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Research Article

The distribution and ecological role of *Corbicula fluminea* (Müller, 1774) in a large and shallow reservoir

Chase H. Patrick[1,*], Matthew N. Waters[1+] and Stephen W. Golladay[2]
[1]*Valdosta State University, 1500 N. Patterson St., Valdosta, GA 31698, USA*
[2]*Joseph W. Jones Ecological Research Center, 3988 Jones Center Dr., Newton, GA 39870, USA*
[+]*Current address: Auburn University, 201 Funchess Hall, Auburn, AL 36849, USA*

**Corresponding author*
E-mail: chpatrick@valdosta.edu

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Abstract

Invasive species can change ecosystem services, cause loss of biodiversity, alter biogeochemical processes, and significantly affect global economics. *Corbicula fluminea* is an invasive bivalve found globally in lotic and lentic systems. This study aimed to examine the distribution, density, and potential ecological effects of *C. fluminea* in Lake Seminole, a large shallow, polymictic reservoir in the S.E. USA by investigating: 1) the density and distribution of *C. fluminea*; 2) abiotic factors determining abundance; and 3) heavy metals and nutrients accumulating within whole body tissue. This study calculated *C. fluminea* abundance at 55 ± 29 (mean ± SD) per m^2, leading to a reservoir-wide estimate of ~4.3 billion. Multivariate analysis showed water depth as the leading factor determining *C. fluminea* occurrence. *Corbicula fluminea* siphon large volumes of Lake Seminole potentially playing a role in benthic/pelagic biochemical coupling. Compared to surrounding sediments, *C. fluminea* whole body tissue had significantly greater concentrations of Zinc, Copper, and Phosphorus. Results show that *C. fluminea* can thrive in large, shallow reservoirs as well as provide linkages between pelagic and benthic environments.

Key words: invasive bivalves, heavy metals, nutrients, distribution density, biochemical coupling

Introduction

With escalating global trade and changing climate, effects of invasive species on aquatic ecosystems are ever more relevant (Ibanez et al. 2014; Lopez et al. 2006). Invasive species can change aquatic ecosystem services, cause loss of biodiversity, alter biogeochemical processes, and have significant impacts on global economies (McDermott et al. 2013; Warziniack et al. 2013; Basen et al. 2012). Specifically, invasive filter-feeding species (e.g., bivalves) affect aquatic ecosystems by transferring carbon to benthic sediments (Pigneur et al. 2014), and reducing primary productivity (Lopez et al. 2006). One invasive species affecting fresh water ecosystems is the Asian clam, *Corbicula fluminea* (Müller, 1774) (Atkinson et al. 2010). With wide habitat tolerance (Vohmann et al. 2010), *C. fluminea* inhabit environments across North America and around the globe (Gatlin et al. 2013).

Introduced to North America in the early 20th century from southeastern Asia, *C. fluminea* is found in diverse lotic and lentic ecosystems (Basen et al. 2012). *Corbicula fluminea* currently inhabits 41 of the lower 48 continental United States, Hawaii, and the District of Columbia (Foster et al. 2014) as well as parts of Mexico (Karatayev et al. 2003) and Canada (Simard et al. 2012). Dresler and Cory (1980) report that the spread of *C. fluminea* throughout the U.S. has caused major ecosystem disturbances and generated significant economic costs, including hydro-electrical generator failure due to water intake blockage (Williams and McMahon 1986). Lovell and Stone (2005) reported that since 1980, *C. fluminea* cost an estimated $1 billion in total damages each year.

Environmental warming and habitat alterations (i.e., river dredging or water level reduction) favor rapidly reproducing bivalves like *C. fluminea* (Weitere et al. 2009; McMahon 1999). High filtration and assimilation rates enable *C. fluminea* to grow rapidly, allowing for greater reproductive potential than native freshwater bivalves (McMahon 2002). With fewer individuals than native bivalves, *C. fluminea*'s highly fecundate hermaphroditism permit rapid dispersion in new habitats (McMahon and Bogan 2001). *Corbicula fluminea* also have the ability to extract resources from the water column (filter-feeding) and/or feed on organic material within sediments (pedal-feeding) (Hakenkamp et al. 2001). This enables *Corbicula* to achieve great densities, often calculated in the thousands per square meter (Franco et al. 2012; Hubenov et al. 2013; Modesto et al. 2013).

