) used in 30 day experiments to evaluate the effects of silver carp (*Hypophthalmichthys molitrix*) on native mussels. Shell surface area was measured in cm^2. Measurements were made from photographs taken at the beginning and end of the experiment

Each independent replicate consisted of two rectangular tanks: a 113.5 L opaque, plastic tank and a 7.5 L acrylic aquarium. Water from the bottom of the larger tank was pumped through plastic tubing from the larger tank to the smaller tank via an aquarium pump. Water flowed out of the smaller tank through a standpipe and back into the larger tank. Flow rates (mL s^{-1}, mean ± SE) of aquarium pumps were similar among treatments: silver carp only 47.6 ± 3.4, fatmucket only 46.1 ± 6.0 and fatmucket + silver carp 49.8 ± 1.3. Silver carp (one individual per tank) were housed in the larger, opaque tanks during the experiment to allow the fish to change their orientation within the tank and to reduce their reactions (i.e. jumping) in response to changes in the laboratory environment outside of the tanks. Fatmucket (five individuals per tank) were housed in the smaller acrylic aquaria lined with a 3.8 cm-thick layer of sterilized aquarium gravel (grain size distribution = 3.2 mm × 7.9 mm; sterilized at 300°C for 2 hr). Mussels may respond to stressful environments (e.g. lack of food) by increasing movement rates (Balfour & Smock, 1995; Schwalb & Pusch, 2007). To assist in monitoring mussel movement, a 1 cm^2 grid was marked on the edges of each acrylic tank to monitor the location of each mussel daily. The number of 1 cm^2 grid squares that each mussel moved vertically and horizontally through the tank was recorded each day to estimate the linear daily movement of each individual. Every mussel was not located every day owing to occasional burial in the sediment. The larger tank in each replicate received ~7.5 L of bioballs from a larger, existing recirculating system and 7.5 L of new bioballs (surface area of each bioball = 25.3–315 cm^2; Integrated Aqua Systems Inc., Escondido, CA, USA). Bioballs were allowed to acclimate for 2 months prior to the start of the experiment. Bioballs provide a surface area upon which the bacteria responsible for nitrification and denitrification may colonize, thereby maintaining ammonia concentrations at levels that are not lethal to fish.

Water used in the experiment was city of Carbondale, IL (USA) water subjected to a reverse osmosis process and then supplemented to increase water hardness. A combination of sodium bicarbonate, calcium chloride and calcium sulphate was added at a ratio of 1:0.59:0.66 to the water until total hardness was at least 150 mg L^{-1} as determined using a Hach total hardness test kit (model 5-EP MG-L, Hach, Loveland, CO, USA). Fifteen days into the experiment, hardness-amended water was added to each replicate to replace water lost to evaporation and suspended particle sampling.

Silver carp and fatmucket were fed a mixture of commercially available diets which consisted of 37 mL *Chlorella* spp. (Natural Foods Inc., particle size about 120 μm, Toledo, OH, USA), 37 mL *Spirullina* spp. (Natural Foods Inc., particle size about 110 μm, Toledo, OH, USA) and 5 mL microalgae mix (Shellfish diet 1800, particle size 4–20 μm, Reed Mariculture Inc., Campbell, CA, USA) in 1 L water. This food concentration was estimated from the diet fed to silver carp at the US Geological Survey, Columbia Environmental Research Center and amounts were meant to be limiting. The food mixture was mixed fresh every 5 days and stored in a refrigerator between feedings. The food mixture was added daily to both the large and small tanks in each replicate at a rate of 0.5 mL food per 3.8 L tank water. Every 5 days, the diet mixture was measured to assure consistency over time. A

0.5 mL aliquot of the food mixture was filtered through a pre-weighed glass fibre filter (Whatman GF/A glass fibre filter, General Electric Healthcare Life Sciences, Pittsburgh, PA, USA), dried at 60°C for 24 hr, and re-weighed. The mass of the food mixture was (mean ± SE) 0.04 ± 0.006 g mL^{-1}, indicating that 0.69 g dry weight of food was added to each replicate daily.

