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Stable isotopic signatures, tissue stoichiometry, and nutrient cycling (C and N) of native and invasive freshwater bivalves

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Abstract. Filter-feeding mussels historically comprised most of benthic biomass in many streams. They contribute to stream ecosystem functioning by linking the water column and benthic habitats. Both native and nonnative species coexist in many streams, but their ecological roles are not well quantified. The invasive bivalve, *Corbicula fluminea*, has the potential to alter profoundly organic matter dynamics and nutrient cycling in streams. We compared stable isotope ratios and tissue and biodeposit stoichiometry of the native freshwater mussel, *Elliptio crassidens*, and *C. fluminea* in a Coastal Plain stream (Ichawaynochaway Creek, a tributary to the lower Flint River, Georgia, USA) to assess their trophic niche space and potential effects on nutrient cycling. We hypothesized that *C. fluminea* would assimilate a larger range of materials than *E. crassidens*. To determine dietary overlap of *C. fluminea* and *E. crassidens*, we measured the elemental and stable isotopic compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of their tissue. *Corbicula fluminea* showed lower trophic fidelity than *E. crassidens* and was able to acquire and assimilate a wide range of resources, as illustrated by their wide range of $\delta^{13}\text{C}$ values. *Corbicula fluminea* also might alter nutrient cycling in the benthic environment of streams because they retain less N than *E. crassidens*, as reflected by their higher tissue C:N. In the laboratory, we measured C and N in biodeposits (feces and pseudofeces) from the 2 species. *Corbicula fluminea* released more N through their biodeposits relative to *E. crassidens* by mass, a result implying that *C. fluminea* might modify nutrient cycling in streams. Our results show important differences in the food resources assimilated and the nutrients deposited as feces and pseudofeces by these 2 bivalves. Furthermore, our results demonstrate how invasive species, such as *C. fluminea*, can alter aquatic environments through differences in species traits within a functional group.

Key words: trophic niche space, trophic fidelity, stable isotope, functional role, unionid, *Corbicula fluminea*, *Elliptio crassidens*, nutrient cycling.

Native and invasive species can have similar functional roles but potentially process materials differently. If an introduced species can alter ecosystem-level processes, such as productivity or nutrient cycling, then they potentially can change the functioning of whole ecosystems (Vitousek 1990, Taylor et al. 2006, Gonzalez et al. 2008). Bivalves are ideal models for exploring potential impacts of species replacements on ecosystem characteristics because they can

be abundant and filter large quantities of water (Strayer et al. 1999). Filter-feeding by freshwater mussels is important in aquatic ecosystems because it transfers organic materials and nutrients from the water column to the surrounding benthic area and stimulates primary and secondary production (Howard and Cuffey 2006, Spooner and Vaughn 2006, Vaughn et al. 2007). *Corbicula fluminea*, the invasive Asian clam, is similar to native unionid mussels in that it is a filter-feeding consumer that depends heavily upon microbes, algae, and detrital material available in the water column and benthic environment.

Historically, freshwater mussels were the dominant invertebrates, in terms of biomass, in many eastern North American streams (Parmalee and Bogan 1998, Williams et al. 2008). Landuse changes, hydrologic alterations, invasive species, and declines in native

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fish species have caused declines in native mussel abundance and diversity in North America. In contrast, *C. fluminea* is widespread in many river basins across the US and is one of the most important invasive species in aquatic ecosystems (Sousa et al. 2008). Thus, unionid numbers have decreased, and *C. fluminea* has become a dominant filtering bivalve in many streams and rivers. However, the rates of ecological processes performed by mussels often scale linearly with biomass (Vaughn et al. 2004), and *C. fluminea* is typically smaller than native unionids. Furthermore, unionids and *C. fluminea* are likely to differ in filtering efficiency because of differences in cilia and other feeding structures (Leff et al. 1990, Way et al. 1990, Silverman et al. 1995). Thus, the change in bivalve species dominance could lead to changes in the structure and function of a stream ecosystem despite similar functional roles of native unionid mussels and *C. fluminea*. Therefore, understanding the role that both native and invasive species play in terms of foodweb structure and nutrient cycling is essential for predicting how streams might be altered if native mussel species continue to decline and invasive species continue to spread and increase. However, few studies have addressed how changing species dominance might alter availability of resources.

Bivalves have the potential to affect nutrient cycling and foodweb dynamics greatly through uptake and selective assimilation of C and N from particulate matter during filtration (reviewed in Vaughn et al. 2008). However, few studies have addressed the potential trophic role or trophic niche space that bivalve species occupy. Unionid mussels and non-native *C. fluminea* are in the same functional feeding group (filter-feeders). Species with generalized diets might have higher probabilities of successful invasion than specialist species because food availability is less likely to be a limiting factor (Moyle and Light 1996). Thus, invasive species might occupy a larger trophic niche space than native species (Moyle and Light 1996). For example, an invasive crayfish species in Sweden occupies a larger niche width than a native crayfish species (Olsson et al. 2009).

