

Christine C. Hakenkamp · Margaret A. Palmer

Introduced bivalves in freshwater ecosystems: the impact of *Corbicula* on organic matter dynamics in a sandy stream

Received: 5 October 1998 / Accepted: 6 February 1999

Abstract Previous research on *Corbicula fluminea* (a well-established, non-native bivalve) has clearly shown that this single species impacts ecosystem processes such as nutrient and dissolved organic carbon cycling in the water column of streams. Surprisingly, little was known about how *Corbicula* might influence similar processes in streambed sediments. Here, we used both laboratory and field experiments to determine how filter- and pedal-feeding by *Corbicula* impact organic matter dynamics in the sandy streambed (Goose Creek, Virginia). *Corbicula* consumed significant quantities of organic material in the streambed when conditions favored pedal-feeding but increased buried organic matter stores when filter-feeding promoted deposition of organic matter (by production of feces and pseudofeces). *Corbicula* contributed significantly to total benthic community respiration (and thus carbon dioxide production), and used pedal-feeding on benthic organic material to grow at a faster rate than that possible by filter-feeding alone. *Corbicula* should be an important coupler between benthic and pelagic processes because this bivalve uses organic matter from both the water column and the stream sediments. Given the widespread occurrence of this species, we speculate that the introduction of *Corbicula* may have had major implications for organic matter dynamics in this and many other streams in the United States.

Key words *Corbicula fluminea* · Organic matter · Streams · Non-native bivalve

C.C. Hakenkamp (✉)¹ · M.A. Palmer
Department of Biology,
University of Maryland,
College Park, MD 20742, USA

Present address:

¹Department of Biology,
James Madison University,
Harrisonburg, VA 22807, USA,
e-mail: hakenkcc@jmu.edu

Introduction

A central goal of ecology is to elucidate factors controlling important ecological processes. Recent work has shown that in some instances the effect of a single species on ecological processes may be profound (Grime 1997; Hooper and Vitousek 1997). While terrestrial and aquatic ecologists often focus on species impacting community interactions (Paine 1969; Krebs 1985; Power et al. 1996), less attention is given to how individual species and species interactions influence resource availability and maintenance of habitat (Jones et al. 1994; Freckman et al. 1997). A focus on how organisms influence resource availability allows us to link whole-system “performance” (e.g., rates of decomposition) to underlying biological mechanisms (Baskin 1994; Grimm 1995). Admittedly, such a focus requires that one identify “important” ecosystem processes. In aquatic ecosystems primary production, respiration, decomposition, and organic matter retention are generally viewed as important to ecosystem integrity (Angermeier and Karr 1994; Freckman et al. 1997; Palmer et al. 1997).

Species that have recently colonized an ecosystem can impact ecosystem processes if they become abundant and dominate resource use (Baskin 1994; Williamson and Fitter 1996) or if they alter food web structure (D’Antonio and Dudley 1995). While exotic species often negatively impact communities and ecosystems (OTA 1993), the outcome of species invasion is often unpredictable and thus may or may not have obvious consequence (see Moyle and Light 1996; Williamson and Fitter 1996).

Here we focus on the functional role of a non-native bivalve, *Corbicula fluminea* Müller (= *Corbicula manilensis*) in a stream ecosystem. *Corbicula* has been a very successful invasive species in North American streams and lakes since its introduction in the 1930s (McMahon 1991). In some sandy streams, this bivalve can dominate the benthic invertebrate community both numerically and in terms of biomass (Lauritsen and Mozley 1989;

Poff et al. 1993), and can increase nutrient mineralization rates and water clarity (Buttner 1986; Lauritsen and Mozley 1989; Phelps 1994). Our study was designed to determine if the invasion of *Corbicula* had altered organic matter cycling in Goose Creek, a fourth-order, sandy-bottom stream in Northern Virginia.

Corbicula is already known to be an important filterer of phytoplankton and seston from the water column (Lauritsen 1986a; Leff et al. 1990; Boltovsky et al. 1995). Recently, *Corbicula* has also been shown to collect food within the streambed through pedal-feeding (using cilia on the foot to collect subsurface organic matter; Cleland 1988; Reid et al. 1992). However, the relative importance of pedal-feeding and filter-feeding has not been examined, and nothing is known about how pedal-feeding could affect the streambed. From the perspective of organic matter cycling, pedal- and filter-feeding by *Corbicula* has the potential to impact the rates at which organic matter is transformed in both the streambed and the overlying water column. Thus, where *Corbicula* dominates stream biomass, we predict that: (1) *Corbicula* will decrease the total amount of organic matter in streambed sediments (through consumption of buried organic matter); (2) *Corbicula* growth rates should be greater for bivalves allowed to both pedal- and filter-feed, compared to those restricted to filter-feeding only; and (3) *Corbicula* will dominate benthic metabolism (as measured by respiration) due to high biomass and high metabolic rates relative to other streambed fauna.

