

DOMINANCE OF THE ASIATIC CLAM, *CORBICULA FLUMINEA* (MÜLLER), IN THE BENTHIC COMMUNITY OF A RESERVOIR

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ABSTRACT *Corbicula fluminea* dominated the benthic community of Lake Nacogdoches, East Texas, composing 97% of the total biomass of benthic invertebrates. *C. fluminea* appears to be restricted to the littoral zone. Lower depths have lower oxygen, especially during the stratified period, which may restrict the distribution of *C. fluminea*. *C. fluminea* was found only down to a depth of 4 m and had an extremely patchy distribution. The greatest density within a patch was found at 1 m depth ($35.8 \pm 13.8 \text{ m}^{-2}$) and the greatest biomass within a single patch was at 2 m ($137.17 \pm 69.21 \text{ g} \cdot \text{m}^{-2}$). *C. fluminea* density differed significantly among substrate types. The maximum density ($43 \pm 14 \text{ m}^{-2}$) was found in sediments with dead *C. fluminea* shells and coarse detritus, and the lowest density ($3.6 \pm 3.6 \text{ m}^{-2}$) was found in silt. The spatial distributions of *C. fluminea* and three species of unionids were similar both in depth and across substrates in the reservoir. We found no correlation between the densities of *C. fluminea* and other benthic invertebrates. Finally, we contrasted the effect of *C. fluminea* on benthic communities to what is known about the impacts of another invasive bivalve, the zebra mussel.

KEY WORDS: *Corbicula fluminea*, benthic community, *Hydrilla*, invasive species

INTRODUCTION

Asiatic clams [*Corbicula fluminea* (Müller)] are native to Southeast Asia and have been successfully invading North American water bodies since the beginning of the 20th century. They currently occur in 36 states in the United States and northern and central Mexico; however, they are not found in Canada (McMahon 1982, McMahon 1999, McMahon & Bogan 2001). *C. fluminea* invaded Texas in the 1960s and has now spread statewide (Howells 1992). *C. fluminea* is a simultaneous hermaphrodite that is ovoviviparous. Fertilized eggs are brooded in the interlamellar spaces of the gills through the trochophore and veliger stage and released at the nonswimming pediveliger stage (McMahon 1999). Because of a high reproductive potential ($<68,000$ pediveligers $\text{adult}^{-1} \text{y}^{-1}$), *C. fluminea* can rapidly increase in population density within a short period of time (Aldridge & McMahon 1978, McMahon 1991, McMahon 1999, McMahon & Bogan 2001). *C. fluminea* is infaunal, usually burrowing in soft sediments. Adults can grow to 50–70 mm in size and can live for 3–4 y (reviewed in McMahon 1999). One of the reasons for its success may be the ability of *C. fluminea* to feed both from the water column (using siphons; Cohen et al. 1984, Boltovskoy et al. 1995), and from the sediments (using the foot to pedal-feed; Reid et al. 1992, Hakenkamp et al. 2001).

Carried into raw water systems on intake flows, *C. fluminea* nonswimming pediveligers and juveniles may settle in places with water currents below $1.2\text{--}1.5 \text{ m sec}^{-1}$ and form adult populations $>20,000 \text{ m}^{-2}$ (McMahon 1999). The total damage caused by *C. fluminea* for US industries in 1986 was estimated at \$1 billion (Isom 1986). *C. fluminea* can also play an important role in aquatic ecosystems as a benthic–pelagic coupler (Lauristen 1986, Hakenkamp & Palmer 1999). *C. fluminea* can reduce phytoplankton levels (Cohen et al. 1984), seston concentration (Leef et al. 1990), particulate phosphates (Greer & Zeibell 1972) and chlorophyll *a* levels (Beaver et al. 1991). Water clarification by clam filtering

favors the growth of rooted macrophytes, shifting primary production from planktonic to benthic communities (Phelps 1994, McMahon 1999). As a consequence, *C. fluminea* is becoming a major component of benthic communities in freshwater environments across North America (McMahon 1983, Counts 1986, Poff et al. 1993, McMahon 1999).