Large populations of *C. fluminea* may also contribute to biogeochemical changes in lakes and reservoirs. Majdi et al. (2014) note that through pedal feeding, *C. fluminea* rework benthic sediments. This reworking, or bioturbation, may resuspend sediments and contribute to internal loading and eutrophication in shallow aquatic environments (Scheffer 2004). Conversely, *C. fluminea* have been shown to reduce chlorophyll *a* concentrations in a shallow Florida lake (Beaver et al. 1991). *Corbicula fluminea* have also been shown to reduce seston concentrations in streams (Leff et al. 1990). Invasive species like *C. fluminea* may provide an important transfer route of nutrients and energy between pelagic and benthic habitats (Sousa et al. 2014). Given *C. fluminea*'s global distribution and economic liability, studies are needed to better understand its role in pelagic/benthic coupling (Sousa et al. 2008). Few studies have focused on *Corbicula* within reservoirs (Neptae and Phalaraksh 2009; Bagatini et al. 2007; Karatayev et al. 2003), with even fewer studies focusing on reservoirs containing *C. fluminea* in the subtropical SE USA (Abbott 1979; Bates 1962).

This study aimed to examine the distribution, density, and potential effects of *C. fluminea* within Lake Seminole, a large and shallow reservoir in the S.E. USA. Our objectives were to: 1) determine the density and distribution of *C. fluminea* in Lake Seminole; 2) examine how abiotic factors (such as: water depth, sediment type, organic matter, nutrients, and heavy metals) influence the distribution of *C. fluminea* within Lake Seminole; and 3) determine whether metals and/or nutrients were accumulating in *C. fluminea* whole body tissue creating the potential for transfer across trophic levels.

Methods

Study site

The Apalachicola-Chattahoochee-Flint (ACF) River Basin (Figure 1) drains an area of 51,800 km^2 (Frick et al. 1996) including the northern and western parts of Georgia, the eastern border of Alabama, and a portion of the Floridian panhandle (Peterson et al. 2013). A subset of the ACF, the Chattahoochee and Flint Rivers collectively drain 44,625 km^2 (Sammons and Maceina 2005; Dalton et al. 2004) but have differing land uses and degree of regulation. The Chattahoochee River has a large urban (Atlanta and Columbus, GA) and industrial influence, whereas the Flint River is more rural and agricultural, particularly in the lower reaches (Frick et al. 1996). The Chattahoochee River is highly regulated with 13 dams, while the Flint River contains only two run-of-the-river reservoirs. The two rivers meet at the Jim Woodruff Lock and Dam forming Lake Seminole (Dalton et al. 2004). Lake Seminole is a large (152 km^2), shallow (mean depth = 3 m, max depth = 10 m) reservoir used for hydroelectric power production, recreation, and navigation. The reservoir was divided into three different sampling zones indicating areas of potential drainage influence: Flint-Spring Creek and Chattahoochee zones, and dam pool (Figure 1).

Field collection

Benthic sampling was conducted from spring 2012 to spring 2014 with 33 sampling sites covering all tributaries into the reservoir (Figure 1). *Corbicula fluminea* and sediment samples was collected using a PONAR sampler (sample area = 0.0768 m^2). At each collection site, three sediment grabs were sieved using a standard 2.00 mm sieve and converted to the average number of clams per square meter using the sampling area of the PONAR. Sieved sediments were subsampled from the first PONAR sample and stored in plastic whorl bags on ice. We measured shell length using a handheld caliper, recording the distance between the posterior and anterior edges of the shell (Dresler and Cory 1980).

Laboratory analysis

Following a method of original design, frozen tissue and sediment samples were dried in a Labconco Freeze Drier at −52 °C for 2 hours. Once dried, *C. fluminea* shells were opened and the entire soft tissue was ground to a homogenous consistency and stored at −25 °C.