Materials and methods

Study site and *Corbicula* life history

Goose Creek, a fourth-order stream in northern Virginia, is a wide (c. 20 m), low gradient stream dominated by long stretches of sandy bottom (median grain size = 1 mm). The stream drains approximately 800 km² of farmland and forests and the riparian zone is dominated by deciduous trees including black gum, hackberry, oaks, sycamore, and box alder (for a full description of the site, see Palmer 1990; Poff et al. 1993). Average stream discharge is 8.5 m³ s⁻¹, with summer minimums typically approaching zero discharge, and maximum flows during the spring that often cause bed scour (Palmer et al. 1992).

The biomass of *Corbicula* in Goose Creek is estimated to equal the biomass of all meiofauna in the stream and to exceed the biomass of all other macrofauna combined (Poff et al. 1993). Numerically, the density of *Corbicula* in Goose Creek (c. 1372 m⁻²) falls within the range reported for many other studies (see Isom 1986). In Goose Creek, *Corbicula* reproduces twice during the year, ranges in size from 0.25 to 30 mm and occurs almost exclusively in the top 10 cm of the stream sediments.

Experiment 1: relative importance of *Corbicula* to streambed respiration rates

In March 1997, we conducted a laboratory experiment to compare the amount of oxygen consumed by *Corbicula* with that consumed by all the other combined biota (macrofauna, meiofauna, protists, and microbes) in the streambed sediments. *Corbicula* and stream sediment were collected by gently shoveling sediment into plastic containers. In the laboratory, *Corbicula* was held with stream water

and sediment at the experimental temperature (18°C) until used (<24 h). Stream sediment (50 ml) was added to 150-ml flasks ($n = 16$) wrapped with duct tape to block light. Flasks were filled with commercially available, filtered (0.2 µm) spring water and randomly assigned to one of four treatments: 0, 1, 2, or 3 bivalves added (size 15–20 mm shell length). Treatments were chosen to represent the range of densities in Goose Creek (Poff et al. 1993): 1 bivalve (=625 individuals m⁻²) represented approximately half field density; 2 bivalves (=1250 individuals m⁻²) represented field density; 3 bivalves (=1875 individuals m⁻²) represented more than field density. The high-density treatment was chosen to mimic densities found in other streams (e.g., Isom 1986). To keep the volume of water displaced by bivalves similar in all flasks, control shells (cleaned shells of dead bivalves glued together) were placed in 0-, 1-, and 2-bivalve treatment flasks to bring the total number of bivalves or shells in each flask to three.

After adding bivalves, all flasks were sealed and incubated together for 1 h at 18°C. Oxygen concentrations were measured (OM-1 probe, Microelectrodes, Inc.) at the beginning and end of the incubation. Dry tissue weight of all live bivalves was measured after removing the tissue from shells. Abundance of other fauna in the sediments (bacteria, protists and meiofauna) was not quantified. Regression analysis was used to determine if the amount of oxygen consumed was significantly related to total *Corbicula* dry weight. For this and all other statistical tests, required model assumptions were verified (e.g., homogeneity of treatment variances, normality of model residuals) and all analyses were completed using SAS version 6.10 or 6.12.

Experiment 2: *Corbicula* consumption of sediment organic matter

In April 1996, we conducted a laboratory experiment to determine if pedal-feeding by *Corbicula* could substantially decrease buried organic matter in stream sediments. The day before the experiment, *Corbicula* and stream sediment were collected from Goose Creek and returned to the laboratory where all bivalves were removed from the sediment, patted dry, and weighed. Stream sediment (100 ml) was placed in the bottom of each of 12 plastic containers (volume = 2 l). All containers received 0.75 g of dried, crushed sycamore leaves collected from the riparian zone at the study site (abscised *Plantus* leaves, no particles larger than 1 mm) to provide a single addition of organic carbon. The containers were randomly assigned to either a "no-*Corbicula*" treatment ($n = 6$) or a "with-*Corbicula*" treatment ($n = 6$). For the containers receiving *Corbicula*, approximately 5 g wet mass of live bivalves (± 0.2 patted dry weight with shell) was added (12–14 bivalves ranging in size from 5 to 15 mm; approximates field densities). Containers were randomly assigned a place in an incubator outfitted with a grow-light (12-h light/dark cycles) and maintained at 19°C. Oxygen and water levels were maintained using aquarium air pumps and by adding fresh, commercially available, filtered (0.2 µm) spring water every few days (container water volume = 1.7 l). It is important to point out that pedal-feeding was favored in these flasks since no suspended particulate material (e.g., seston) was added experimentally or was resuspended by aeration. This was tested by sampling 200 ml water from each container 1 week into the incubation; pelagic organic matter concentration (percent weight loss on ashing) was not significantly different from zero (t -test, $P > 0.05$, $n = 12$). Containers were rotated within the incubator every few days to minimize any effects of location. After 3 weeks, sediments were collected and frozen. Bivalves were patted dry and reweighed (with shell). Sediments were dried, weighed, heated to 550°C for 3 h, and reweighed to determine percent weight loss after ashing (=organic matter content). The average initial sediment organic matter concentration was estimated by ashing six sediment samples collected and treated in the same manner (e.g., with 0.75 g added leaf material) except that bivalves had never been added. The change in percent sediment weight loss for the no-*Corbicula* treatment and the with-*Corbicula* treatments was calculated by subtracting final values from the average initial value. Organic matter concentrations were then compared between the two treatments using an ANOVA.