Our goal was to understand the trophic niche space filled by 2 species in the same functional group. The specific objectives of our study were to measure and understand the trophic and nutrient cycling roles of the native mussel *Elliptio crassidens* and *C. fluminea*. We used a 2-step statistical method to compare their trophic roles. First, we determined how similar the 2 species were in their use of suspended organic particulates when feeding in the same location and when feeding in different locations in the drainage

network. We use the term trophic fidelity to describe the ability of an organism or group of organisms to adhere to feeding habits through space and time. We assessed trophic fidelity by determining how isotopic signatures (both the central tendency and dispersion of points) varied by species and their positions in the watershed or study site. We hypothesized that invasive *C. fluminea* would be generalists capable of using and assimilating a larger range of food materials than the more specialized *E. crassidens*. Second, we compared the tissue stoichiometry of both species to the stoichiometry of their feces and pseudofeces to assess nutrient uptake and release. In other systems, tissue C:N of native mussels was ~4.6 (Christian et al. 2008), whereas tissue C:N of *C. fluminea* was ~5.8 (Evans-White et al. 2005). Therefore, we hypothesized that in our system, *C. fluminea* would have a higher tissue C:N and would release more N into the stream than *E. crassidens*.

Methods

Study sites

Ichawaynochaway Creek (IC) is a 5th-order, low-gradient tributary to the lower Flint River on the Gulf Coastal Plain of southwest Georgia (Golladay et al. 2000). The stream discharges into the Flint River ~10 km downstream from the confluence of Chickasawhatchee Creek (CC) and IC (Fig. 1). Much of the IC watershed is situated in the Dougherty Plain physiogeographic district, which is characterized by mantled karst physiography (Hyatt and Jacobs 1996). Row-crop agriculture and managed forests are the dominant land uses within the region (50% agriculture, 30% forests) (Golladay and Battle 2001). *Corbicula fluminea* occurs throughout the entire watershed except for the headwaters. *Elliptio crassidens* appears to be associated with the Dougherty Plain region and is found primarily south of the boundary that divides the Fall Line Hills and the Dougherty Plain (Brim-Box and Williams 2000; Fig. 1).

Field collection and sample analysis

Six sampling sites, chosen on the basis of access to the stream and including 2 on CC, were established in the IC watershed (Fig. 1). Five to 10 individuals of each species were collected from each sampling location between June and August 2007. Length (mm) and wet mass (g) including shell were recorded. Foot-muscle tissue samples were collected from sacrificed individuals and dried (45°C) and ground separately for each individual. Total C and total N content and C and N stable isotope signatures were

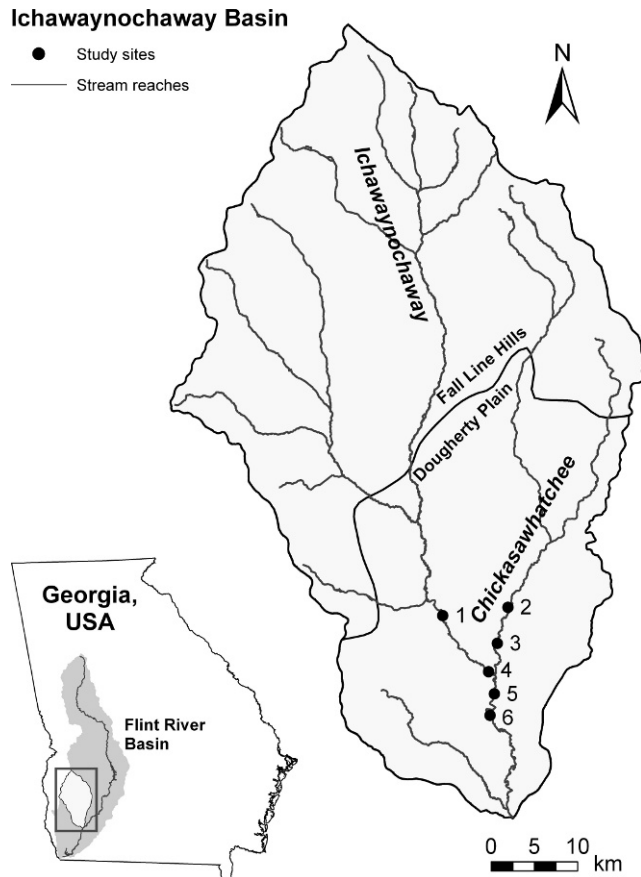


FIG. 1. Map of the Ichawaynochaway Creek watershed in the lower Flint River Basin, sampling sites, and the physiogeographic provinces found within the basin. Sites 1, 4, 5, and 6 were on Ichawaynochaway Creek and sites 2 and 3 were on Chickasawhatchee Creek.

determined for the mussel tissue samples with a Finnigan Delta Plus mass spectrometer (Thermo-Finnigan, Bremen, Germany) in the University of Georgia's Ecology Analytical Laboratory. Isotope ratios were expressed in the delta (δ) format: $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (units of ‰) = $(R_{\text{sample}} - R_{\text{standard}} / R_{\text{standard}}) \times 1000$, where R is the $^{13}\text{C}:^{12}\text{C}$ ratio or $^{15}\text{N}:^{14}\text{N}$ ratio. A bovine protein (peptone) laboratory standard was referenced against an international standard, and precision averaged $\leq 0.1\text{‰}$. The C and N composition was converted to a molar C:N to determine stoichiometric values.

