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The functional role of native freshwater mussels in the fluvial benthic environment

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SUMMARY

1. Freshwater mussels are the dominant consumer biomass in many fluvial systems. As filter feeding grazers, mussels can remove large amounts of particulate matter from the water column and transfer these resources to the substrate as biodeposits (agglutinated mussel faeces and pseudofaeces). Mussel biodeposits are a nutrient rich and easily assimilated food source and therefore may have significant relevance to benthic community structure. This study examines the functional role of *Margaritifera falcata* in the South Fork Eel River, California.
2. We addressed two main questions: (i) Do mussels increase benthic resources in this system? (ii) If so, does this alter macroinvertebrate community structure?
3. Measurements and enclosure experiments in the South Fork Eel River show that mussels can play a significant role in local food webs by increasing available fine particulate matter (both organic and inorganic) on the substrate. We document increased benthic macroinvertebrate biomass for predators and collectors (Leptophlebidae) in the presence of mussels, but only in late summer.

Keywords: benthic, biodeposit, California, fluvial, food web, freshwater mussels, functional role, trophic

Introduction

Freshwater mussels are abundant benthic-pelagic couplers in streams (Leff, Burch & McArthur, 1990; Strayer *et al*., 1999; Vaughn, Gido & Spooner, 2004). As nearly stationary filter-feeders, mussels can remove large amounts of particles from the water column and transfer these resources to the substrate as biodeposits (mussel faeces and pseudofaeces). Small, suspended particles that may not otherwise settle from the water are made available as a food or structural resource at the bed, thereby potentially stimulating benthic productivity.

The cycling of fine particulate matter is critical for the sustenance of stream ecosystems (Vannote *et al*., 1980; Allan, 1999), providing nutrients and energy to both suspension feeders (Wallace & Merritt, 1980) and deposit feeders (Berg, 1994; Wotton, 1994; Zweig & Rabeni, 2001). Deposit feeding organisms have more food available to them if organic content of the substrate is high. Although an important resource, benthic organic standing crops are rarely considered in stream research (Benke *et al*., 1984; Merritt & Cummins, 1996; Wallace & Grubaugh, 1996). Fine benthic organic matter (FBOM) stores vary both spatially and temporally in streams (Martinez *et al*., 1998; Wanner *et al*., 2002; Galas & Dumnicka, 2003; Magana & Bretschko, 2003), with large stores usually associated with pools or debris dams in headwater streams and with low flow conditions (Bilby & Likens, 1980; Smock, Metzler & Gladden, 1989; Magana & Bretschko, 2003). Organic matter deposition under these conditions occurs passively, via physical stream processes, but can also occur via active biological processes. Nutrient recycling and translocation by

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relatively large stream organisms are important biological processes for increasing nutrient standing stocks in recipient habitats and perhaps stimulating new primary production (Vanni, 2002).

The influence of freshwater bivalves on the benthic environment and macroinvertebrate community has not been well studied in lotic systems. Previous studies of the impacts of large filter feeders focus mainly on native bivalves in marine systems (Navarro & Thompson, 1997) and exotic species in lentic and lotic systems (Klerks, Fraleigh & Lawniczak, 1996; Roditi, Strayer & Findlay, 1997; Stewart, Miner & Lowe, 1999). Exotic species, particularly zebra mussels *Dreissena polymorpha*, (Pallas, 1771) increase the amount and nutritional value of benthic matter in lakes and rivers (Roditi *et al*., 1997; Hakenkamp & Palmer, 1999) and in turn increase the abundance of macroinvertebrates (Stewart & Haynes, 1994; Horvath, Martin & Lamberti, 1999; Stewart *et al*., 1999; Greenwood *et al*., 2001). In marine systems, bivalves increase benthic organic matter, the abundance and diversity of macroinvertebrates and production of macrophytes (Reusch, Chapman & Groger, 1994; Peterson & Heck, 2001).

For mussel biodeposits to be important in lotic systems, deposition rates must exceed advective losses (Strayer *et al*., 1999). In the South Fork Eel River in California, mussels occur almost exclusively in low velocity pools (Howard & Cuffey, 2003). This will certainly restrict advective losses during the summer/autumn low flows, favouring accumulation.