Sediment samples were ground to an even consistency using a mortar and pestle, transferred to glass scintillation vials, and stored at −25 °C. To measure sediment particle composition, 40 g of sediment from each sample site was mixed with 100 ml of Na metaphosphate solution following the methods

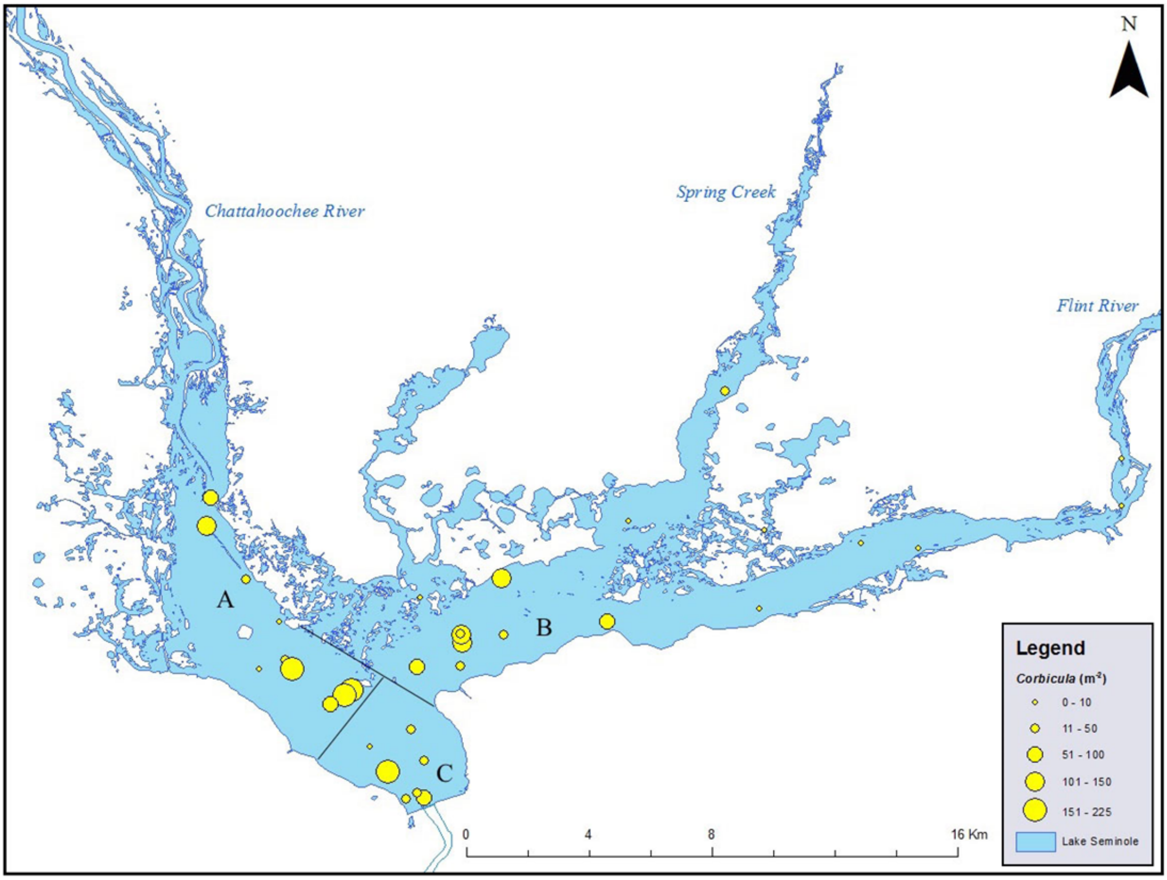

Figure 1. 2012–2014 sampling sites in Lake Seminole and tributaries. Chattahoochee and Flint/Spring Zones are denoted by the letters “A” and “B”, respectively. The dam pool zone is signified by the letter “C”. All circles indicate sampling sites and population estimates. Black lines indicate borders between described zones.