Laboratory

Biodeposition experiments were used to determine the amount and composition of materials excreted as feces and pseudofeces (biodeposits). *Corbicula fluminea* ($n = 12$) and *E. crassidens* ($n = 12$) were collected in July 2008 at site 5. Immediately after collection,

bivalves were taken to the laboratory in a bucket containing stream water. Total wet mass (g) of each individual was measured and converted to tissue wet mass with a regression equation generated from previous data on these species (Atkinson 2008). Individuals were scrubbed and rinsed to remove any attached particles and were placed in separate containers filled with deionized water (which has been shown not to cause mortality to unionids; McCorkle and Dietz 1980, Scheide and Dietz 1982), and held at 25°C (typical summer stream temperature) in an incubator.

The experiment was set up as a completely randomized block design. The main effect was bivalve treatment (*E. crassidens* and *C. fluminea*) with time (0, 1, 2, and 3 h) as a covariate. Each treatment was replicated 4 times ($n = 32$). At the end of the experiment, the water in each container was filtered through separate, precombusted, preweighed glass-fiber filters (GFF; nominal pore size = 0.3 μm , Sterlitech Corp., Kent, Washington) to remove excreted particles. The samples were dried and weighed to the nearest 0.0001 mg to determine the total dry mass (DM) released. The total amount of C and N on the filter was analyzed on a Finnigan Delta Plus mass spectrometer. Mussels were returned to the stream.

Data analyses

Trophic niche space and trophic fidelity.—Multiple response permutation procedures (MRPP), which can be used to compare bivariate data sets, were used to compare the central tendency and dispersion of stable isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) between species across all sites and among sites (Biondini et al. 1985, Zimmerman et al. 1985). The MRPP was analyzed with the FORTRAN program FIDELITY (L. M. Conner, Joseph W. Jones Ecological Research Center). Van Valen's test was used to calculate dispersion (mean distance between bivariate medians; Van Valen 1978) as a way to quantify the size of the trophic niche space occupied by each species. A small dispersion around the central tendency of all isotopic points of a species or a small trophic niche demonstrated that a species had high trophic fidelity across all the sites. The distribution and dispersion of the bivariate isotopic points for each individual site was another measure of trophic fidelity. The smaller the distances for each species between sites on the MRPP plot, the greater the trophic fidelity. This approach allowed us to determine the distribution of both species at each site and to compare the dispersion of these points at each site. Larger differences in dispersion indicated greater within-site dispersion and suggested large

differences between the 2 species at that location. The distribution and dispersion of the bivariate isotopic points for each individual site also was determined. The smaller the distance was for an individual species between the given sites, the greater the trophic fidelity. Bootstrapping (sampling with replacement, 1000 bootstraps) was used to sample for the median values of the isotopic signatures of each species at each site and among sites to determine the distance between the bivariate medians (in ‰) and lower and upper confidence intervals (95% CIs) of this distance. The CIs of the 2 species were compared for each site. Nonoverlapping CIs indicated significant differences between species across sampling sites. In addition, larger values demonstrated greater distances between the medians of the sampling sites. A smaller value indicated greater central tendency and was characteristic of greater trophic fidelity. Comparisons of CIs between pairs of sites for each species also were made. To illustrate the trophic niche spaces of the 2 species, isotopic signatures were plotted in ArcMap (version 9.1; ESRI, Redland, California), and Hawth's Analysis Tools (available from: <http://www.spatial ecology.com/htools>) were used to create minimum convex polygons around points representing each species, and then around points representing each sampling site (as in Layman et al. 2007).

Tissue stoichiometry.—Two-way analyses of variance (ANOVA) were used to determine if tissue %C, %N, and C:N differed between species or among sites. Significant ANOVAs were followed by Tukey's Honestly Significant Difference (HSD) multiple comparisons ($\alpha = 0.05$; Littell et al. 2002). These analyses were followed by Tukey's HSD multiple comparison tests for 1 factor at each level. One-way ANOVAs were used to determine if tissue %C, %N, and C:N differed within species among sampling sites. Paired *t*-tests were used to identify significant differences between the species at each pair of sites.