Mussels cycle nutrients via translocation, excretion and egestion. Translocated nutrients (pseudofaeces) and egested nutrients (faeces) may enrich the substrate (Nalepa, Gardner & Malcyk, 1991; Roditi *et al*., 1997; Greenwood *et al*., 2001). This enrichment may in turn result in alteration of the local distribution and abundance of benthic invertebrates (Riccardi, Whoriskey & Rasmussen, 1997). Excreted nutrients are released as solutes and provide nutrients for primary producers (Nalepa *et al*., 1991; Davis, Christian & Berg, 2000). Mussel biodeposits are a nutrient rich and easily assimilated food source (Nalepa *et al*., 1991) and are known to be an important source of both phosphorus (Nalepa *et al*., 1991) and nitrogen (Roditi *et al*., 1997; Greenwood *et al*., 2001).

This study examines the functional significance of native freshwater mussels in the benthic environment. We conducted a series of measurements and experiments in 2002 and 2003 to address the food web implications of mussels as pelagic-benthic couplers. We aimed to determine whether freshwater mussels increase fine benthic resource and, if so, whether macroinvertebrate community structure is altered as a result. We hypothesised that increases in mussel biodeposits will result in increases in collector/gatherers, which in turn will increase predators. We also asked whether characteristics of fine benthic resources associated with mussels might yield information about the cycling of organic matter on the substrate.

Methods

Study site and biota

The research was conducted in the upper reaches of the South Fork Eel River (a fourth order channel) in the northern California Coast Range (Howard & Cuffey, 2003). The study area is located within the 1600-ha Angelo Coast Range Reserve. Vegetation in the study area is primarily old growth Douglas fir (*Pseudotsuga menziesii*) and redwood forest (*Sequoia sempervirens*) with little human modification. The reserve, founded in 1952, was the first Nature Conservancy site west of the Mississippi River. Consequently, this reach of river currently has few human impacts, except for fine sediments from upstream logging from the 1950s to 1970s.

The hydrology of the basin is characteristic of a Mediterranean climate: a seasonal cycle of warm and dry summers but wet and cool winters. The hydrological consequence is a seasonally predictable cycle of flooding in winter and near drought in summer. Lowest flows occur in September with means for the last 35 years ranging from 0.03 to 0.25 $m^3 s^{-1}$ (US Geological Survey 2002), compared with mean January discharge of 1 to 40 $m^3 s^{-1}$.

Two species of mussels are found within the Angelo Coast Range Reserve, *Margaritifera falcata* (Gould, 1850) and *Anodonta californiensis* (Lea, 1852). The location and number of individuals in all mussel aggregations within the study area were documented in 2000 and 2001 (Howard & Cuffey, 2003). The distribution of both species is patchy, with a few local areas of exceptionally high density (Howard & Cuffey, 2003). Using a definition of aggregation as a group of 10 or more individual mussels with <1 m separation between neighbours, there are approximately 120 aggregations (totalling 12 000 individuals) of *M. falcata* and 15

aggregations of *A. californiensis* (totalling 8000 individuals) within the study area. The frequency distribution of aggregate size is approximately exponential, with most aggregations having between 50 and 100 individuals. Mussels in this system occur primarily near channel banks in pools (Howard & Cuffey, 2003). Because of their widespread distribution in the study area we considered only *M. falcata* in the research reported here. Individual *M. falcata* used in the following experiments occur in areas of the channel where *A. californensis* do not occur.

The river channel in our study area is hydraulically rough, with extensive eroded bedrock exposures, coarse bedload and sedge root mats. In this setting, in contrast to low gradient rivers studied elsewhere (Vaughn *et al*., 2004), the physical presence of mussel shells makes no important enhancement of channel roughness and is therefore unlikely to impact the supply of fine particulate matter to the benthic environment through enhancement of channel roughness. For example, Wolman-style pebble counts at various cross-sections with mussels showed that half of substrate clasts (D_{50}) were coarser than 64 mm, whereas mussels are typically burrowed in sediment patches and rock crevices and protrude from the substrate no more than approximately 20 mm (J. Howard, personal observation). Thus in manipulation experiments reported below we did not use control treatments of 'shells only' as carried out by Vaughn *et al*. (2004). Instead our control treatments contain sediment or sections of riverbed with zero mussels.