C. fluminea may also influence bottom fauna as a result of pedal-feeding via bioturbation of sediments or consuming benthic fauna directly (Hakenkamp & Palmer 1999, McMahon 1999, Hakenkamp et al. 2001). Although there are some reports that the Asiatic clam can compete with native unionid bivalves (Kraemer 1979, Leef et al. 1990, Howells 1992), there are no data about the impact of this invasive bivalve on biodiversity and functioning of the macroinvertebrate community or productivity and food web interactions. Hakenkamp et al. (2001) found that an increasing abundance of *C. fluminea* was negatively associated with the abundance of benthic bacteria and flagellates but had no apparent effect on other benthic protists or meiofauna. This contrasts with studies of another invading bivalve, the zebra mussel, *Dreissena polymorpha* (Pallas) (reviewed in Karatayev et al. 1997, Karatayev et al. 2002).

We determined the abundance and distribution of *C. fluminea* along depth gradients and among substrate types and their role in the benthic community, especially possible impacts on native fauna including unionid bivalves. We also compared patterns of the distribution of *C. fluminea* and its impact on bottom invertebrates with those found for zebra mussels.

METHODS

Study Area

Studies were conducted at Lake Nacogdoches, a monomictic reservoir in East Texas ($31^{\circ}37' \text{N}$, $94^{\circ}49' \text{W}$). Lake Nacogdoches is the municipal water supply reservoir for the city of Nacogdoches, Texas. The dam-forming Lake Nacogdoches was completed in July 1976. The reservoir has a surface area of 8.94 km^2 , maximum

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storage capacity of 49.7 million m³, maximum depth of 13 m, and an average depth of 5.6 m.

The upper shallow (<5 m depth) and more eutrophic part of the reservoir is situated north of an island in the lake and constitutes approximately 40% of the water body (Fig. 1). Bottom sediments in this shallow part are mainly silt and a mixture of silt and clay. The lower part of the reservoir is less eutrophic, deep (up to 13 m), and has a variety of substrates, including sand, gravel, clay, shells, coarse detritus, and silt, as well as various combinations of these. The drainage area of the reservoir is 231 km², and Loco Bayou is the primary tributary (Prater 1991). During December to March, there is a long period of homeothermy. In spring, summer, and fall the water column of the reservoir is stratified. A lack of mixing and high productivity in the reservoir cause complete oxygen depletion below the thermocline by late spring. As a result, the oxygen content at depths greater than 6 m never exceeds 1 mg L⁻¹ from May to August (Taylor 1980).

In the early 1980s, *Hydrilla verticillata* (l.f.) Royal was accidentally introduced into the Lake Nacogdoches and by 1989 covered approximately 45% of the reservoir (Prater 1991). *H. verticillata* spread mainly in the upper shallow part of the water body, where it completely covered the reservoir. In contrast, in the lower part less than 3% of the reservoir is covered with *H. verticillata* (Fig. 1).

Sampling Protocol

To determine the distribution of *C. fluminea* and its effect on the benthic community of Lake Nacogdoches, a total 96 bottom

samples were taken in September (transect 1) and October (transects 2–6) 2001 (Fig. 1). For each transect, samples were collected from 1, 2, 3, 4, 6, and 8 m, except for transects 5 and 6, where samples were collected at depths of 1, 2, 3, and 4 m. These last two transects were situated at the upper shallow part of the reservoir with a maximum depth less than 5 m. In addition, the deep (profundal) part of the lake was sampled separately (6 and 10 m depth). Three or more replicate samples were taken at each depth with an Ekman grab (sampling area = 0.0233 m²) and washed through a 550- μ m mesh. At each sampling point, water transparency, bottom temperature, pH, oxygen, and conductivity were recorded (Table 1). After sampling, all macroinvertebrates were transferred to containers with 10% neutral-buffered formalin and labeled. All macroinvertebrates were identified to the genus or species level, counted, and weighted to the nearest 0.0001 g after being blotted dry on absorbent paper (wet mass). For oligochaetes, only *Branchiura sowerbyi* Beddard and *Stylaria lacustris* (Linnaeus) were identified to species level. All *C. fluminea* and unionids were cut open with a scalpel to remove water from the mantle cavity, measured, weighed (wet mass), and identified to species. The average mass of individual *C. fluminea* in a sample was calculated by dividing the total mass by the number of clams in the sample. Because several samples contained no *C. fluminea* (density = 0), we used nonparametric Kruskal–Wallis test to analyze the data. When multiple statistical tests were conducted on the same data, we used a Bonferroni correction to determine the critical alpha for significance.

RESULTS

Corbicula fluminea Distribution

During our September sampling, the reservoir was still well stratified for temperature and oxygen to around 6 m depth (Table 1). In October, the lake was well mixed and both temperature and oxygen did not vary appreciably with depth. Oxygen content was low only at the deepest sampled site (10 m depth). Water pH and conductivity did not show sharp changes across the thermocline (Kruskal–Wallis test, $P = 0.20$).