Biodeposit stoichiometry.—ANCOVA was used to identify differences in the mass, %C, and %N of deposited particles between species over time (time was a covariate). Significant ANOVAs were followed by Tukey's HSD multiple comparisons to determine if significant differences existed between species ($\alpha = 0.05$; Littell et al. 2002). These analyses were followed by Tukey's HSD multiple comparison tests for 1 factor at each level. One-way ANOVAs were used to determine if mass, %C, and %N of excreted particles differed between species within times or within species among times. The composition of biodeposited materials was converted to a biodeposition rate ($\mu\text{mol C or N g}^{-1} \text{ h}^{-1}$) for each species, and biodeposition rates were compared between species

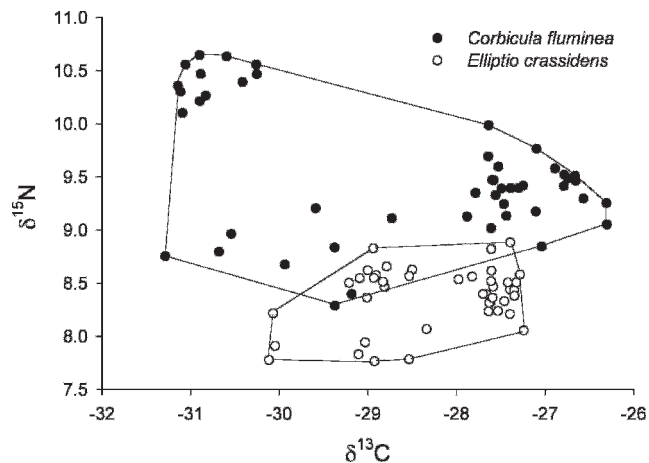


FIG. 2. Tissue stable isotopic signatures of *Corbicula fluminea* ($n = 42$) and *Elliptio crassidens* ($n = 42$) at all sites. A minimum convex polygon is drawn around all points for each species.

with *t*-tests. All parametric statistical analyses were done with SAS (version 9.1; SAS Institute, Cary, North Carolina).

Results

Stable isotopes

Isotopic signatures differed between species (MRPP, $p < 0.00001$; Fig. 2). *Corbicula fluminea* had a more enriched $\delta^{15}\text{N}$ and more depleted $\delta^{13}\text{C}$ signature (mean values: $\delta^{13}\text{C} = -28.98 \pm 0.28$, $\delta^{15}\text{N} = 9.69 \pm 0.08$) than *E. crassidens* (mean values: $\delta^{13}\text{C} = -28.23 \pm 0.11$, $\delta^{15}\text{N} = 8.38 \pm 0.03$). The dispersions of the isotopic signatures differed significantly between species (Van Valen's test, $t_{70} = 4.99$; $p < 0.00001$). The distance between group medians was 1.06 (95% bootstrap CI = -0.39 – 1.12). Dispersion was 1.72 (95% CI = 1.38 – 2.06) for all *C. fluminea* points and 0.79 (95% CI = 0.63 – 0.95) for all *E. crassidens* points. The difference in dispersion was 0.93 (95% CI = 0.56 – 1.31), and *C. fluminea* had a greater dispersion among isotopic signatures. Because Van Valen's test was significant and the distance between group bivariate medians was large, the significant MRPP statistic reflects both a change in dispersion of isotopic points and differences in central tendency between the species. This result implies major differences in feeding and trophic fidelity.

Isotopic signatures differed significantly among sites when species were grouped together (Fig. 3). Using bootstrapping techniques, we found significant differences between the distances between *E. crassidens* and *C. fluminea* median values among sampling sites (Table 1, Fig. 3), and site medians for each

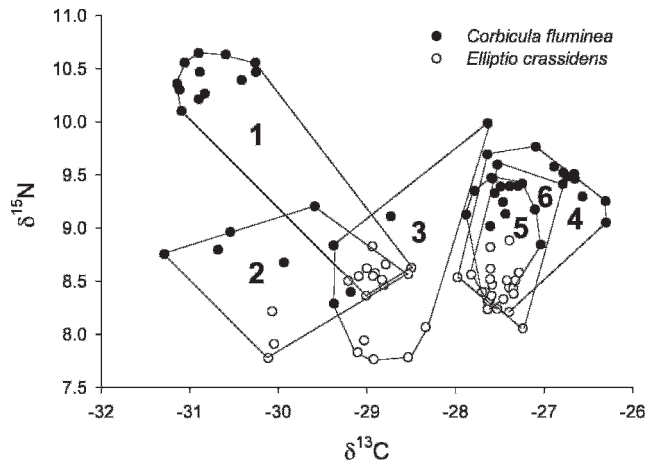


FIG. 3. Tissue stable isotopic signatures of *Corbicula fluminea* ($n = 42$) and *Elliptio crassidens* ($n = 42$) at all sites. A minimum convex polygon is drawn around all points for both species at each sampling site.

species differed significantly for many between-site comparisons. *Corbicula fluminea* had a significantly greater dispersion of isotopic points across sites than *E. crassidens*. Moreover, the CIs for species and site medians were larger and differed more among sites that were more geographically separated, i.e., we found larger CI among sites that were further apart in comparison to sites 4, 5, and 6, which were closer together (Figs 1, 3). These results indicate that isotopic signatures varied with location. However, the values for *E. crassidens* were more tightly clustered than the values of *C. fluminea* (Van Valen's test; Fig. 3), indicating greater trophic fidelity among *E. crassidens* than among *C. fluminea* across sites.