Assessing mussel contribution to benthic environment

Biodeposition rates. To assess the potential for *M. falcata* to supply biodeposits to the substrate, we directly measured biodeposition rates for mussels taken from the river channel. Although filtering rates have been calculated for many freshwater bivalves (Kryger & Riisgard, 1988; Fanslow, Nalepa & Lang, 1995), we know of no studies that have examined biodeposition rates of *M. falcata* and it is necessary in any case to measure filtering rates from river water at the study site.

To quantify biodeposition rates (both faeces and pseudofaeces), plastic containers (30 in 2002 and 40 in 2003) filled with 1 L of river water filtered through a 63-μm mesh sieve were placed on the river shore in October 2002 and 2003. Fifteen mussels in 2002 and 20 mussels in 2003 (ranging in size from 40 to 80 mm) were removed by hand from the river channel and scrubbed with a scouring pad to remove algae and sediment from the shell. Mussels were then measured to the nearest 0.01 mm and placed in individual containers. Half of the containers in each year were left as controls with no mussels. Half of the mussels were allowed to filter for 1 h, the other half for 2 h. Timing began when mussel siphons were visibly open. When the filtering periods ended, mussels were removed from the containers and the entire contents of all containers filtered onto individual pre-ashed and preweighed glass fibre filters.

To determine dry mass of the biodeposits, the filtered samples were oven dried (50 °C for 24 h), desiccated (24 h) and weighed on an analytical balance. To determine ash-free dry mass, the filters were ashed in a muffle furnace (500 °C for 1 h), desiccated (24 h) and weighed on an analytical balance. Masses provide measures of total dry matter, organic matter or ash free dry mass (dry mass − ash mass) and inorganic matter. We determined biodeposit mass as the difference between masses from buckets with mussels and control buckets. The mass from control buckets proved to be very small (see Results).

In situ *comparison.* We next asked whether this sort of concentrated biodeposition might be causing spatial variation in the concentration of FBOM within the river channel at our study site. To quantify the differences in the concentration of FBOM between mussel and non-mussel areas, a simple in-situ comparison was conducted in summer 2003. Fine benthic matter was collected at eight haphazardly selected sites within known mussel beds and eight selected outside the beds.

Benthic matter was collected using a modified version of the protocol for field collection of fine benthic matter developed by Wallace & Grubaugh (1996). We temporarily emplaced a 26-cm diameter polyvinyl chloride (PVC) pipe extending from above the water surface into the substrate. Using a paddle, we agitated the water within the pipe to dislodge surface benthic matter. The agitation was standardised by using the same number of rotations and a similar rotation rate for each sample. We removed water within the pipe with a 7-cm diameter bailer. Three bails of material were collected and placed in a bucket. The pipe was removed and placed at another

haphazardly selected place within the site and the bailing procedure repeated. We pooled the collected material to obtain a representative sample of the benthic matter at the site. Volume of water in the pipe was calculated from water depth measured with a stadia rod and volume of water in the bailed subsamples was measured using a graded container.

The removed water and material were then filtered through nested 1-mm and 63-μm sieves. The sieves were positioned over a bucket to retain water and small particles that passed through the sieve. Material collected on the 1-mm sieve was discarded because it was too coarse for mussels to process (Nichols & Garling, 2000). Material collected on the 63-μm sieve was washed with distilled water into preweighed, labelled filters. Sample water that passed through the 63-μm sieve was then reagitated to guarantee suspension of the particles and a 1-L subsample collected. The samples were taken back to the laboratory and processed within 24 h.

Three replicates from each 1-L sub-sample were vacuum-filtered onto precombusted and preweighed 47-mm diameter glass-fibre filters with a pore size of 0.5 μm. The volume of water filtered varied between 100 and 300 mL depending upon the concentration of particles on the filters. The filtered samples (both less and greater than 63-μm) were oven dried (50 °C for 24 h), desiccated (24 h) and weighed on an analytical balance. To determine ash-free dry mass (inorganic matter), the filters were ashed in a muffle furnace (500 °C for 1 h), desiccated (24 h) and weighed on an analytical balance. By subtracting ash-free dry mass from total, we obtained a measure of organic matter per sample.