Water quality was measured at the start of the 30 day period and every 5 days thereafter: dissolved oxygen (mg L^{-1}), temperature (°C), NO_3, NO_2 and NH_4 concentration (mg L^{-1}), total hardness (mg L^{-1}), alkalinity (mg L^{-1}) and pH. Phosphate concentrations were also measured but remained below detection limits (0.15 mg L^{-1}). Dissolved oxygen and temperature were measured using a YSI 550A (YSI/Xylem Inc., Yellow Springs, OH, USA) and pH was measured using a handheld pH meter (EcoTestr pH 1, Oakton Instruments, Vernon Hills, IL, USA). Dissolved oxygen was measured in both tanks of each replicate and averaged for each water quality monitoring event. Nitrate, NO_2 and NH_4 concentrations, and alkalinity were measured from water that was pumped from the larger tank to the smaller tank, using Hach TNTPlus water chemistry cuvettes (Hach, Loveland, CO, USA).

Potential differences in availability of food particles among treatments (e.g. silver carp faecal material; Yallaly, Seibert, & Phelps, 2015) may affect the strengths of competitive interactions observed and, therefore, required quantification. To quantify available potential food resources in each replicate, suspended solids were measured every 5 days: (a) before feeding (background particulate levels); (b) 1 hr after feeding; and (c) 2 hr after feeding. Water samples of 100 mL each were collected from each replicate at each of the three timepoints. Samples were filtered through pre-weighed glass fibre filters, oven dried at 60°C for 24 hr, and re-weighed. Change in particulate matter was calculated by taking the percentage difference between the background particulate mass and the mass of the filtrate of the 1 and 2 hr post-feeding water samples.

2.1 | Statistical analyses

Mussel growth metrics (e.g. length, height, surface area) over the 30 day experiment were normally distributed and showed equal variance. Growth metrics (mm day^{-1} or cm^2 day^{-1}) were tested using a linear mixed-effects model with treatment (fatmucket + silver carp and fatmucket only) as the fixed effect and tank as a random effect.

The 30 day mean daily distance moved and the total distance moved were estimated based on observed movements for each mussel. Mussel movements were normally distributed with equal variance and were compared among treatments using linear mixed-effects models with treatment as a fixed effect and tank as a random effect.

Percentage change in total length (mm) and wet mass (g) of silver carp were compared between treatments using one-way ANOVA. The dry mass of suspended particles in each tank before feeding was compared through time and among treatments using a repeated measures ANOVA. In addition, differences in the amounts of suspended particles from 1 hr before feeding to 2 hr after feeding were compared among treatments using a repeated measures ANOVA with time, treatment, and a time × treatment interaction as factors. Suspended particle data were log(x + 1) transformed before analysis to achieve normality. Nitrate and nitrite concentrations were evaluated using repeated measures ANOVAs with time, treatment and time × treatment interaction as factors. Nitrite concentrations were natural log-transformed before analysis to achieve normality. Ammonia concentrations were analysed with a Friedman test, as normality could not be achieved via transformations. One-way and repeated measures ANOVAs were completed in SAS (v 9.4; SAS Institute, 2013); all other analyses were completed in R (v. 3.4.0; R Core Team, 2017). All analyses used an $\alpha = 0.05$.

3 | RESULTS

Over the course of this study, no mussel mortality occurred. Length ($F_{6,32}$ = 22.5, P = 0.0100; Tukey's, P = 0.000240) and surface area ($F_{6, 32}$ = 21.4, P = 0.00510; Tukey's, P = 0.0000180) of mussels varied significantly between treatments (Figure 2). The height of mussels did not differ between treatments ($F_{2,32}$ = 0.110, P = 0.910; Figure 2). The mean daily rate of mussel movement ($F_{6,32}$ = 660, P = 0.024; Tukey's, P = 0.0026) and total distance moved ($F_{6, 32}$ = 820, P = 0.0200; Tukey's: P = 0.00180) differed significantly between treatments. Mussels moved at a higher rate and covered a greater distance in the silver carp and mussel treatment than in the mussel-only treatment (Figure 3).