of Bouyocos (1962). The Na metaphosphate solution was 50 g of Na metaphosphate in 1000 ml of deionized (DI) water. The sediment mixture was stirred for approximately 3 minutes and allowed to settle for 24 hours at room temperature. The supernatant was then poured into a 1000 ml graduated glass cylinder and DI water added until the volume equaled 1000 ml (Gee and Bauder 1986). The solution was mixed until all sediment was suspended. Forty seconds after mixing, the first hydrometer reading was recorded. A second hydrometer reading was taken approximately 2.5 hours after the first reading. The second hydrometer reading time was chosen according to the 21 °C room temperature and its effects on the viscosity of water. A third hydrometer placed in 1000 ml of DI water was used to calibrate the hydrometer reading before measuring each sediment sample. Percentages of clay, silt, and sand were calculated for each benthic sampling site (Gee and Bauder 1986).

Organic matter content of sediment was analyzed using mass loss of ignition (LOI) by combusting samples at 550 °C in a muffle furnace for 4 hours (Hakanson and Jansson 1983). Nutrients and metals in *C. fluminea* tissue and benthic sediment were analyzed by Waters Agricultural Laboratory in Camilla, GA, USA (www.watersag.com) using an iCAP 6000 ICP analyzer following an acid digestion using standard EPA methods (Waters et al. 2009).

Estimation of C. fluminea *population and filtration*

At each site, three sediment samples were collected. Next, the number of *C. fluminea* in each of the three PONAR samples was averaged. All sampling sites were then averaged to estimate how many *C. fluminea* could likely be found at any given site. In order to obtain the average amount of *C. fluminea* per m^2, the average number of *C. fluminea* was divided by the PONAR area. Benthic sediment sampling within *Hydrilla verticillata* beds was compromised by vegetation preventing complete closure of the PONAR sampler. In 2013, the coverage by *H. verticillata* in Lake Seminole was 48% of the reservoir's surface area (Shivers 2016). Uncertainty with *C. fluminea* collection within *H. verticillata* beds led to the exclusion of these areas when estimating Lake Seminole's *C. fluminea* population. Therefore, the number per m^2 was multiplied by 78.5 million m^2 (52% of the total surface area or the area not covered by *H. verticillata*, Bayne et al. 1974) providing a conservative estimation of the population of *C. fluminea* in Lake Seminole at the time of sampling.

The population estimate was then used to examine the potential impact of *C. fluminea* water filtering. We used filtration rates stated in Viergutz et al. (2012) because of similar shell size, ambient water temperature, and multiple sampling seasons to this study.

Baseline nutrients and metals within Corbicula *tissue*

Corbicula fluminea used in baseline metal and nutrient tissue analysis were transported in reservoir water to the laboratory within 48 hours and kept in clean fish tanks for 14 days to measure baseline metals within whole body tissue. Dechlorinated tap water was replaced every two days (Atkinson et al. 2010) and clams were given half a frozen herpetological food cube containing plant material every three days. After two weeks, *C. fluminea* were frozen at −25 °C for 24 hours then freeze-dried. Once dry, all body tissue was ground to an even consistency. Samples were transferred to individual glass scintillation vials. Nutrients and metals within whole body tissue were measured using the same methods as sediment nutrient/metal analysis.

Analysis

Statistical analysis and graphical representation of the data including Principal Component Analysis (PCA) (live *Corbicula*; sediment Calcium; sediment Phosphorus; percent organic matter; water depth; sediment sand, clay, and silt; and heavy metals) was conducted using JMP version 8.0.2 (SAS Institute Inc.). The orientation of eigenvectors of the abiotic factors for principle components 1 and 2 were compared to live *C. fluminea*'s orientation to better understand any influence on population dispersal in the reservoir. Microsoft Excel version 14.4.5 (Microsoft Corporation) was used to produce One-way ANOVA and Tukey HSD test with *C. fluminea* whole body tissue and benthic sediment being the dependent variables and nutrients/metals (phosphorus, potassium, magnesium, calcium, sulfur, boron, zinc, manganese, iron, copper, sodium, molybdenum, chromium, lead, cadmium, cobalt, nickel, aluminum) being the independent variables; p values less than 0.05 were considered significant. Significant results were assessed using Tukey's HSD to understand where greater levels of nutrients/metals were concentrating.