Experiment 3: the influence of pedal- and filter-feeding on *Corbicula* growth

In July 1995, we conducted a field experiment to determine if pedal-feeding increased *Corbicula* growth rates. Bivalves (10 groups of 10 individuals) were collected by hand from the study site the day before the experiment. Each group of bivalves was weighed (patted dry wet mass) and was assigned to either a water column ("water-column") or water column and sediment ("water-column + sediment") treatment. In the field, the water-column + sediment bivalves were placed in the bottom half of a plastic cage partially buried in the streambed (see Fig. 1 for cage details) allowing the bivalves to both filter- and pedal-feed. Bivalves in the top of the cage (water-column treatment) were separated from the sediments by a permeable plastic partition *c.* 15 mm off the stream bottom and could only filter-feed. A total of five cages were used. Daily high temperature at the stream varied between 15–18°C. After 2 weeks, the bivalves were returned to the laboratory, patted dry, and reweighed. Within a cage, the difference in total weight gained (g) between the group of ten bivalves in the top of the cage and the group of ten bivalves in the bottom of the cage was calculated (patted dry wet mass, with shell). The mean differences in growth were compared with zero (i.e., no difference in weight gained between treatments) using a paired *t*-test.

Two experimental assumptions for this field experiment were examined with laboratory and field experiments. Water velocity was low at the site ($< 5 \text{ cm s}^{-1}$), minimizing cage artifacts but allowing sufficient water movement through the cages to ensure that the bivalves in the bottom half of the cage did not receive significant fecal or pseudofecal material from bivalves in the top of the cages. To check this assumption, the dry weight of fine particulates reaching the bottom of the cages (in 2 h) was compared between cages with live bivalves and with control shells only. Weight of particulates entering the lower half of a cage was not significantly different between live bivalve cages and control cages (mean for both cages identical = $0.09 \pm 0.02 \text{ mg}$, *t*-test, $P = 0.96$, $n = 4$). We also examined the assumption that filtration rates did not vary between buried and unburied bivalves by measuring filtration rates on suspended colloidal carbon (graphite, as measured with spectrophotometry). Single bivalves were placed in 500-ml flasks with either no sediment ("no-sediment") or with 50 ml of sediment ("with-sediment"). To estimate how much graphite was lost from the water due to passive settlement (i.e., not filtration), we also ran a set of controls. Control shells (dead bivalves glued together) were placed in flasks with or without sediment ("with-sediment control"; "no-sediment control"). Flasks ($n = 14$ for each of the 4 treatments) were incubated at 18°C, water was kept in motion using aerators and initial and final ab-

sorbance values (after 2 h) determined for each flask. Percent change in absorbance was corrected for settling using the control flask results, and for the amount of dry tissue weight of the bivalve. Filtration rates were not significantly different for bivalves buried in sediments compared to unburied bivalves (buried mean percent change in absorbance = 0.33 ± 0.11 , unburied mean percent change in absorbance = 0.39 ± 0.11 ; ANCOVA, $P = 0.66$, $R^2 = 0.01$).

Experiment 4: impact of *Corbicula* on streambed organic matter concentrations

In August 1997, we completed a field experiment to examine whether the presence of *Corbicula* resulted in a net change in streambed organic matter concentrations. To examine this, cages (same cages as in experiment 3, with central plastic partition removed) were filled with streambed sediment from which all visible *Corbicula* had been removed. To each cage, no, two, four, or six live bivalves (collected on site at the start of the experiment, all *c.* 15 mm in size) were added along with enough control shells (glued valves) to bring the total number of bivalves in each cage to six ($n = 4$ cages per treatment). Cages were gently pushed into the stream sediments leaving *c.* 2 cm of the cage above the streambed to allow bivalves to filter-feed. Cages were arranged 30 cm apart in four complete blocks. Blocks were *c.* 5 m apart and perpendicular to flow. Daily high temperature at the study site varied between 18 and 30°C during the field study.

After 3 weeks, bivalves were collected from each cage and then two sediment cores (2.5 cm diameter) were taken from within each cage to measure organic matter concentration. Ambient cores from surrounding sediments were also collected in each block (2 cores per block) to determine whether there was a cage effect on organic matter concentrations. Samples were returned to the laboratory on ice. *Corbicula* biomass (dry tissue weight, without shell) and sediment organic matter (percent weight loss after ashing) were determined. Data were analyzed as a randomized complete block ANCOVA where blocks were modeled as random factors, the treatment main effect was tested using the block by treatment interaction as the error term, and *Corbicula* biomass was a covariate. Means were compared using an LSD means comparisons test.