Silver carp survival was 100%. The percentage change in silver carp total length was similar between treatments (initial length [mean ± SE] = 337 ± 4 mm and final length = 336 ± 4 mm; $F_{1,6}$ = 3.88, P = 0.0940). Percentage change between mean initial (334 ± 9 g) and final (331 ± 9 g) wet mass for silver carp followed a similar pattern ($F_{1,6}$ = 0.600, P = 0.467).

Pre-feeding suspended particle dry mass fluctuated over time ($F_{5,45}$ = 6.32, P = 0.000200), peaking for each treatment on day 20; however, there was no effect of treatment ($F_{2,9}$ = 0.280, P = 0.761)

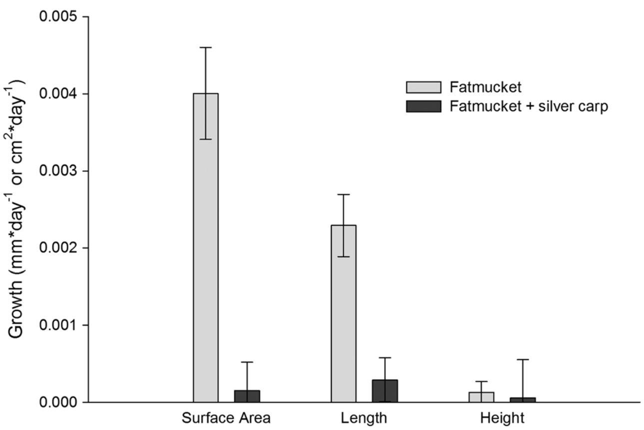

FIGURE 2 Changes (tank mean ± SE) in surface area (cm^2 day^{-1}), length (mm day^{-1}) and height (mm day^{-1}) of fatmucket mussels (*L. siliquoidea*) over a 30 day experiment to determine potential competition between fatmucket and silver carp (*H. molitrix*) in fatmucket only (n = 20) and fatmucket + silver carp (n = 20) treatments

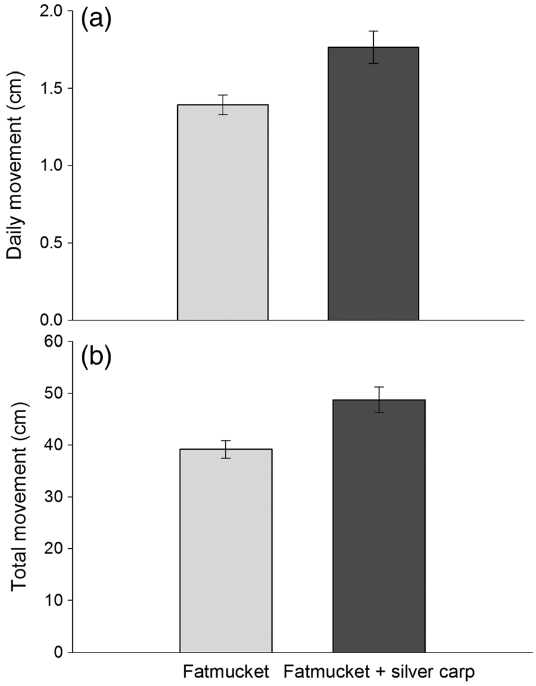

FIGURE 3 Tank mean (± S.E) (a) daily movement and (b) total movement of fatmucket (*L. siliquoidea*) over a 30 day study to examine potential competition between fatmucket and silver carp (*H. molitrix*) in fatmucket only (n = 20) and fatmucket + silver carp (n = 20) treatments

or time × treatment interaction ($F_{10,45}$ = 0.810, P = 0.623; Figure 4a). The change in suspended particle dry mass from 1 to 2 hr after feeding did not differ through time or by treatment (time effect, $F_{4,28}$ = 0.800, P = 0.534; treatment effect, $F_{2,9}$ = 2.03, P = 0.188; time × treatment interaction, $F_{8,28}$ = 1.42, P = 0.230).