Tissue stoichiometry

Retention of C and N from food sources differed significantly between species as reflected by differences in tissue %C (ANOVA, $p < 0.04$; Fig. 4A), %N ($p < 0.0001$; Fig. 4B), and C:N ($p < 0.0001$; Fig. 4C). C:N values also differed significantly among sites ($p < 0.04$), and the species \times site interaction term was significant ($p < 0.009$). C:N values of *C. fluminea* were always higher than the C:N values of *E. crassidens*. Differences in tissue C:N between *E. crassidens* and *C. fluminea* were significant at sites 1 ($p < 0.0001$), 4 ($p < 0.001$), and 5 ($p = 0.005$), but not at sites 2 ($p = 0.077$), 3 ($p = 0.734$), and 6 ($p = 0.235$). The differences in tissue C:N between species were primarily driven by differences in %N (Fig. 4B). The C:N ratio of *C. fluminea* differed among sites ($p < 0.05$), but Tukey's HSD was unable to resolve those differences. The C:N ratio of *E. crassidens* differed significantly among sites

($p < 0.0001$). Individuals at site 1 (upstream of CC) had significantly lower tissue C:N than individuals at sites 2 and 3 (on CC). Individuals at site 4 (downstream of CC) had significantly lower tissue C:N than individuals at site 2. Individuals at site 5 had significantly lower C:N than individuals at all sites except site 1.

Feces and pseudofeces stoichiometry

Differences in tissue C:N were consistent with differences in C:N of biodeposits. Over time, *E. crassidens* biodeposited more material/individual than did *C. fluminea* (Fig. 5). However, when this value was corrected for bivalve wet tissue mass, *C. fluminea* had higher biodeposition rates than *E. crassidens*, although this difference was not statistically significant ($p = 0.07$).

Percent C and N of biodeposits differed significantly between species. Percent C differed among treatments (overall ANOVA; $p = 0.004$; Fig. 6A). Significant differences were found between species ($p < 0.006$), but the time effect ($p < 0.09$) and the species \times time interaction term ($p = 0.07$) were not significant. Multiple comparisons revealed that %C of *C. fluminea* biodeposits was significantly higher than %C of *E. crassidens* biodeposits only at 2 h ($p < 0.04$). Percent N of the biodeposits differed among treatments (overall ANOVA, $p = 0.004$; Fig. 6B). Percent N of biodeposited material decreased significantly over time ($p < 0.05$), but the species \times time interaction term was not statistically significant ($p > 0.05$). Multiple comparisons revealed that %N of *C. fluminea* biodeposits was significantly higher than %N of *E. crassidens* biodeposits only at 2 h ($p < 0.04$).

Significantly more C and N per mass was released in *C. fluminea* biodeposits than in *E. crassidens* biodeposits (C: $p = 0.028$, N: $p = 0.033$; Fig. 7). On average, *C. fluminea* released $1116 \pm 473 \mu\text{mol C g}^{-1} \text{DM h}^{-1}$ and $171 \pm 75 \mu\text{mol N g}^{-1} \text{DM h}^{-1}$ more than *E. crassidens*.

Discussion

Isotopic signatures

Differences in central tendency of the isotope data indicate that the 2 species were assimilating dissimilar food resources. The dispersion of isotopic signatures differed between species across all sites. *Corbicula fluminea* used a more diverse pool of resources (shown by the larger dispersion of isotopic points) than *E. crassidens*, a result indicating that *C. fluminea* has lower trophic fidelity than *E. crassidens*. Isotopic signatures of basal resources can vary because of

TABLE 1. Lower and upper confidence intervals (CIs) determined from 1000 bootstraps comparing the median distances of isotopic signatures between sites for *Corbicula fluminea* and *Elliptio crassidens*. Statistically significant differences among bivariate medians of the 2 species between sites are indicated by nonoverlapping values (bold). Larger values for the CIs indicate greater differences in stable isotopic signatures for individual species.

Site comparisons	<i>C. fluminea</i>		<i>E. crassidens</i>	
	Lower CI	Upper CI	Lower CI	Upper CI
1 vs 2	1.195	1.524	0.931	1.89
1 vs 3	1.725	2.742	0.623	0.848
1 vs 4	4.035	4.596	1.116	1.448
1 vs 5	3.508	3.75	1.377	1.66
1 vs 6	3.399	3.667	1.096	1.413
2 vs 3	0.846	1.272	0.567	1.567
2 vs 4	3.661	4.455	1.989	3.827
2 vs 5	3.227	3.981	2.178	3.334
2 vs 6	2.995	3.619	2.225	3.058
3 vs 4	2.251	3.118	1.307	1.793
3 vs 5	1.631	2.522	1.471	2.288
3 vs 6	1.558	2.323	1.019	1.695
4 vs 5	0.278	0.885	-0.102	0.256
4 vs 6	0.656	1.434	-2.079	0.138
5 vs 6	-0.243	9.166	-0.037	0.273