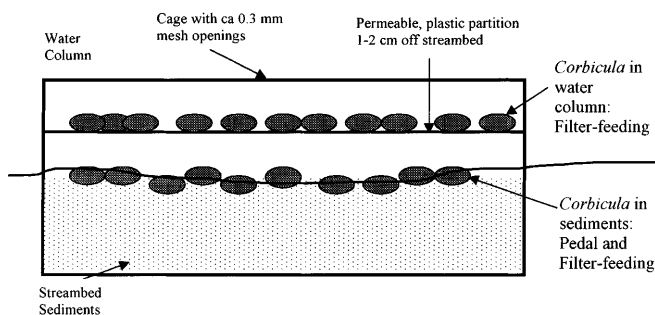


Fig. 1 Diagram of plastic cage (Whitlock-Vibert box, American Fly Fishers Association) used for field experiments (experiments 3 and 4). Cage dimensions are 15 cm wide by 6 cm deep and 9 cm high. For experiment 3, bivalves in the top half of the cage were held 1–2 cm above streambed sediments by a permeable plastic partition. This partition was removed for experiment 4. Top of cage extended less than 5 cm into water column

Results

Experiment 1: relative importance of *Corbicula* to streambed respiration rates

Increasing the biomass of *Corbicula* in sediments significantly increased the amount of oxygen consumed in flasks ($R^2 = 0.76$, H_0 : slope = 0 rejected, $P < 0.01$; Fig. 2). The *Y*-intercept on Fig. 2 (0.19 mg h^{-1}) represents the best estimate of the amount of respiration that can be attributed to organisms other than *Corbicula* in the flask sediments ($= c. 4 \text{ cm}^3$ of streambed). These organisms include all other macrofauna, meiofauna (including meiofaunal-sized *Corbicula*), protists, and microbes. At average *Corbicula* field abundances (*c.* 0.1 g dry weight), oxygen consumption in the flasks was *c.* 0.35 mg h^{-1} . Thus, *Corbicula*'s contribution to total oxygen consumption in the shallow streambed sediments is approximately 46% $\{[(0.35 - 0.19 \text{ mg h}^{-1}) / 0.35 \text{ mg h}^{-1}] \times 100\}$, suggesting that *Corbicula* is an important oxygen consumer in the streambed.

Experiment 2: *Corbicula* consumption of sediment organic matter

After incubation, a significantly greater decrease in sediment organic matter concentration was found for the with-*Corbicula* treatment compared to the no-*Corbicula* treatment (ANOVA: $F_{1,11} = 6.10$, $P < 0.05$, Fig. 3). Loss of organic matter was greater in the with-*Corbicula* (=0.22% weight loss) than in the no-*Corbicula* treatment (=0.15% weight loss) after 3 weeks. The presence of *Corbicula* increased the rate of organic matter loss by 0.07%, which is roughly equal to 50 mg of organic matter per bivalve per day (given that 1 ml sediment = 1.4 g dry weight). Thus, when conditions favored pedal-feeding (i.e., no material available to filter out of water column), *Corbicula* consumed

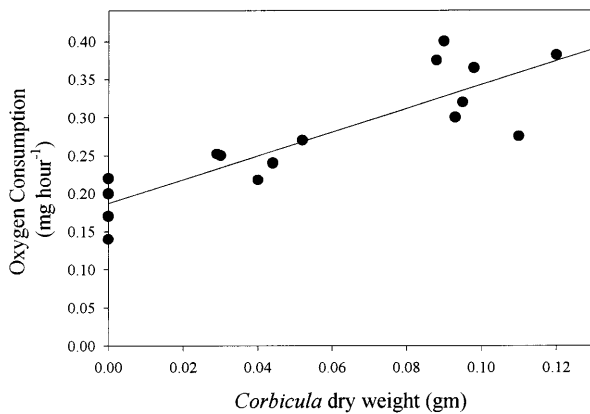


Fig. 2 Experiment 1: regression of oxygen consumption rate on *Corbicula* dry weight (tissue weight without shells). Both slope and intercept are significantly different from zero ($P < 0.05$). Equation for best fit line is: Oxygen consumed = $0.19 + (1.58 \times \text{Corbicula dry weight})$

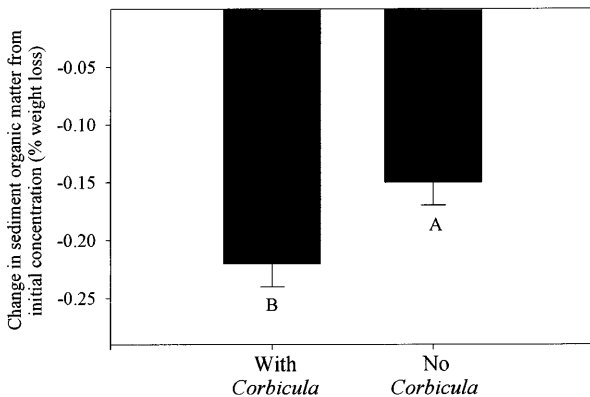


Fig. 3 Experiment 2: comparison of the change from initial concentrations in sediment organic matter (% weight loss after ashing) for containers with *Corbicula* or without *Corbicula* ($n = 6$ per treatment). No suspended food (for filter-feeding) was added to containers to allow quantification of pedal-feeding on buried organic matter concentration. Standard error bars are shown; means sharing letters are not significantly different ($P > 0.05$, ANOVA comparing two means)

detectable amounts of organic material in stream sediments by pedal-feeding.