Water quality measurements fluctuated throughout the experiment and often varied significantly among treatments (Table 1). Alkalinity fluctuated through time (time effect: $F_{6,63}$ = 8.66, P < 0.000100), but did not differ by treatment (treatment effect, $F_{2,63}$ = 1.79, P = 0.175; time × treatment interaction, $F_{12,63}$ = 0.564, P = 0.863). Similarly, hardness differed through time but not by treatment (time effect, $F_{6,\ 63}$ = 4.72, P = 0.000500; treatment effect, $F_{2,63}$ = 1.42, P = 0.249; time × treatment interaction, $F_{12,63}$ = 0.625, P = 0.813). Nitrate concentration increased throughout the experiment (time effect, $F_{5,45}$ = 21.3, P < 0.000100), but did not differ by treatment (treatment effect, $F_{2,9}$ = 0.150, P = 0.859; time × treatment interaction, $F_{10,45}$ = 1.77, P = 0.0948; Figure 4b). Nitrite concentration differed both by treatment ($F_{2,9}$ = 10.3, P = 0.00470; Tukey's, P = 0.00360) and over time ($F_{5,45}$ = 12.9, P < 0.000100), with concentration increasing more in the fatmucket + silver carp treatment than other treatments; however, there was no time × treatment interaction ($F_{10,45}$ = 1.45, P = 0.192; Figure 4 c). Ammonia concentrations remained low (<0.64 mg L^{-1}) throughout the study and differed among treatments (P = 0.0118), but not time (P = 0.113; Figure 4d).