location, stream flow, and season (Finlay et al. 1999, McNeely et al. 2006, Atkinson et al. 2009). Seston varies in isotopic ratio and quality (C:N) spatially and temporally across the IC watershed (Atkinson et al. 2009), and the isotopic signatures of the 2 species indicate that the resources they used varied among sites. However, isotopic signatures of *E. crassidens* were less variable than those of *C. fluminea*, and bivariate distances between sites were always smaller for *E. crassidens* than for *C. fluminea*. Thus, *E. crassidens* had greater trophic fidelity than did *C. fluminea*. The lower trophic fidelity of *C. fluminea* probably favors successful invasion because this species can use a wider spectrum of food resources than the native species.

Determining the exact sources of food used by bivalve species can be difficult because of the heterogeneity of materials in suspension at any given time. Seston composition is diverse and variable and can include phytoplankton, bacteria, and nanoflagellates (Wotton 2007, Atkinson 2008). Moreover, in addition to suspension feeding, many bivalves can pedal feed on sedimentary particles (McMahon and Bogan 2001). Laboratory studies indicate that bivalves preferentially ingest living materials, such as algae and bacteria (Brillant and MacDonald 2003, Atkinson 2008). Moreover, bivalves might selectively assimilate bacteria over the fine particulate organic matter (FPOM) to which they are attached (Nichols and Garling 2000, Christian et al. 2004). Smaller seston particles in the IC watershed have a more enriched $\delta^{15}\text{N}$ signature than larger particles (Atkinson et al.

2009), and we expect that both species feed on a diverse assemblage of microorganisms from bacteria to protozoans and associated materials based on their $\delta^{15}\text{N}$ signatures. However, *C. fluminea* might be more efficient than *E. crassidens* at assimilating microbial sources as evidenced by their more enriched $\delta^{15}\text{N}$ signature, which often indicates assimilation of microbial-enriched materials (Macko and Estep 1984, Angradi 1994, Goedkoop et al. 2006).

Tissue and biodeposit stoichiometry

Our laboratory study had 2 limitations. First, our experiment was done in deionized water, which probably caused osmotic stress. However, unionids and *C. fluminea* can survive in deionized water for extended periods (McCorkle and Dietz 1980, Scheide and Dietz 1982), and our experiments were conducted over a 3-h period. Moreover, tissue and biodeposition stoichiometric values in our study were very similar to those reported by Christian et al. (2008) for other unionid species. Thus, we think our results are meaningful. Second, we measured stoichiometry of biodeposits, but not of dissolved excretion products, so we could have underestimated release of N into the environment. To increase environmental relevance, future studies should measure stoichiometry of both biodeposition and excretion products of bivalves held in more natural water conditions.

Differences in the biodeposits of the 2 species were consistent with differences in their tissue stoichiometry. *Corbicula fluminea* retained less N relative to the