Experiment 3: the influence of pedal- and filter-feeding on *Corbicula* growth

Bivalves able to both pedal- and filter-feed gained more weight than bivalves only able to filter-feed (Fig. 4); the difference was statistically significant (paired t -test on difference between growth in top of cage and bottom of cage, $H_0: \mu_{\text{difference}} = 0$ was rejected, $t_{0.05,4} = 4.11$, $P < 0.02$). The weight gain (after 2 weeks) was considerably greater (by 55%) for bivalves with access to stream sediments. The difference between the amount of weight gained during the experiment (0.68 g water-column + sediment treatment vs. 0.38 g water-column treatment) is an estimate of added growth attributable to pedal-feeding (=0.30 g for ten bivalves over 2 weeks, or $c. 2 \text{ mg bivalve}^{-1} \text{ day}^{-1}$). Individuals able to supplement filter-feeding with pedal-feeding on buried organic material grew at a faster rate than individuals that could only filter-feed.

Experiment 4: impact of *Corbicula* on streambed organic matter concentrations

When *Corbicula* was allowed to both pedal- and filter-feed, the concentration of organic matter in nearby

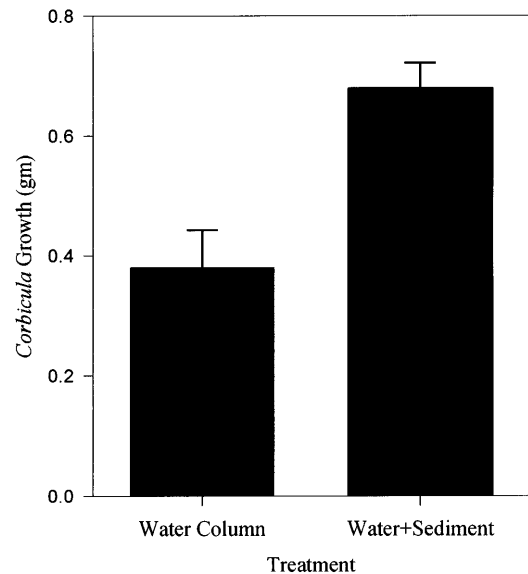


Fig. 4 Experiment 3: *Corbicula* growth (g weight gained in 2 weeks) when bivalves were able to feed from the water only, or from the water and sediments (bivalve number = 10 for each treatment within a cage, $n = 5$ cages). Standard error bars are shown. Growth means shown for comparison; statistical analysis computed on difference between treatments within a cage. Growth was significantly greater in bivalves with access to both water and sediments (paired t -test, $P < 0.05$, $t_{0.05,4} = 4.107$)

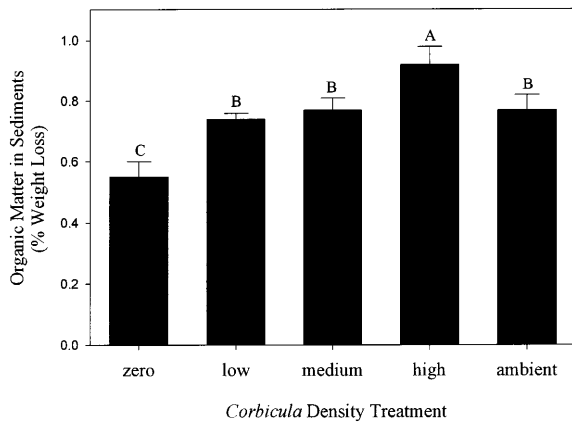


Fig. 5 Experiment 4: comparison between sediment organic matter (% weight loss after ashing) in cages with varying densities of *Corbicula* (0, 2, 4, 6) or from nearby ambient sediments ($n = 4$ per treatment). Means and SEs are shown; means sharing the same letter are not significantly different (LSD means comparison tests, $P > 0.05$)

streambed sediments was significantly greater in cages with large abundances of *Corbicula* (treatment main effect: $F_{4,13} = 5.04$, $P < 0.02$), and decreased as the abundance of bivalves decreased (Fig. 5). Treatments with no *Corbicula* (but with meiofauna, macrofauna, and so on) had the lowest organic matter concentrations. The low- and medium-density treatments were not significantly different in organic matter concentration from the ambient treatments. *Corbicula* biomass was not a significant covariate ($F_{1,13} = 1.66$, $P = 0.22$); however, inclusion of the covariate did decrease residual variance and so was left in the model. In the field, the net result of filter- and pedal-feeding is an increase in sediment organic matter.

Discussion

C. fluminea, a species of bivalve that is well established, but not native to Goose Creek, impacts organic matter dynamics in this ecosystem in a number of important ways. *Corbicula* contributed strongly to total metabolism in streambed sediments as shown by their high rates of respiration. Since every 1 mole of oxygen consumed by *Corbicula* is roughly equivalent to the release of 1 mole of carbon in the form of carbon dioxide (e.g., Bott 1996), the high respiration rate found for *Corbicula* reflects significant utilization of organic matter resources. To meet this resource need, *Corbicula* both filter-feeds on organic matter in the water column and pedal-feeds on organic matter in the streambed sediments. These dual feeding modes support this bivalve's rapid growth rate. These results, added to the fact that *Corbicula* dominates this stream's metazoan biomass (Poff et al. 1993), suggest that with respect to carbon dynamics, *Corbicula* may be the single most important species in this stream. Below, we examine the experi-

mental results as they relate to the functional role of *Corbicula* in this stream.