C. fluminea was found only in the lower part of Lake Nacogdoches (transects 1–4; Fig. 1). We did not find any live *C. fluminea*, or even their dead shells, in the upper part of the reservoir, which was covered with *H. verticillata* (transects 5 and 6).

We found a significant difference in some chemical parameters between regions of the lake with *C. fluminea* (transects 2–4, 1–4 m) and the area of the lake with *H. verticillata*, where we did not find clams (transects 5–6, 1–4 m). The pHI was slightly higher in the upper region (7.96 ± 0.009 , $n = 12$) vs. 7.86 ± 0.011 ($n = 7$); Kruskal–Wallis test, $P = 0.0005$). Dissolved oxygen was slightly lower in area covered with *H. verticillata* (9.26 ± 0.06 ($n = 7$) vs. 9.76 ± 0.15 mg L⁻¹ ($n = 12$); Kruskal–Wallis test, $P = 0.016$), but this difference was only marginally significant (critical alpha with the Bonferroni Correction = 0.012). Conductivity was lower in the upper part of the reservoir (93.11 ± 0.28 ($n = 7$) vs. 95.66 ± 0.53 m Siemens cm⁻¹ ($n = 12$); Kruskal–Wallis test, $P = 0.002$). Transect 1 was not included in these analyses as it was sampled 20 days earlier.

The average (\pm SE) *C. fluminea* density and biomass in the lower portion of the reservoir (transects 1–4, depths 1–8 m) was 15.6 ± 5.3 m⁻² and 71.9 ± 18.8 g m⁻², respectively. There were no significant differences in density or biomass of *C. fluminea* between the four transects (Kruskal–Wallis test, $P > 0.44$). In addi-

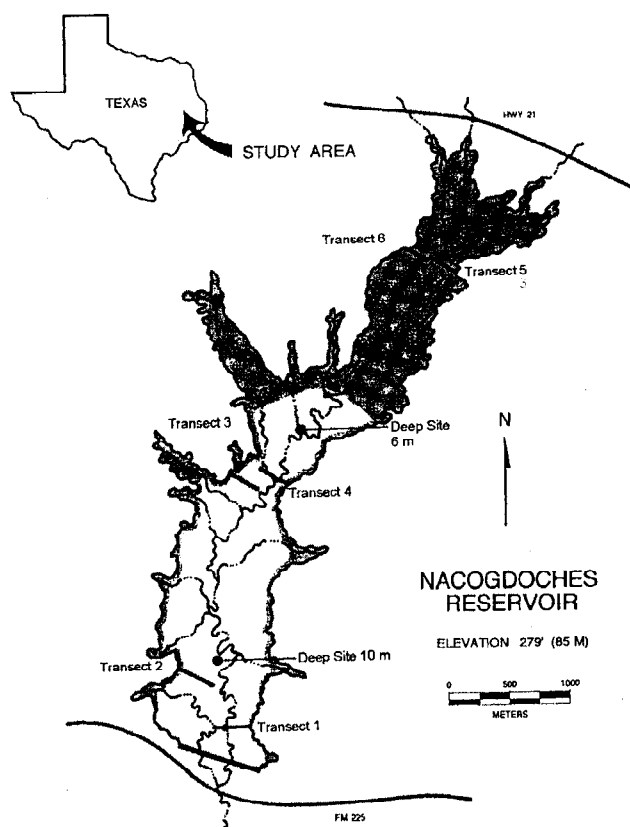


Figure 1. Location of transects sampled in Lake Nacogdoches. Shaded area represents the extent of the reservoir covered by *Hydrilla verticillata*.

TABLE 1.
Oxygen concentration, temperature, conductivity and pH in Lake Nacogdoches.