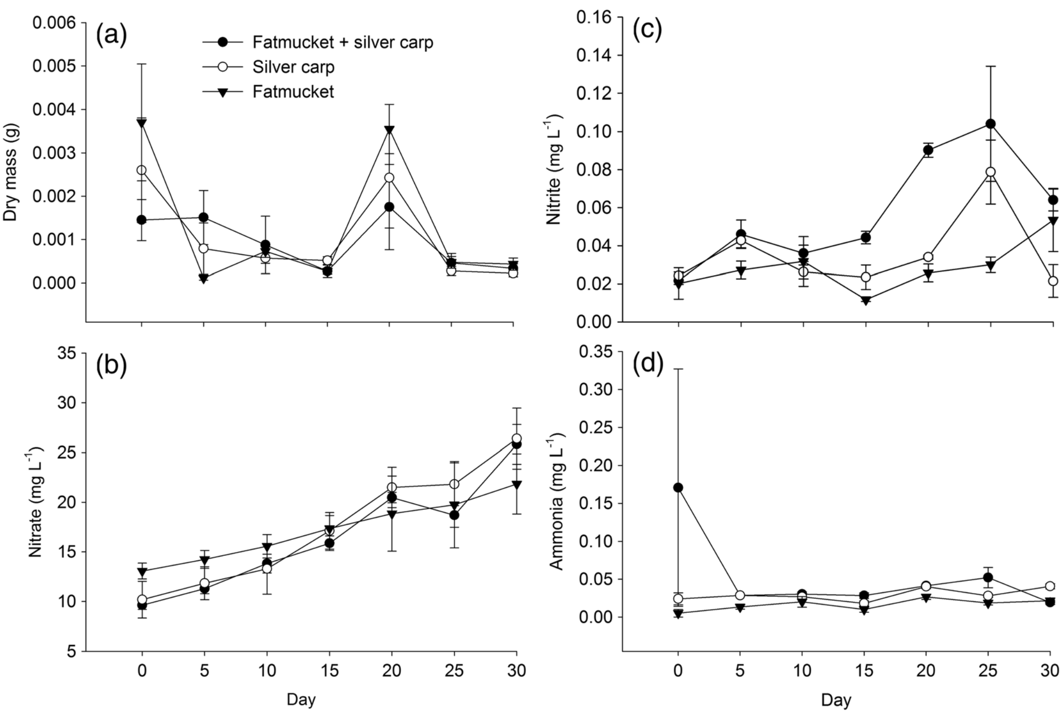

FIGURE 4 Temporal patterns in water chemistry and suspended particles in an experiment to examine potential competition between fatmucket mussels (*L. siliquoidea*) and silver carp (*H. molitrix*). Mean (± SE) (a) pre-feeding suspended particle dry mass, (b) nitrate concentration, (c) nitrite concentration and (d) ammonia concentration in the silver carp only (n = 4), fatmucket only (n = 4), and famucket + silver carp treatments (n = 4). Water chemistry and suspended particles were measured every 5 days

TABLE 1 Water quality in experimental tanks used to examine potential competition between invasive silver carp (*Hypophthalmichthys molitrix*) and fatmucket (*Lampsilis siliquoidea*) in a 30 day laboratory experiment. Each treatment consisted of four replicate tank set-ups

	Treatment					
	Silver carp		Fatmucket		Fatmucket + silver carp	
	Initial	Final	Initial	Final	Initial	Final
Temperature (°C)	22.9 ± 0.03	22.1 ± 0.04	22.0 ± 0.14	21.0 ± 0.0	22.3 ± 0.07	21.7 ± 0.03
pH	7.9 ± 0.05	8.1 ± 0.06	7.9 ± 0.08	7.8 ± 0.0	7.7 ± 0.06	7.9 ± 0.03
Total hardness (mg L^{-1})	230 ± 13	245 ± 19	210 ± 6	245 ± 15	220 ± 20	245 ± 10
Alkalinity (mg L^{-1})	90.8 ± 6.3	48.0 ± 7.8	93.7 ± 12.2	33.7 ± 8.2	103.0 ± 12.0	63.7 ± 1.8
Dissolved oxygen (mg L^{-1})	7.7 ± 0.2	8.1 ± 0.2	7.6 ± 0.5	8.1 ± 0.2	7.3 ± 0.06	7.8 ± 0.2
Ammonia (mg L^{-1})	0.17 ± 0.16	0.02 ± 0.003	0.005 ± 0.005	0.02 ± 0.0009	0.02 ± 0.008	0.04 ± 0.004
Nitrate (mg L^{-1})	10.2 ± 0.4	26.4 ± 2.0	13.1 ± 0.8	21.9 ± 3.0	9.6 ± 1.9	25.8 ± 3.1
Nitrite (mg L^{-1})	0.02 ± 0.002	0.02 ± 0.006	0.02 ± 0.002	0.05 ± 0.02	0.02 ± 0.002	0.06 ± 0.008

4 | DISCUSSION

This study provides experimental evidence of an invasive planktivore adversely affecting native sub-adult mussels and may be the first evidence of direct vertebrate competition with freshwater mussels in North America. Although the literature on potential silver carp–mussel interactions is limited, previous work suggests that the distinct size range of particles filtered by each species would limit potential competition (Mueller et al., 2004; Yan et al., 2009), but this study suggests that diet overlap exists. Growth of mussels in the absence of silver carp was lower than growth observed in other studies. For example, Pullum (2015) found that sub-adult *Lampsilis* mussels increased in length by an average of 0.026 mm day^{-1} under control conditions, which is greater than the average growth in length under control conditions in this study. This suggests that food availability was limiting in this study, as was intended to induce competition between mussels and silver carp. Although growth still occurred for most mussels in both treatments, mean growth was lower in the presence of silver carp than without silver carp. Although slight, the lower growth of mussels, if continued over time, may reduce survival, recruitment, or condition in the presence of silver carp, especially if coupled with other stressors. Moreover, this effect may be exacerbated in younger mussels which have higher growth rates compared with adults (Haag, 2012).