As predicted (Introduction), our results show that *Corbicula* is an important component of the aerobic community in these stream sediments: the addition of 0.1 g dry weight of *Corbicula* (c. ambient field density) almost doubled respiration (Fig. 2). The increased respiration should be attributable directly to *Corbicula* metabolism given that the experiment was too short in duration for indirect effects (e.g., bioturbation) to have been a confounding factor. Respiration by *Corbicula* has been previously predicted to exceed respiration by other metazoa in this stream using biomass-based respiration conversion coefficients (Poff et al. 1993). This research confirms that prediction and further shows that respiration by *Corbicula* was also greater than protist and microbial respiration under normal field densities (comparison of 0 and 0.1 g dry weight of *Corbicula*, Fig. 2). These respiration rates are reasonable for *Corbicula* given its large body size compared to other invertebrates in Goose Creek (Banse 1982).

Corbicula is abundant in many streams (Isom 1986) and, given the considerable magnitude of *Corbicula* respiration, may play an important role in benthic metabolic processes. While *Corbicula* is common in the top 10 cm of Goose Creek sediments, the streambed or hyporheic zone may actually extend to about 50 cm deep and respiration by the hyporheic fauna (e.g., invertebrates, protists and bacteria) can be considerable (Grimm and Fisher 1984). However, even when we estimated hyporheic respiration rates for the entire streambed using the community respiration rates measured for the surficial sediments (Fig. 2), *Corbicula* still comprised $> 10\%$ of total respiration in these streambeds.

The magnitude of respiration by *Corbicula* suggests that this bivalve requires a considerable amount of organic matter to support high metabolism. Thus, the ability of *Corbicula* to pedal-feed on benthic pools of organic matter in this stream helps support high metabolism as well as rapid growth rates (Aldridge and McMahon 1978; McMahon 1991). While pedal-feeding by marine bivalves on buried organic matter has already been shown (e.g., *Nucula proxima*; Cheng and Lopez 1991), pedal-feeding by freshwater bivalves has been less extensively documented (Cleland 1988; Reid et al. 1992). Given the ability of *Corbicula* to feed on buried organic matter, the effect of pedal-feeding by freshwater bivalves (both native and non-native species) deserves further attention as a potentially important form of deposit-feeding in streams.

In this study, two of the experiments attempted to quantify the importance of pedal-feeding relative to filter-feeding (experiments 2 and 3). To compare these experiments, we contrasted the amount of organic matter consumed by pedal-feeding in the laboratory (experiment 2) and the amount of growth measured when pedal-feeding occurred in the field (experiment 3) using literature values for net production and assimila-

tion efficiencies. When *Corbicula* was only allowed to feed on buried organic matter (experiment 2), organic matter was consumed at a rate of 50 mg bivalve⁻¹ day⁻¹ (Results). Previous research on *Corbicula* has estimated its net production efficiency as *c.* 70% (Aldridge and McMahon 1978; Lauritsen 1986b), and while unstudied for *Corbicula*, assimilation efficiency on buried organic matter is generally thought to be low across most taxa (e.g., 10–30%, Valiela 1995). Given these estimates, we would have predicted that pedal-feeding allowed 3.5–10.5 mg weight gain bivalve⁻¹ day⁻¹ given the consumption rate observed (experiment 2). While growth was not measured in the laboratory experiment, weight gain attributable to pedal-feeding in the field study was lower than this estimate (Results, experiment 3; 2 mg bivalve⁻¹ day⁻¹). There are several reasons why this discrepancy is probably due to higher than expected loss rates on buried organic matter in the laboratory experiment. First, the presence of *Corbicula* may have stimulated the metabolic activity of other organisms (i.e., bioturbation of protists and bacteria; Levinton 1995) and thus increased organic matter use in containers with *Corbicula* relative to those without *Corbicula*. Second, since bivalves in the laboratory experiment could only feed on buried organic matter (no seston), growth was entirely dependent on pedal-feeding, and consumption rates may have exceeded those in the field where filter-feeding also supported growth.

While our experiment shows that pedal-feeding by *Corbicula* can decrease sediment organic matter under specific laboratory conditions (no seston), in the field, the effect of filter-feeding has the opposite effect. When filter-feeding could occur (experiment 4), there was a net gain in the amount of organic matter in sediments, presumably due to deposition of unassimilated material (feces and pseudofeces). Thus, while *Corbicula* does consume buried organic matter, our prediction that *Corbicula* would decrease the total amount of organic matter in the streambed under natural conditions was not met. The increase in sediment organic matter suggests that *Corbicula* enhances removal of suspended material in the water column and increases deposition of organic matter to sediments.

Thus, from a functional point of view, *Corbicula* has probably changed the physical structure of the stream sediments in a manner similar to that found for some marine deposit-feeding bivalves (Levinton 1995; Dame 1996), as well as for freshwater zebra mussels (Roditi et al. 1997). This may include changing the size, bio-availability, quantity, and quality (e.g., nitrogen content) of sediment organic material (Roditi et al. 1997), or by influencing factors such as sediment stability and interstitial water chemistry (e.g., oxygen concentrations; Levinton 1995; Dame 1996). Given that organic matter concentrations in this stream are small (often *c.* < 1% weight loss on ashing, Hakenkamp 1997), species that can influence organic matter distribution may play an important role in controlling availability of that resource for themselves and other organisms.