Parameter	Depth (m)						
	1	2	3	4	6	8	10
Transect 1							
Oxygen, mg · L ⁻¹	9.72 (1)	9.57 (1)	9.40 (1)	9.26 (1)	3.03 (1)	0.45 (1)	—
Temperature, °C	27.8 (1)	27.7 (1)	27.6 (1)	27.6 (1)	26.3 (1)	24.3 (1)	—
Conductivity, mSiemens cm ⁻¹	96.9 (1)	95.3 (1)	94.3 (1)	94.2 (1)	97.7 (1)	116.7 (1)	—
pH	7.87 (1)	7.90 (1)	7.90 (1)	7.87 (1)	7.76 (1)	7.60 (1)	—
Transects 2-4							
Oxygen, mg · L ⁻¹	10.24 ± 0.36 (3)	9.62 ± 0.39 (3)	9.64 ± 0.30 (3)	9.52 ± 0.25 (3)	7.83 ± 0.40 (3)	6.25 ± 2.15 (2)	—
Temperature, °C	23.10 ± 0.17 (3)	22.69 ± 0.30 (3)	22.83 ± 0.12 (3)	22.82 ± 0.12 (3)	22.45 ± 0.05 (3)	22.30 ± 0 (2)	—
Conductivity, mSiemens cm ⁻¹	96.27 ± 1.77 (3)	95.2 ± 0.95 (3)	95.2 ± 0.68 (3)	95.97 ± 1.06 (3)	95.70 ± 0.20 (3)	97.65 ± 2.25 (2)	—
pH	7.87 ± 0.03 (3)	7.86 ± 0.02 (3)	7.86 ± 0.01 (3)	7.84 ± 0.02 (3)	7.84 ± 0.03 (3)	7.80 ± 0.02 (2)	—
Transects 5-6							
Oxygen, mg · L ⁻¹	9.30 ± 0.20 (2)	9.20 ± 0 (2)	9.33 ± 0.12 (2)	9.15 (1)	—	—	—
Temperature, °C	22.30 ± 0.20 (2)	22.31 ± 0.16 (2)	22.41 ± 0.27 (2)	22.7 (1)	—	—	—
Conductivity, mSiemens cm ⁻¹	92.60 ± 0 (2)	93.5 ± 0.50 (2)	93.55 ± 0.75 (2)	92.50 (1)	—	—	—
pH	7.96 ± 0.03 (2)	7.95 ± 0.04 (2)	7.96 ± 0.005 (2)	7.97 (1)	—	—	—
Profundal							
Oxygen, mg · L ⁻¹	—	—	—	—	8.45 (1)	—	0.85 (1)
Temperature, °C	—	—	—	—	23.4 (1)	—	21.3 (1)
Conductivity, mSiemens cm ⁻¹	—	—	—	—	93.6 (1)	—	123.0 (1)
pH	—	—	—	—	7.14 (1)	—	7.80 (1)

Transect 1 was sampled in September; all other transects were sampled in October. Transects 5 and 6 were in an area of the lake covered with *Hydrilla verticillata* and no *Corbicula fluminea*. Transects 2-4 had *C. fluminea* and no *H. verticillata*. In addition, we sampled two sites deep in the lake (profundal, 6 and 10 m). Average values ± standard errors of mean are given, sample sizes are in parentheses, — = no data.

tion, density and wet mass did not differ significantly with depth down to 4 m (Kruskal-Wallis test: density: $P = 0.29$; biomass: $P = 0.40$; Figs. 2 and 3). This lack of significance is probably caused by the high degree of patchiness (Index of Dispersion Test; $I = 59.7$; $\chi^2 = I * (n - 1) = 59.7 * (48 - 1) = 2805$. $\chi^2_{0.025, 47} = 67.8$, $P < 0.001$). Many samples had no *C. fluminea*, which resulted in an increase in the variance in observed means. The

mean density of *C. fluminea* was greatest at 1 m ($35.8 \pm 13.8 \text{ m}^{-2}$), and the maximum biomass was at 2 m ($137.17 \pm 69.21 \text{ g m}^{-2}$). The maximum density of *C. fluminea* in a single sample was 172 m^{-2} (transect 4, 1 m) and maximum wet mass (soft body + shells) in a single sample was 770 g m^{-2} (transect 2, 2 m).

The average individual mass for *C. fluminea* (total sample mass/density) differed significantly with depth (ANOVA,

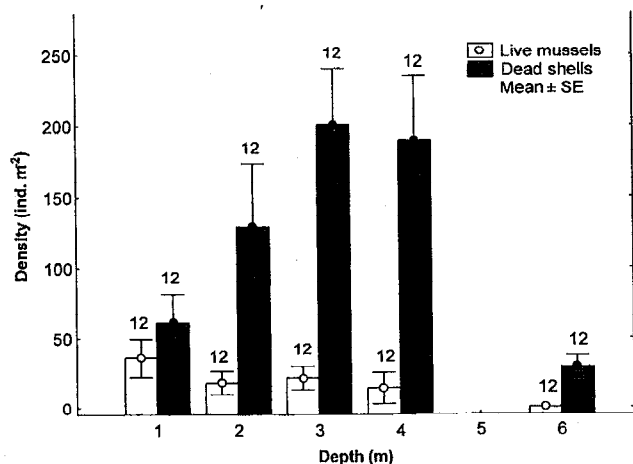


Figure 2. Density of live and dead shells of *Corbicula fluminea* at different depths in Lake Nacogdoches. Averages, standard errors of mean, and sample sizes are given.