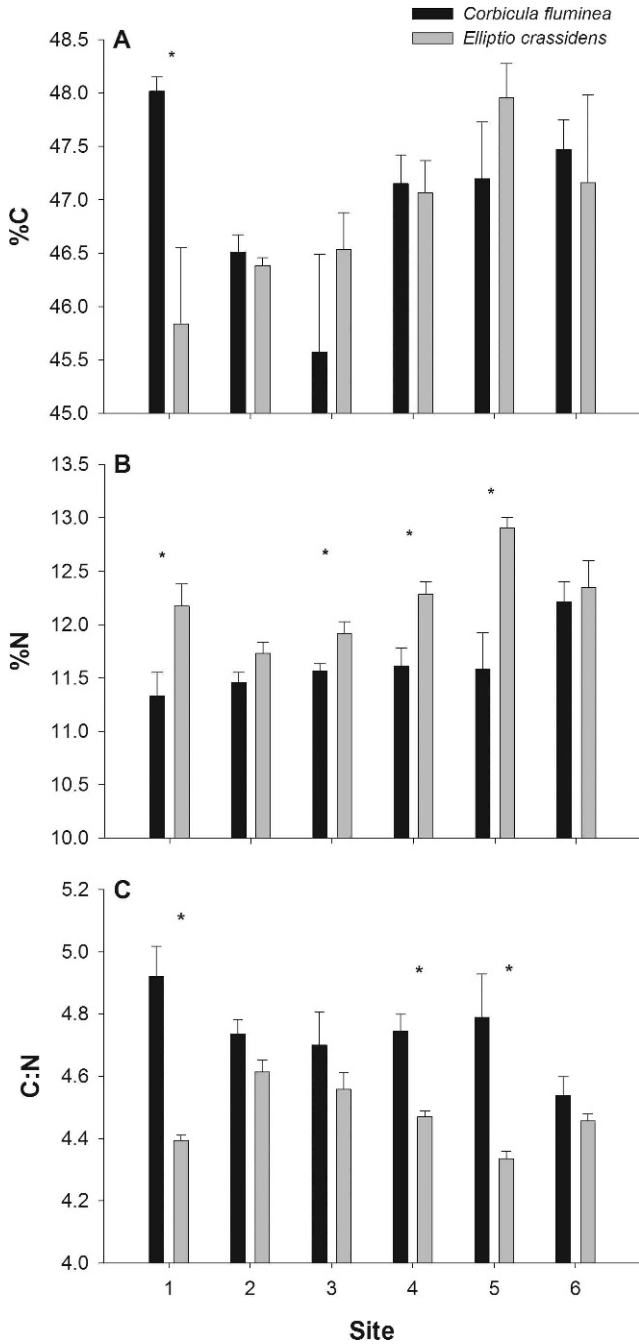


FIG. 4. Percent C (A), %N (B), and C:N (C) values of bivalve tissue at the 6 sampling sites. Asterisks indicate significant differences at $\alpha = 0.05$ between the 2 species at the site (Tukey's Honestly Significant Difference multiple comparisons).

amount of C they retained, whereas *E. crassidens* retained more N relative to the amount of C they retained. Thus, relative to *C. fluminea*, *E. crassidens* released less N into the benthic environment through biodeposition. In addition, unionid mussels are typi-

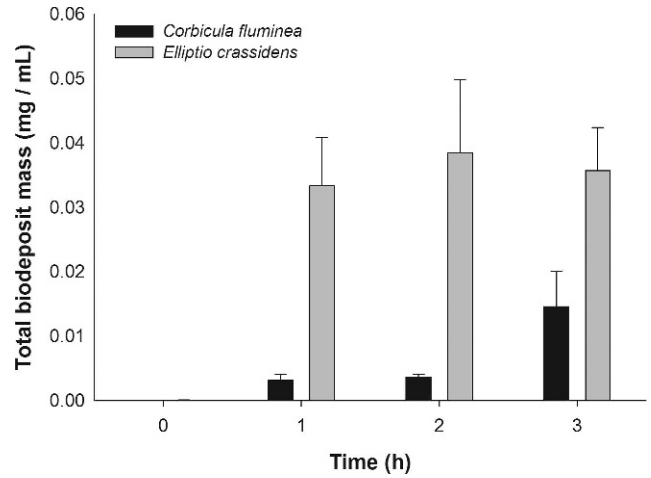


FIG. 5. Mean (+1 SE) total dry mass (DM) of materials released by bivalves as biodeposits.

cally long lived (typically 30–70 y maximum age = 200 y; Williams et al. 2008), whereas *C. fluminea* are much shorter-lived (maximum age = 3–4 y; Vaughn and Hakenkamp 2001). The long lifespan of *E. crassidens* and its ability to retain N suggest that this native species can store more nutrients longer than *C. fluminea*. Historically, freshwater mussels were the dominant invertebrates in many southeastern streams, and *E. crassidens* is the most dominant native species throughout most of the IC watershed. However, *C. fluminea* has become widespread (McMahon and Bogan 2001, Sousa et al. 2008) and might now outnumber *E. crassidens*. Thus, the shorter life span, higher C:N ratio, and higher amounts of N in the biodeposits of *C. fluminea* than of *E. crassidens* has potentially serious implications for stream nutrient cycling.

The invasion of *C. fluminea* is likely to change concentrations of available nutrients in the water column and in particles available as food. C:N of biodeposits (7.65–11.86) was lower than C:N of 10 to 45- μ m seston (12.08–21.75; Atkinson et al. 2009) in the IC watershed. Low C:N values in food increases nutritional quality by reducing elemental imbalances (Frost et al. 2002, Cross et al. 2005). Thus, biodeposits are a higher-quality food source than are seston particles. Moreover, *C. fluminea* biodeposits (C:N = 7.65–11.14) are of higher nutritional value than *E. crassidens* biodeposits (C:N = 8.14–11.86). Variation in bivalve tissue C:N also has implications for stream food webs. For example, Barbour map turtles (*Graptemys barbouri*) consume bivalves as a primary diet component during part of their lives (Lindeman 2006). A diet switch from native mussels (tissue C:N = 4.22–4.71) to *C. fluminea* (tissue C:N = 4.24–5.71) could affect growth of these turtles.