The greatest impact of pedal-feeding by *Corbicula* on sediment organic matter stores probably occurs during long periods of low flow (4–6 months of the year in Goose Creek) which are typical of many sandy-bottom streams. In streams, variability in organic matter stores is often assumed to be primarily associated with high flow events that bury organic matter and may resuspend into the water any material deposited by bivalves (Roditi et al. 1997). While *Corbicula*'s influence may be modest during these flood periods, between floods and during baseflow periods, organic material stores may be significantly influenced by *Corbicula*.

From this study and others, it is clear that *Corbicula* is important in these systems as a benthic-pelagic coupler (Lauritsen 1986a). Where *Corbicula* is abundant, these bivalves have been shown to influence seston size (Leff et al. 1990), and cause large decreases (20–70%) in suspended chlorophyll *a* levels (Cohen et al. 1984). For Goose Creek, *Corbicula* functions almost uniquely in the streambed, in part, because all other metazoan filter-feeders occur in much lower abundances and biomass compared to *Corbicula* (Poff et al. 1993). These “other” filter-feeders include native bivalves (extremely rare), insects such as caddisflies, mayflies, and black flies inhabiting riffles (which are a rare habitat in our study system) and other invertebrates inhabiting the sandy channels (e.g., rotifers and chironomids). Further, *Corbicula* is the only species of filter-feeder in this system that also deposit-feeds, so *Corbicula* occupies a place in the Goose Creek trophic web that differs functionally from the native assemblage of species.

Our experimental results strongly suggest that *Corbicula* has important impacts on carbon dynamics in Goose Creek, and similar impacts are likely in other sandy streams where this bivalve species is abundant. Further, *Corbicula* is an important coupler between the water column and the stream sediments because this bivalve dominates filter-feeding in this stream and also pedal-feeding on buried organic material. Thus, feeding and metabolism by *Corbicula* may have significant impacts on the concentration of stored organic matter in stream sediments. Further research is needed to explore what effect *Corbicula* may have on other members of the streambed community (e.g., microbes, protists, meiofauna), either through consumption or as a result of *Corbicula*'s affect on organic matter dynamics. Given that *Corbicula* occurs in large densities throughout the southern and middle latitudes in the United States (McMahon 1991), limited only by cold temperatures (McMahon 1991) and acidic conditions (Stites et al. 1995), *Corbicula* has the potential to influence ecosystem function in hundreds, if not thousands of streams.

Acknowledgements We thank Matthew Goodman, Nolana Kabwit, Suzanna Ribblett, and Chris Smith for help in the field and laboratory. We also thank Irv Forseth, Diane Lauritsen, Bob McMahon, LeRoy Poff, Marjorie Reaka, Skip Pierce, Dave Strayer and the Maryland Stream Group (Kären Nelson, Brad Cardinale, Marcia Shofner, and Chris Swan) for discussion and comments that improved the manuscript. This research was

supported by the Washington Biologists' Field Club to Chris Hakenkamp and NSF grants DEB 9318060 and 9741101 to Margaret Palmer.