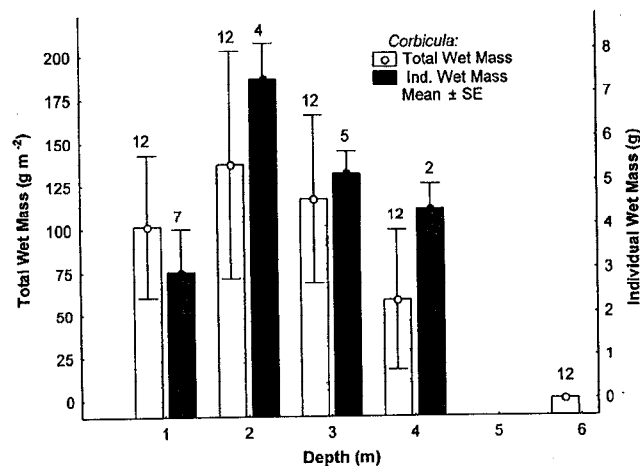


Figure 3. Total wet mass (left axis) and average individual wet mass (total wet mass divided by the number of clams in the sample, right axis) of *Corbicula fluminea* at different depths in Lake Nacogdoches. Averages, standard errors of mean, and sample sizes are given.

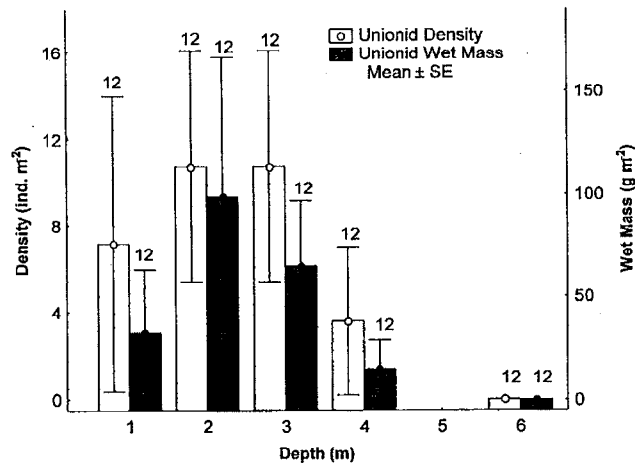


Figure 4. Density (left axis) and total wet mass (right axis) of unionids at different depths in Lake Nacogdoches. Averages, standard errors of mean, and sample sizes are given.

$P < 0.029$; Fig. 3). The smallest average individual mass (2.95 ± 1.02 g) was at 1 m, and the largest average individual mass (7.33 ± 0.86 g) was at 2 m.

C. fluminea shells were found down to 6 m (Fig. 2). The distribution of shells with depth was not uniform (Kruskal-Wallis test, $P = 0.0002$) and differed from the distribution of live *C. fluminea* (Kolmogorov-Smirnov test, $P < 0.001$).

C. fluminea density differed significantly among substrate types (Kruskal-Wallis test, $P = 0.04$). Dead *C. fluminea* shells and course detritus had the highest density (43 ± 14 m⁻²), and the lowest density (3.6 ± 3.6 m⁻²) was found in silt (Table 2). Dead *C. fluminea* shells were not found uniformly among substrate types, and were most abundant in clay with stones (272 ± 56 m⁻²; Kruskal-Wallis test, $P = 0.0008$).

Distribution of Benthic Animals

We found 38 taxa (species, genera or higher taxa), including 17 chironomids (identified to the species or genus level). The average density of benthic animals, excluding bivalves, over the entire reservoir was 901 ± 91 m⁻² with a biomass of 2.76 ± 0.29 g m⁻². The most abundant insect larvae were the chironomid *Coelotanyptus tricolor* (Lowe) (185 ± 25 m⁻², total number of samples = 96), *Chironomus* sp. (69 ± 17 m⁻²), and the phantom midge *Chaoborus punctipennis* (Say) (137 ± 35 m⁻²). Among oligochaetes, *Branchiura sowerbyi* Beddard was dominant (71 ± 12 m⁻²). Only a single species of amphipod, *Hyalolella azteca* (Saussure), was found (24 ± 11 m⁻²).