Results

C. fluminea *density, population, and filtration*

Corbicula fluminea abundance in Lake Seminole was 55 ± 29 (mean ± SD) individuals per m^2. Shell size averaged 20 ± 5 mm indicating an estimated age of 2–3 years old (Ciutti and Cappelletti 2009; Williams and McMahon 1986). Thus, an estimated 4.3 ± 2.3 billion adult *C. fluminea* were present in macrophyte-free areas of Lake Seminole.

Using the filtration rates reported by Viergutz et al. (2012), we estimate that 4.3 billion *C. fluminea* could filter the equivalent volume of Lake Seminole over 6 to 181 days, depending on high or low water temperatures, respectively. Low water temperature refers to ~2 °C, while high temperature refers to ~20 °C.

Influential benthic parameters

In the PCA of reservoir parameters (live *Corbicula*, sand silt and clay %, depth, sediment Ca, sediment P, heavy metals, and organic matter %), principal component 1 accounted for 58.3%, while PC 2 accounted for 17.7% of the variability. The PCA indicated that depth is the primary factor determining *C. fluminea* occurrence (Figure 2), with *C. fluminea* more likely to be found in shallow waters. Other parameters such as Ca, P, organic matter %, and heavy metals are likely secondary influences on *C. fluminea* occurrence. Substrate (sand, silt, and clay percentage) does not appear to be a major determinant of bivalve occurrence.

Metals and nutrients within Corbicula *tissue*

Metal/nutrient concentrations in reservoir sediments compared to *C. fluminea* whole body tissue directly from Lake Seminole, and whole body tissue flushed with dechlorinated water, showed that Zinc and Copper were significantly greater in whole body tissue than in reservoir sediments (One-way ANOVA, followed by Tukey's HSD, for each metal, Figure 3a, p = 0.0001). There was no significant difference in metal/ nutrient concentrations between *C. fluminea* whole body tissue directly from Lake Seminole and whole body tissue flushed with dechlorinated water.

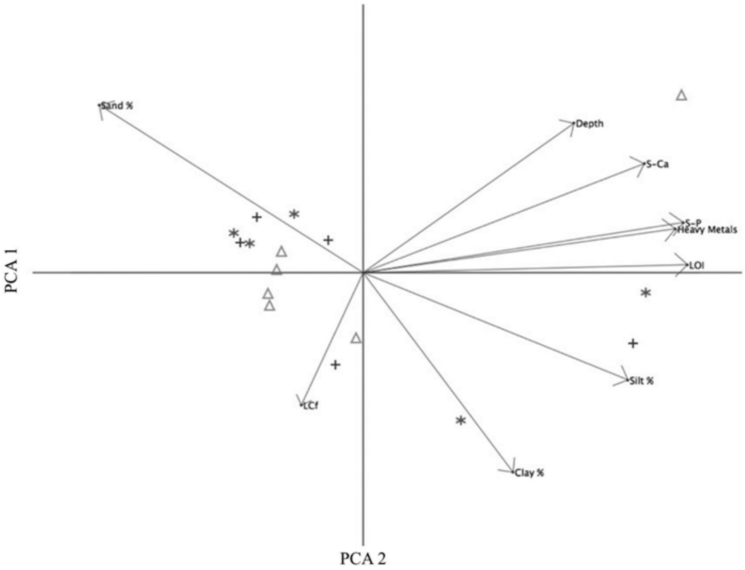

Figure 2. Principal Component Analysis of Lake Seminole parameters and number of *Corbicula fluminea*. LCf represents live *Corbicula*. S-Ca represents calcium in sediment. S-P represents phosphorus in sediment. LOI indicates loss on ignition (% organic matter). Asterisks represent sites in the Flint River basin of influence. Triangles represent sites within the Dam pool. Plus signs represent sites in the Chattahoochee River basin of influence. PCA 1 = 58.3% and PCA 2 = 17.7%.