References

- Aldridge DW, McMahon RF (1978) Growth, fecundity, and energetics in a natural population of the Asiatic freshwater clam, *Corbicula manilensis* Philippi, from north central Texas. *J Molluscan Stud* 44:49–70
- Angermeier PL, Karr JR (1994) Biological integrity versus biological diversity as policy initiatives. *BioScience* 44:690–697
- Banse K (1982) Mass-scaled rates of respiration and intrinsic growth in very small invertebrates. *Mar Ecol Progr Ser* 9:281–297
- Baskin Y (1994) Ecosystem function of biodiversity. *BioScience* 44:657–660
- Boltovskoy D, Izaguirre I, Correa N (1995) Feeding selectivity of *Corbicula fluminea* (Bivalvia) on natural phytoplankton. *Hydrobiologia* 312:171–182
- Bott TL (1996) Primary productivity and community respiration. In: Hauer FR, Lamberti GA (eds) *Methods in stream ecology*. Academic Press, San Diego, pp 533–556
- Buttner JK (1986) Biology of *Corbicula* in catfish rearing ponds. In: Britton JC (ed) *Proceedings of the Second International Corbicula Symposium* (American Malacological Bulletin special edition 2). American Malacological Union, Hattiesburg, pp 211–218
- Cheng I-J, Lopez GR (1991) Contributions of bacteria and sedimentary organic matter to the diet of *Nucula proxima*, a deposit-feeding protobranchiate bivalve. *Ophelia* 34:157–170
- Cleland JD (1988) Ecological and physiological considerations of deposit-feeding in freshwater bivalve, *Corbicula fluminea*. Masters Thesis, University of Texas, Arlington
- Cohen RRH, Dresler PV, Phillips EPJ, Cory RL (1984) The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol Oceanogr* 29:170–180
- Dame RF (1996) *Ecology of marine bivalves: an ecosystem approach*. CRC, Boca Raton
- D'Antonio CM, Dudley TL (1995) Biology of invasions as agents of change on islands versus mainlands. In: Vitousek PM, Loope LL, Adersen H (eds) *Islands* (Ecological Studies, vol 115). Springer, Berlin Heidelberg New York, pp 103–121
- Freckman DW, Blackburn TH, Brussaard L, Hutchings P, Palmer MA, Snelgrove PVR (1997) Linking biodiversity and ecosystem functioning of soils and sediments. *Ambio* 26:556–562
- Grime JP (1997) Biodiversity and ecosystem function: the debate deepens. *Science* 277:1260–261
- Grimm NB (1995) Why link species and ecosystems? A perspective from ecosystem ecology. In: Jones CG, Lawton JH (eds) *Linking species and ecosystems*. Chapman Hall, New York, pp 5–15
- Grimm NB, Fisher SG (1984) Exchange between interstitial and surface water: implications for stream metabolism and nutrient cycling. *Hydrobiologia* 111:219–228
- Hakenkamp CC (1997) Oxygen consumption in streambeds: examining the impacts of environmental factors and hyporheic fauna. PhD Dissertation, University of Maryland, College Park
- Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305
- Isom BG (1986) Historical review of Asiatic clam (*Corbicula*) invasion and biofouling of waters and industries in the Americans. In: Britton JC (ed) *Proceedings of the Second International Corbicula Symposium* (American Malacological Bulletin special edition 2). American Malacological Union, Hattiesburg, pp 1–6
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Krebs CJ (1985) *Ecology. The experimental analysis of distribution and abundance*. Harper and Row, New York
- Lauritsen DD (1986a) Filter-feeding in *Corbicula fluminea* and its effect on seston removal. *J N Am Benthol Soc* 5:165–172
- Lauritsen DD (1986b) Assimilation of radiolabeled algae by *Corbicula*. In: Britton JC (ed) *Proceedings of the Second International Corbicula Symposium* (American Malacological Bulletin special edition 2). American Malacological Union, Hattiesburg, pp 219–222
- Lauritsen DD, Mozley SC (1989) Nutrient excretion by the Asiatic clam *Corbicula fluminea*. *J N Am Benthol Soc* 8:134–139
- Leff LG, Burch JL, McArthur JV (1990) Spatial distribution, seston removal, and potential competitive interactions of the bivalves *Corbicula fluminea* and *Elliptio complanata*, in a coastal plain stream. *Freshwater Biol* 24:409–416
- Levinton JS (1995) Bioturbators as ecosystem engineers: control of the sediment fabric, inter-individual interactions, and material fluxes. In: Jones CG, Lawton JH (eds) *Linking species and ecosystems*. Chapman Hall, pp 29–36
- McMahon RF (1991) Mollusca: Bivalvia. In: Thorp JH, Covich AP (eds) *Ecology and classification of North American freshwater invertebrates*. Academic Press, San Diego, pp 315–399
- Moyle PB, Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. *Biol Conserv* 78:149–161
- OTA (1993) *Harmful nonindigenous species in the United States*. Office of Technology and Assessment, United States Congress, Washington
- Paine RT (1969) A note on trophic complexity and community stability. *Am Nat* 103:91–93
- Palmer MA (1990) Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek, Virginia. *J N Am Benthol Soc* 9:17–25
- Palmer MA, Bely AE, Berg KE (1992) Response of invertebrates to lotic disturbance: a test of the hyporheic refuge hypothesis. *Oecologia* 89:182–194
- Palmer MA, Covich AP, Finlay BJ, Gibert J, Hyde KD, Johnson RK, Kairesalo T, Lake S, Lovell CR, Naiman RJ, Ricci C, Sabater F, Strayer D (1997) Biodiversity and ecosystem processes in freshwater sediments. *Ambio* 26:571–577
- Phelps HL (1994) The Asiatic clam (*Corbicula fluminea*): invasion and system-level ecological change in the Potomac River estuary near Washington, D.C. *Estuaries* 17:614–621
- Poff NL, Palmer MA, Angermeier PL, Vadas Jr RL, Hakenkamp CC, Bely A, Arensburger P, Martin AP (1993) The size structure of a metazoan community in a Piedmont stream. *Oecologia* 95:202–209
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills S, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *BioScience* 46:609–620
- Reid RGB, McMahon RF, Foighil DO, Finnigan R (1992) Anterior inhalant currents and pedal feeding in bivalves. *Veliger* 35:93–104
- Roditi HA, Strayer DL, Findlay SEG (1997) Characteristics of zebra mussel (*Dreissena polymorpha*) biodeposits in a tidal freshwater estuary. *Arch Hydrobiol* 140:207–219
- Sites DL, Benke AC, Gillespie DM (1995) Population dynamics, growth, and production of the Asiatic clam, *Corbicula fluminea*, in a blackwater river. *Can J Fish Aquat Sci* 52:425–37
- Valiela I (1995) *Marine ecology processes*. Springer, Berlin Heidelberg New York
- Williamson MH, Fitter A (1996) The characters of successful invaders. *Biol Conserv* 78:163–170