Corbicula fluminea dominated the benthic biomass in the littoral zone from 1–4 m in the lower part of the reservoir (transects 1–4) and was responsible for more than 97% of the total wet mass of the benthic community. At depths ≥ 6 m, *Chironomus* sp., *C. punctipennis*, and *B. sowerbyi* were responsible for 43%, 17%, and 26% of the total benthic biomass, respectively.

In the upper region of the reservoir (transects 5 and 6) the average density (1165 ± 216 m⁻²) and average biomass (3.57 ± 0.54 g m⁻²) of benthic animals were marginally higher (Kruskal-Wallis test, density: $P = 0.073$; biomass: $P = 0.061$) than in the lower part (excluding *C. fluminea* and unionids density 843 ± 104 m⁻², biomass 2.60 ± 0.35 g m⁻²). However, because of the presence of *C. fluminea* in the lower region of the reservoir, the total macrobenthos (including *C. fluminea*) biomass (74.5 ± 18.9 g m⁻²) was 20 times greater than in the upper part.

There were three species of unionids in the lake, *Pyganodon grandis* (Say), *Ligumia subrostrata* (Say), and *Toxolasma texansis* (Lea). Two *P. grandis*, one *L. subrostrata*, and six *T. texansis* were found on transects 2, 3, and 4 on depths of 1–4 m (Fig. 4). These unionids completely overlapped with the distribution of *C. fluminea* (Kolmogorov-Smirnov test, $P > 0.10$).

For transects 1–4, the maximum density and biomass of unionids was in clay (17.9 ± 8.3 m⁻², 97.5 ± 42.8 g m⁻², total number of samples $n = 12$) and in course detritus with *C. fluminea* shells (10.8 ± 5.6 m⁻², 98.4 ± 71.1 g m⁻², $n = 12$). The lowest density and biomass of unionids was in silt (3.6 ± 3.6 m⁻², 14.9 ± 14.9 g m⁻², $n = 12$). There were no significant correlations between the *C. fluminea* density or the density of *C. fluminea* shells and any invertebrate taxon.

DISCUSSION

C. fluminea Distribution

The exotic plant *Hydrilla verticillata* covers approximately 45% of Lake Nacogdoches and is the dominant macrophyte species in this community (Prater 1991). Another exotic species, *C. fluminea*, dominated the benthic community of this reservoir. However, the spatial distribution of these two nuisance species did not overlap. During our study, neither live *C. fluminea* nor dead shells were found in the upper part of the reservoir, which is covered with *H. verticillata*. Prater (1991) sampled the benthos of Lake Nacogdoches monthly over 12 mo in 1989–1990 and never found *C. fluminea* in the *H. verticillata* region of the reservoir as well. Two factors may contribute to the absence of *C. fluminea* in the upper part of the reservoir. First, dense *H. verticillata* mats may deplete the oxygen in the water to levels below those critical for *C. fluminea* survival. We found a significant decrease in oxygen in

TABLE 2.
Abundance of live *Corbicula fluminea* and shells in various substrata in Lake Nacogdoches in 2001.

Substrate Type	Density, Ind. m ⁻²	Biomass, g · m ⁻²	<i>C. fluminea</i> Shells m ⁻²
<i>C. fluminea</i> shells and course detritus	43.0 ± 14.0 (12)	162.68 ± 56.01 (12)	71.7 ± 25.6 (12)
Clay and stones	19.1 ± 14.5 (9)	95.36 ± 63.75 (9)	272.3 ± 55.5 (9)
Clay	25.1 ± 8.3 (12)	149.93 ± 66.26 (12)	100.3 ± 21.4 (12)
Sand	14.3 ± 14.3 (3)	45.87 ± 45.87 (3)	28.7 ± 28.7 (3)
Silt	3.6 ± 3.6 (12)	17.77 ± 17.77 (12)	112.9 ± 28.6 (24)

The abundance of live *C. fluminea* was estimated from transects 1–4, from 1–4 m. The abundance of dead shells was estimated from transects 1–4 and 1–6 m. Average values ± standard errors of the mean are given. Sample size in parentheses.

the portions of the lake covered with *H. verticillata*, but this difference was relatively small. Second, bottom substrates in the upper part of the reservoir are predominantly silty clay, which may be unfavorable for *C. fluminea*.