The complexity of natural ecosystems may provide mechanisms for reducing or eliminating competition between these species (e.g. greater variety of resources, dispersal away from competition). Food particles in this study ranged from about 10 to 120 μm, which is within the observed range for silver carp consumption (Smith, 1989) and were fed at a level that was meant to induce potential competition. The lack of silver carp growth throughout the study suggests that food resources may have been limited, thereby facilitating a competitive interaction between the two species. In natural ecosystems, a greater abundance and variety of particle sizes and quality may allow mussels to consume a narrower range of particle sizes, with selectivity toward food <25 μm in size (Baker & Levinton, 2003), which may reduce competition with silver carp. However, particles approaching 10 μm in size are within the range of particle sizes silver carp can consume (Smith, 1989), and their feeding can cause plankton communities to shift to smaller sizes, indicating that competition could still occur in a natural ecosystem. An established silver carp population would contain individuals across a variety of size classes, feeding on a range of particle sizes (Walleser et al., 2014), which could augment the adverse effects of silver carp on mussels. Further work to quantify feeding selectivity in both silver carp and mussels at varying sizes is necessary to understand fully the situations in which silver carp and mussels may overlap in diet. Moreover, although the potential for stress was minimized as much as possible in this study, being housed in a tank may have reduced silver carp growth, perhaps reducing their competitive effect.

Although the lack of silver carp growth and reduced fatmucket growth in the presence of silver carp suggest limited food resources during the experiment, the amounts of suspended particles (an estimate of available food) were similar among treatments and time points. Suspended particle availability may have been affected by silver carp and fatmucket egestion, or fatmucket movement may have disturbed settled particles. Suspended particles were introduced into the tanks via egestion. However, they may not have provided an adequate food source for the fatmucket because of mussel feeding selectivity (Mueller et al., 2004; Stuart, Eversole, & Brune, 2001), or they may have contained lower nutrient content. Although recent experimental evidence indicates that *Hypophthalmichthys* spp. may supplement benthic nutrients (Collins & Wahl, 2017; Yallaly et al., 2015), which may have positive impacts on mussels, further analysis of the size and nutritional quality of egested particles from silver carp may elucidate the impact of silver carp egestion on food availability for mussels.

Increased horizontal movement of fatmucket individuals in the presence of silver carp further suggests competitive interactions between the species. Energy used to complete horizontal movements may also have contributed to the reduced growth observed in fatmucket in the fatmucket + silver carp treatment. Horizontal movement in mussels is often linked to feeding behaviour, including pedal sweeping to draw food particles into the pedal gape and locomotion to locate high-quality food resources (Yeager, Cherry, & Neves, 1994). Such movements may be important in feeding, as mussels may rely more heavily on pedal feeding than suspended particle feeding during certain conditions and specific life stages (Raikow & Hamilton, 2001; Vaughn & Hakenkamp, 2001). Declines in food resources caused by silver carp feeding may have necessitated increased mussel movement as individuals searched for limited food particles. Alternatively, the increased movements observed in fatmucket may have been due to stress (Balfour & Smock, 1995; Schwalb & Pusch, 2007) resulting from lack of food or some unquantified response to silver carp presence. Although the silver carp were not able to interact physically with the fatmucket, it is possible that chemical cues or changes in nutrient levels from silver carp excretion may have induced fatmucket movements similar to other chemical cues (Balfour & Smock, 1995; Schwalb & Pusch, 2007). Further research is needed to determine whether the increased movement of fatmucket in the fatmucket + silver carp treatment was a feeding behaviour or a response to a biological or chemical stressor.