Phosphorus was significantly greater within whole body tissue than in benthic sediments (Figure 3b, $p < 0.0001$). No significant difference ($p > 0.05$) in concentrations of P was observed between the two *C. fluminea* tissue treatments.

Discussion

Invasive species threaten freshwater ecosystems and are a costly challenge for natural resource managers (Sousa et al. 2006; Wittmann et al. 2012). *Corbicula fluminea* populations are known to vary widely (Prokopovich 1969; Sousa et al. 2006), and few studies have recorded densities within reservoirs (Abbott 1979; Karatayev et al. 2003; Taylor 1973). The wide distributions observed in Lake Seminole may be due to *C. fluminea*'s high reproductive potential and wide physiological tolerances (McMahon and Bogan 2001) thus allowing *C. fluminea* to populate many areas of the reservoir and possibly be a major component within the ecosystem.

Lake Seminole has many abiotic factors capable of supporting large numbers of *C. fluminea*. The polymictic reservoir permits *C. fluminea* populations to thrive in shallow areas (~3 m), as well as deeper (~10 m) portions of the reservoir. Very few periods where water temperatures are below *C. fluminea*'s tolerance level of 0–2 °C have occurred since the formation of the reservoir in 1952 (Janech and Hunter 1995). The short cold season may allow extended reproductive periods, which increases the chances of survival for juveniles (Weitere et al. 2009); while stable inflows from agricultural and urban drainage basins likely provide a steady source of food and nutrients aiding *C. fluminea* survival. Waters et al. (2015) found substantial nutrients in the reservoir's sediments. This large pool of benthic nutrients, coupled with readily available detritus from substantial beds of *H. verticillata*, likely afford *C. fluminea* an abundant and reliable food source for growth and reproduction.

The PCA of abiotic factors indicated depth most likely influences *C. fluminea* distribution within the reservoir. This may be due to lower levels of dissolved oxygen in deeper (6–10 m) regions of Lake Seminole. *Corbicula* have been shown to poorly regulate oxygen consumption with decreasing O_2 levels (McMahon 1979). Shallower areas of Lake Seminole that also exhibit low benthic DO levels are in *H. verticillata* beds (Shivers 2016). A study on a Texas' reservoir by Karatayev et al. (2003 and references therein) found no *C. fluminea* within *H. verticillata* beds during multiple population surveys, supporting our decision to exclude areas of *H. verticillata* when we estimated *C. fluminea* density. Very fine flocculent sediment is also found within these macrophyte beds (CH Patrick, pers. obs.), a sediment type not supportive of *Corbicula* (Sickel 1986). Deeper areas of Lake Seminole were found to have more silt in benthic sediments than shallow areas exhibiting sandier substrates. Additionally, Karatayev et al. (2003) found higher densities of *C. fluminea* in