C. fluminea was found in all four transects in the lower part of Lake Nacogdoches at depths up to 4 m, and *C. fluminea* dead shells were found up to 6 m depth. Deeper in the reservoir, *C. fluminea* was probably limited by low oxygen, especially during the summer, when the water column is stratified and the oxygen content deeper than 6 m never exceeds 1 mg L^{-1} (Taylor 1980). *C. fluminea* is known to be intolerant of even moderate hypoxia (McMahon 1991, McMahon & Bogan 2001), and low oxygen is considered to be one of the main sources of mortality for *C. fluminea* (Sieckel 1986). Although live *C. fluminea* were most dense at 1 m depth and had highest total biomass at 2 m, their dead shells were most abundant at 3 and 4 m (Fig. 2), which suggested that the depth of maximum *C. fluminea* abundance may vary with time or that dead shells were transported to deeper water by water motion.

C. fluminea density and biomass also varied among substrate types. Clams were most abundant in sediments formed by shells and coarse detritus and least abundant on silt. The mean population density and biomass of *C. fluminea* we found were very similar to those found 10 years earlier by Prater (1991). He found that clam density in 1989–1990 varied from 0 to 60 m^{-2} (average $24.4 \pm 5.5 \text{ m}^{-2}$). This suggests that the population density of *C. fluminea* in Lake Nacogdoches is rather stable. *C. fluminea* can occur in dense aggregations, exceeding 2000 m^{-2} (Gardner et al. 1976, Phelps 1992). These densities are much higher densities than those that have been recorded in Lake Nacogdoches. However, these higher densities were reported for a limited period of time, shortly after initial invasion (Phelps 1994) or from a local spot in a water body (Eng 1979). For example, after the initial invasion in the Potomac River in 1977, *C. fluminea* reached a maximum density in 1986 (722 g m^{-2} wet weight, including shell) but then sharply declined, and in 1992 was at 24.8% of 1986 levels (Phelps 1994). In the sediment bars of the Delta-Mendota Canal, the maximum density of *C. fluminea* at one site was $131,200 \text{ m}^{-2}$; however, the average density was much smaller (Eng 1979). In another Texas lake, Lake Arlington, the mean density of *C. fluminea* in 1975 was very similar to the densities we found in Lake Nacogdoches ($32.1 \pm 16.5 \text{ m}^{-2}$, Aldridge & McMahon 1978).

Dominance in Benthos

C. fluminea appears to dominate the benthic community of water bodies it invades (McMahon 1983, Counts 1986, McMahon 1991, Poff et al. 1993, McMahon 1999). We found that in littoral zone of Lake Nacogdoches *C. fluminea* comprises more than 97% of the total wet mass of the macrobenthic community. We found no correlations between *C. fluminea* density and biomass and other nonmolluscan invertebrates.

Impact on Unionids

Whether *C. fluminea* and native bivalves compete is controversial (McMahon 1999, Strayer 1999). According to some authors, *C. fluminea* may out compete native unionids (Kraemer 1979, Belanger et al. 1985, Leef et al. 1990, Howells 1992). The competitive advantage of *C. fluminea* over native bivalves has been suggested because it has a much higher filtering rate than native species (Mattice 1979, Lauristen 1986). In addition, by being able to use both filter and pedal feeding, *C. fluminea* may have an

advantage over native bivalves that are only able to filter feed (Hakenkamp & Palmer 1999). However, most of the evidence for the competitive impacts of *C. fluminea* on native bivalves is based on an analysis of their spatial distributions, and much of these data are anecdotal and qualitative rather than quantitative (Strayer 1999). According to many authors (reviewed in Strayer 1999), *C. fluminea* and native bivalves have nonoverlapping spatial distributions, implying that *C. fluminea* can out compete other bivalves. However, we found that in Lake Nacogdoches unionids and *C. fluminea* are both abundant and occupied the same areas. The depth distribution of *C. fluminea* and unionids was completely overlapping. In addition, both unionids and *C. fluminea* were abundant in the same type of substrate (course detritus with *C. fluminea* shells and clay). The lowest numbers and biomass of both *C. fluminea* and unionids were in silt.

Several other authors have found that unionids and *C. fluminea* coexist (Clarke 1988, Beaver et al. 1991, Miller & Payne 1994). These data may suggest that the impact of *C. fluminea* on native unionids is not as strong as the impact of zebra mussels, which can cause mass mortality of unionids (reviewed in Karatayev et al. 1997).