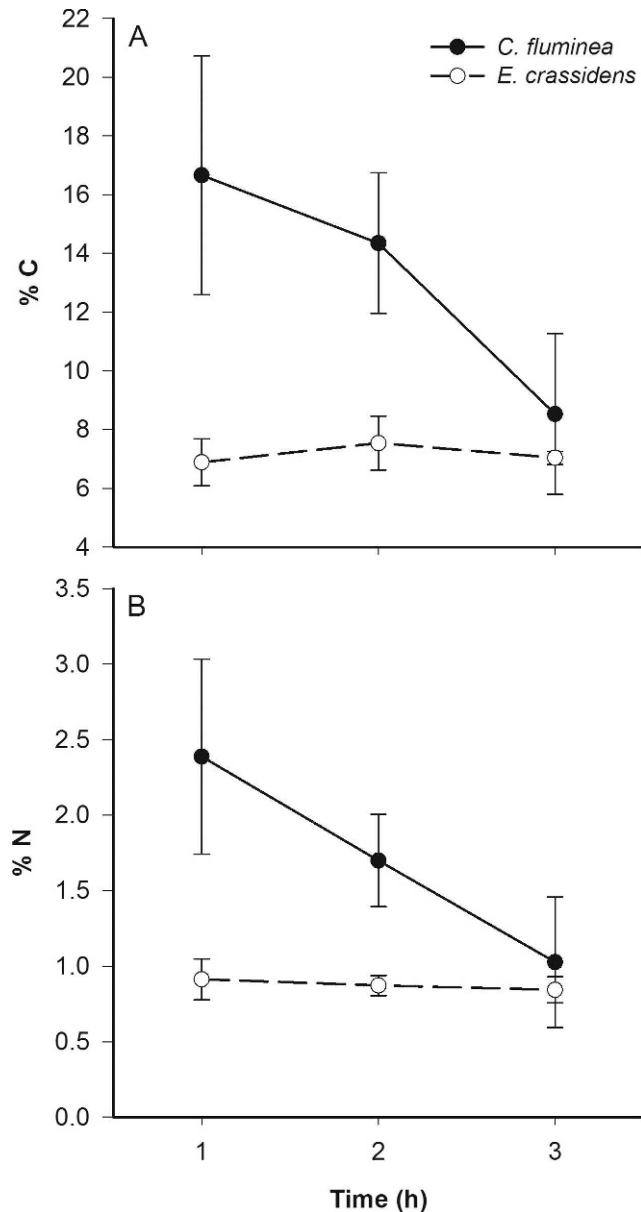


FIG. 6. Percent C (A) and %N (B) of biodeposits left by *Corbicula fluminea* and *Elliptio crassidens* over time. A linear relationship was found between %C ($y = -4.0657x + 21.31$; $r^2 = 0.94$) and %N ($y = -0.6807x + 3.0653$; $r^2 = 0.99$) and time for the *C. fluminea* treatments. No significant linear relationship was found in the *E. crassidens* treatments.

Effects of *C. fluminea* on ecosystem function in the IC watershed

Invasive species can have strong effects on the ecosystems they invade, especially when they have functional roles similar to those of native species. Few researchers have documented the functional effects of *C. fluminea* on North American waterways (but see Hakenkamp and Palmer 1999, Vaughn and Haken-

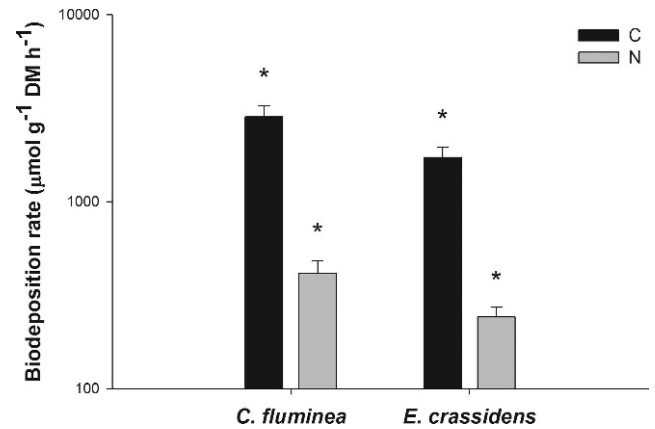


FIG. 7. Mean (+1 SE) biodeposition rates of *Corbicula fluminea* and *Elliptio crassidens*. DM = dry mass. * indicates a significant difference between species for rates of C or N deposition ($\alpha = 0.05$).

kamp 2001). In our system, *C. fluminea* occupies a larger trophic niche space and has lower trophic fidelity than *E. crassidens*. We suspect that *C. fluminea* ingests some of the same materials as native species, but *C. fluminea* has the ability to assimilate a broader range of food resources than *E. crassidens* and are able to change their feeding habits more readily given the availability of materials.

An exotic species that alters ecosystem properties does not merely compete with native species; it also alters the fundamental rules of existence for all organisms in the area (Vitousek 1990). *Corbicula fluminea* has a trophic strategy (i.e., filter feeding) similar to that of native mussels, but its different functional abilities suggest that *C. fluminea* has the ability to alter nutrient cycling dynamics and the availability of materials in the water column. In addition, biodeposition of filtered materials into the sediments could cause competition among filter feeders because of reduction of materials in the water column. Moreover, *C. fluminea* die-offs and tissue decomposition can alter water quality for native mussel species, especially during periods of low flow and warm waters during prolonged drought, by further depleting dissolved O₂ and producing toxic NH₃ (Cherry et al. 2005, Cooper et al. 2005). Clearly, more attention should be focused on the functional roles invasive species play in aquatic ecosystems to understand fully the implications of their introduction.

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