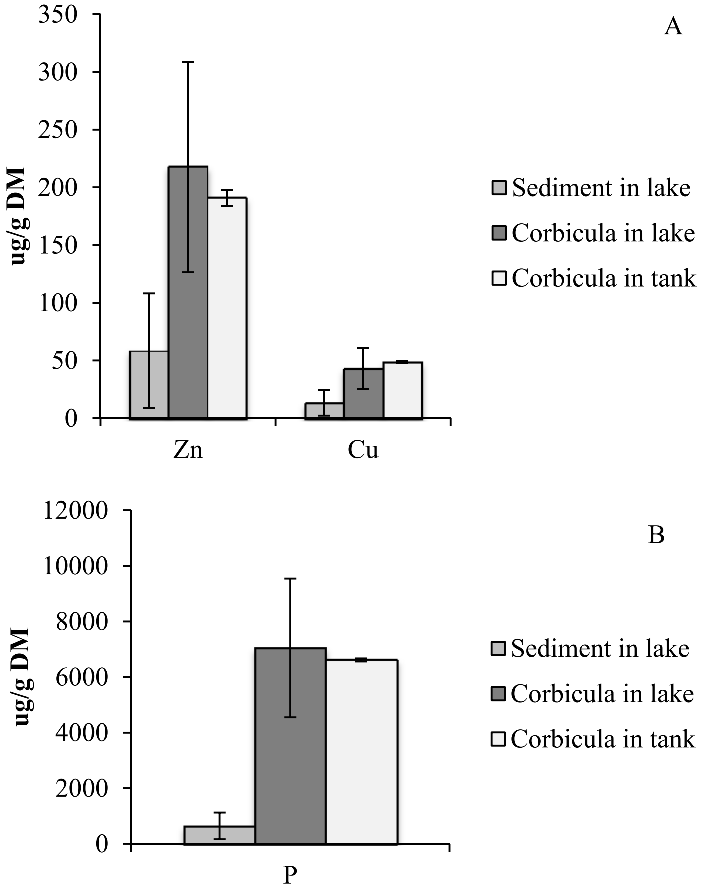

Figure 3. Metal and nutrient content of *C. fluminea* whole body tissue:
A) trace metal concentrations of Cu and Zn in whole body tissue and sediment samples directly from Lake Seminole and flushed with dechlorinated tap water ($p<0.05$);
B) Phosphorous concentration in reservoir sediment, *C. fluminea* directly from the reservoir, and *C. fluminea* flushed with dechlorinated tap water ($p<0.05$) (ug/g DM).

shallow (1–2 m) areas of Lake Nacogdoches. They also noted that *C. fluminea* occurred in the highest densities among courser (i.e., containing more sand) substrates, a benthic trait of shallow areas of Lake Seminole. While this study did not find substrate type to be a main driver of *C. fluminea* in the reservoir, other studies (Schmidlin and Baur 2007) have found substrate type to be important suggesting it to be a potential driver of reservoir populations.

Nutrients and trace metals within whole body tissues

Benthic sediment is an important sink for aquatic pollutants (Stoica et al. 2014). Waters et al. (2015) reported substantial amounts of P within the Flint arm sediments of Lake Seminole. Whole body tissue analysis shows *C. fluminea* are concentrating significantly larger amounts of P than surrounding sediments. Given that *C. fluminea* filter particulate material, their collective filtering efforts may be acting as a pathway for P and other elements moving from a pelagic to a benthic environment. These materials would be either added to the sediments or bioaccumulated into biomass. This potential pathway could be a factor in Lake Seminole's extremely clear water, when such large amounts of nutrients are found in benthic sediments. In addition, previous monitoring efforts in Lake Seminole did not show periods of high phytoplankton productivity (McIntire 2006).

Although essential to normal physiological functions, increased exposure to trace metals such as Cu and Zn can cause acute and chronic toxic effects reducing growth, fecundity, and increasing mortality in freshwater bivalves (Shoults-Wilson et al. 2009). *Corbicula fluminea* have the ability to accumulate and eliminate trace metals through waste (Cory and Dresler 1981). Abaychi and Mustafa (1988) noted that metal concentrations in *C. fluminea* tissue correlate more strongly with concentrated sediment signals rather than diluted concentrations in overlying water. Our findings of Zn and Cu concentrations within *C. fluminea* whole body tissue are comparable to Zn and Cu levels found in *Dreissena polymorpha*

(Pallas, 1771) (Voets et al. 2009) and of populations of *C. fluminea* in neighboring drainage basins (Shoults-Wilson et al. 2009). In static and artificial stream bioassays, *C. fluminea* are capable of resisting exposure to heavy metals such as Cu and Zn (Cairns and Cherry 1983). This tolerance of heavy metal exposure suggests that *C. fluminea* could be important in nutrient cycling, especially in large shallow reservoirs with large amounts of nutrients and metals in benthic sediments. Sousa et al. (2014) and Atkinson et al. (2010) have shown *C. fluminea* influence nutrient cycling within freshwater systems, though influence is dependent on multiple factors including: size, reproductive stage, temperature, and food availability (Vaughn and Hakenkamp 2001). *Corbicula fluminea* can also transfer trace element concentrations to higher trophic levels (Peltier et al. 2008) through predation within shallow reservoirs.