Impacts of *Corbicula fluminea* versus *Dreissena polymorpha*

In Lake Nacogdoches *C. fluminea* was never found in areas overgrown by *H. verticillata*. In contrast, zebra mussels are often found at their highest densities on submerged macrophytes, which they use as sites for attachment (Lewandowski 1982, Lyakhnovich et al. 1994, Karatayev et al. 1998). During our study, *C. fluminea* was most abundant on shelly sediment. This sediment is also one of the best substrates for the zebra mussel (Lyakhnovich et al. 1994, Karatayev et al. 1998). Silt is the poorest substrate for both *C. fluminea* (Duarte & Diefenbach 1994) and *D. polymorpha* (Zhadin 1946, Draulans & Wouters 1988, Karatayev & Burlakova 1995) and often limits their distributions. Belanger et al. (1985) found in their field and laboratory studies that *C. fluminea* preferred the following sediments in decreasing order: fine sand, organically enriched fine sand, and coarse sand. *C. fluminea*, a burrowing animal, preferred fine sediments; however, the zebra mussel, which attaches to hard substrate, forms especially high densities on rocks (Lyakhnovich et al. 1994, Burlakova 1998). Low oxygen may be another important limiting factor for both *C. fluminea* (McMahon 1991, McMahon & Bogan 2001) and the zebra mussel (Mikheev 1961, Spiridonov 1972, Shkorbatov et al. 1994).

Both *C. fluminea* (McMahon 1983, Counts 1986, McMahon 1991, Poff et al. 1993, McMahon 1999) and *D. polymorpha* (Sokolova et al. 1980, Karatayev et al. 1994) dominate benthic communities and are responsible for more than 95% of the biomass in lakes where they occur. *C. fluminea* live in soft sediment, crawl through sediment with a foot, and feed both as a filter feeder from the water column (Cohen et al. 1984, Boltovskoy et al. 1995), and from the sediments as a pedal feeder (Reid et al. 1992, Hakenkamp et al. 2001) and thus may negatively impact burrowing detritivores (McMahon 1999). Zebra mussels, in contrast, can live only on the surface of the sediments, where they attach to hard substrates and each other with proteinacious byssal threads creating complex three-dimensional structures (Karatayev et al. 2002). *D. polymorpha* constantly filter the water for both feeding and respiration. Filtered particles are either consumed or bound in mucus, preventing immediate re-suspension. This zebra mussel

activity builds a direct connection between the planktonic portion of water body and the benthos (benthic-pelagic coupling) and greatly enhances the rates of deposition of both organic and inorganic material on the bottom. *D. polymorpha* provide food and shelter for many benthic invertebrates, which have increased density and biomass in zebra mussel beds. Simultaneously other species (mainly filter feeders) may decrease or disappear from the community (Karatayev & Burlakova 1992, Stewart et al. 1998, Stewart et al. 1999). This well-documented effect of zebra mussel on benthic communities contrasts with the unknown impact of *C. fluminea* on composition, structure and densities of native invertebrates. In a recent study Hakenkamp et al. (2001) found that when they experimentally increased *C. fluminea* density in the field, there was no apparent impact on the abundance or taxonomic composition of the meiofauna.

In some circumstances *C. fluminea* may compete with native bivalves for food or substrate. In contrast, the negative impact of *D. polymorpha* on native unionids is more diverse. Besides resource competition, zebra mussels also show direct interference competition through overgrowth of unionids. By attaching to unionids, zebra mussels can make it more difficult for them to burrow and move through the sediment. They can weight down

their host unionid, resulting in burial in very soft sediments, can increase drag and the likelihood of dislodgement by water motion for species living near shore, prevent opening valves for respiration, feeding and reproduction, or preventing the closing valves (reviewed in Karatayev et al. 1997, Burlakova et al. 2000).

Mass mortalities of unionids caused by *D. polymorpha* overgrowth are most common during the initial stages of colonization, when mussel populations are growing rapidly. After initial peaks in zebra mussel abundance, *D. polymorpha* can coexist with unionid bivalves (Nichols & Amberg 1999, Burlakova et al. 2000). Similarly, we hypothesize that the strength of competition between *C. fluminea* and native bivalves may depend on various factors including unionid species, *C. fluminea* density, and time since *C. fluminea* invasion.

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