Water chemistry may have affected the results of this study. Calcium concentrations, as hardness, were maintained, but alkalinity (i.e. buffering capacity) remained relatively low among all treatments. In recirculating aquaculture systems, alkalinities >40 mg $CaCO_3$ L^{-1} often yield higher animal production and concentrations should not go below 20 mg $CaCO_3$ L^{-1} in production ponds (Boyd, Tucker, & Somridhivej, 2016). Even though the alkalinity declined over the 30 day experiment, this was unlikely to be a confounding factor as alkalinity was similar among all treatments, and growth of all animals in the controls was observed under these observed alkalinities. One potential issue that may arise when alkalinity is low is that nitrification efficiency may be reduced, leading to high ammonia or nitrite levels; however, the overall ammonia, nitrate and nitrite concentrations in this experiment were similar to, or lower than, those observed in other studies (Mueller et al., 2004) and did not reach concentrations that are toxic to mussels (Augspurger, Keller, Black, Cope, & Dwyer, 2003). Nitrate increased throughout the experiment among all treatments confirming that nitrification was occurring in the biofilters.

Higher nitrogen concentrations were observed in the presence of silver carp, suggesting that this species increases nitrogen availability in the water column via excretion. Nitrogen availability may stimulate primary production and increase phytoplankton density (Sterner, 1990), thereby contributing food resources to planktivores. In a natural system, such as the Illinois River or the Great Lakes, this could reduce food limitation and, potentially, competition between silver carp and mussels. Alternatively, increased primary production in response to higher available nitrogen concentrations (Sterner, 1990) may further stimulate high densities of herbivorous silver carp, to the potential detriment of native taxa such as mussels. Further research may aid in illustrating how increased nitrogen availability may affect silver carp densities and competition between native mussels and invasive silver carp.

Although mussels provide many ecosystem services in freshwater systems (Vaughn, 2017; Vaughn et al., 2008; Vaughn & Hakenkamp, 2001), mussel populations are continually threatened by numerous stressors, including the spread of invasive competitors (Salonen et al., 2016). The present and predicted (Kolar et al., 2007) distributions of silver carp strongly overlap with the present distributions of fatmucket (Gangloff & Gustafson, 2000; Hoke, 2005). Given that the Mississippi River basin also contains the greatest global diversity of endemic mussels (Ricciardi et al., 1998), there is great potential for silver carp to compete with fatmuckets and other mussel species. Expansion of silver carp beyond their native range may yield both positive and negative effects on populations of native species (Zhang et al., 2016). Food-web models suggest that silver carp may compete with invasive dreissenid mussels (Zhang et al., 2016), which at present threaten Great Lakes biodiversity (MacIsaac, 1996; Strayer et al., 1999). Dreissenids already compete with native mussels (Baker & Levinton, 2003), and competition with silver carp may add additional stress. Such competitive interactions may also lead to changes in available planktonic resources for native mussels and other native planktivores which also compete with mussels. Moreover, competition between invasive carp species and mussels may limit conservation efforts on mussels. Invasive carp may displace native species that serve as hosts for mussel larvae (Salonen et al., 2016), thereby affecting reproduction. In addition, if silver carp populations continue to expand, this may limit the success of mussel relocation efforts by reducing food resources for the newly placed mussels (Patterson et al., 2018). Silver carp have the potential to alter aquatic food webs profoundly (i.e., Zhang et al., 2016), so it is imperative to understand how their presence affects mussels and other native taxa.

ACKNOWLEDGEMENTS

The authors thank Nathan Eckert at the Genoa National Fish Hatchery for providing the fatmucket used in this experiment and A. Coursey of Southern Illinois University–Carbondale for assistance in setting up tanks and replicates. We also thank the Center for Fisheries, Aquaculture, and Aquatic Sciences,Southern Illinois University Carbondale for providing the facilities to conduct this experiment. Funding for this study was provided by the Center for Fisheries, Aquaculture, and Aquatic Sciences,Southern Illinois University Carbondale and the US Geological Survey Fisheries Program. A. Lubejko, A. Porreca and D. Coulter helped with animal care. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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How to cite this article: Tristano EP, Coulter AA, Newton TJ, Garvey JE. Invasive silver carp may compete with unionid mussels for algae: first experimental evidence. *Aquatic Conserv: Mar Freshw Ecosyst*. 2019;29:1749–1757. https://doi.org/10.1002/aqc.3185