Robinson and Wellborn (1988) report that fish consume *C. fluminea* in a Texas reservoir: of the 13 fish species reported, 6 are found in Lake Seminole and 9 occur in the surrounding watershed (Bayne et al. (1974). Other studies have observed *C. fluminea* predation in multiple fauna including ducks, raccoons, flatworms, and crayfish (Covich et al. 1981; Sickel 1986), all of which are found in and around Lake Seminole. This predation from various sources could biomagnify heavy metals in both aquatic and terrestrial fauna around the reservoir. Given their high filtration rates (McMahon 2002), *C. fluminea*'s role in shallow reservoirs could be very important not only to aquatic ecosystems but terrestrial ecosystems as well.

Filtration and a potential role in reservoirs

Previous research indicates *C. fluminea* filtration rates vary according to numerous factors including: temperature, dissolved metals, food availability, phytoplankton abundance, reproductive cycles, and turbidity (Way et al. 1988; Pigneur et al. 2014). McMahon (2002) established that *C. fluminea* have some of the highest filtration and assimilation rates among freshwater bivalves. We demonstrated that *C. fluminea* within Lake Seminole potentially filter a large volume of water. This large filtration volume coupled with Lake Seminole's shallow water suggests that *C. fluminea* could filter a significant portion of the water column, although clearance rates can vary intra- and inter-annually (Viergutz et al. 2012). As a result, *C. fluminea* possibly contribute to sustaining water column clarity, and serve as a "bio-filter", increasing the quality of water released to downstream aquatic ecosystems. How large an impact *C. fluminea* have on water quality likely varies from year to year and should be a focus of future studies. A large population of *C. fluminea* in a hypereutrophic Florida lake reduced chlorophyll *a* concentrations over 7 days (Beaver et al. 1991). Additionally, *C. fluminea* reduce seston concentrations in streams (Leff et al. 1990). The potential high densities of *C. fluminea* in aquatic ecosystems likely serve as an important mechanism for the transfer of materials from the water column to sediments. Given that *C. fluminea* are unlikely to be eradicated from Lake Seminole, efforts should be made to accept these invasive bivalves as a component of the reservoir. Monitoring, legislation, and public awareness are often the most cost-effective management strategies for invasive bivalves (Sousa et al. 2014). *Corbicula fluminea* can be and has been used as a biomonitor in different aquatic ecosystems, including the Minho estuary (Reis et al. 2014). Peltier et al. (2008) used *C. fluminea* to investigate contributions of trace elements from different point sources and land uses. In the nearby Altamaha River system, Shoults-Wilson et al. (2009, 2010) demonstrate that *C. fluminea* can be good biomonitors indicating potential sources of trace elements into aquatic systems and used to approximate trace element levels in co-occurring native mussel species. Interestingly, *C. fluminea* is not only a good biomonitor for nutrients and metals, but also for asbestos (Belanger et al. 1986, 1987). The current worldwide production of asbestos is 2,000,000 tons with the top three producing countries being Russia, China, and Brazil (Marsili et al. 2016). All three countries contain populations of *Corbicula* which therefore could be used to biomonitor reservoir quality, especially reservoirs used to hold drinking water.

Conclusion

This study quantifies the *C. fluminea* population within a shallow reservoir at approximately 4 billion individuals. *Corbicula fluminea* potentially filter a large volume of water suggesting an important role in benthic/pelagic biogeochemical coupling. We show that depth appears to be the main driver of *C. fluminea* occurrence in the reservoir, while substrate type is not influential. *Corbicula fluminea* was shown to have significantly greater levels of Zn and Cu within its body tissue when compared to surrounding sediments. Additionally, P was measured at significantly greater levels within tissue, when compared to surrounding benthic sediment. These findings suggest a possible transport route for nutrients and metals from pelagic to benthic environments in shallow reservoirs. *Corbicula fluminea* can also be used as a biomonitor for pollutants such as heavy metals and carcinogens. While measures should be taken to slow invasion into new ecosystems, *C. fluminea* can be a useful monitoring tool in reservoirs worldwide. With increasing global trade and temperatures expected, *C. fluminea* could continue to increase as a substantial presence in aquatic environments. Our study shows a potential role for *C. fluminea* suggesting a need for further study of its distribution and ecological role.

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