To determine the fine benthic matter concentration at each site, we used the sample water volumes to scale to the total mass of organic matter in the original PVC pipe water columns. Pipe cross-section was then used to scale this total mass to a concentration (mass per area) derived from the bed. Collections were made monthly from July to October 2003. Differences in mean values of benthic material in mussel and non-mussel areas were statistically assessed using the Student's *t*-test ($P = 0.05$).

In-channel experiments. To control for physical habitat variability and to test whether the accumulation of FBOM is because of active biodeposition, we conducted two in-channel experiments. These experiments isolated the impact of mussels on the benthic ecosystem and examined both the quantity of fine benthic deposits and the macroinvertebrate community structure within and outside the aggregations.

The first 'isolation experiment' severely limited water flow rate and isolated the experimental substrate from other stream organisms (see below). The second 'quadrat experiment' allowed nearly unlimited access to other stream organisms and represented more typical channel conditions. Both experiments measured effects of mussels within the channel environment that varies diurnally and seasonally.

1 *Isolation experiment.* In mid-June 2002 we placed in the stream channel twelve 26-cm diameter flow-through buckets with 0.5 mm nylon mesh covering both openings (which faced upstream and downstream). The top edge of the bucket was above the water surface at all times. The buckets were randomly selected for one of three treatments: mussels and sediment, sediment only and neither mussels nor sediment. Four replicates per treatment were placed in the stream. The nylon mesh was scraped at least once per week to remove build up of algae and other debris.

Two litres of river gravels and pebbles were placed in the buckets selected for the mussel and sediment treatments. The gravel and pebbles were scrubbed to remove algae and sediments and were dried before being placed in the buckets.

Ten *M. falcata* were selected and added to each of the buckets selected for the treatment with sediment and mussels. All mussels used in the experiment were measured with digital callipers (length, width and thickness to the nearest 0.3 mm), weighed on a field balance (to the nearest 0.1 g) and labelled with individual plastic tags and adhered to the shell with cyanoacrylate glue. Differences in mean values of shell length among buckets were statistically assessed using one-way analysis of variance (ANOVA; $P = 0.05$). There were no significant differences in the length of mussel shells between replicates.

At 15, 30, 60 and 90 days mussels were removed from the buckets, the mesh screen covered to keep contents within the bucket confined and all bucket contents transferred into a larger tub. Gravels and pebbles were scrubbed to dislodge fine particulate matter and removed from the buckets. The tub contents were then filtered through nested 1-mm

and 63-μm sieves and processed for ash-free dry mass as described above (See *In situ* comparison above).

To determine the total particulate matter in each bucket, we calculated the total volume of water in the bucket. Using this value, the amount of particulate matter in our samples could be scaled up to determine the total amount of particulate matter located on the substrate per bucket [$g(0.05\ m^2)^{-1}$].

Differences in mean values of benthic material (< and >63 μm) between treatments (buckets with mussels, sediment and controls) were statistically assessed using one-way analysis of variance. A posteriori comparisons between treatments were made with the Tukey test ($P = 0.05$).

2 *Quadrat experiment*. To perform a similar set of measurements in a less constrained environment, we also constructed corrals that prevented the escape of mussels but neither restricted the movement of other organisms nor altered the flow of water. This experimental design was also used to explore how varying the density of mussels on the bed influences both benthic matter and macroinvertebrate community structure. In late June 2002, sixteen 0.5 m^2 quadrats (0.71 × 0.71 m) made of PVC pipes (10-cm diameter and 5-mm thick walls) were placed in a relatively shallow reach (maximum depth 0.5 m) with approximately uniform depth and substrate. Quadrats were randomly selected for one of four density treatments: 0, 10, 20 or 40 *M. falcata*. Four replicates per treatment were used. Mussel densities were chosen to be similar to the range of densities within mussel aggregations in the study reach.

Mussels selected for this experiment were collected by hand in the same reach of channel where the experiment took place. All mussels were scrubbed to remove biofilm, measured with digital callipers (length, width and thickness to the nearest 0.3 mm), weighed on a field balance (to the nearest 0.1 g) and labelled with individual plastic tags adhered to the shell with a cyanoacrylate glue. Mussels were placed in the center of the quadrats oriented with siphons upstream. Note that within hours of being placed in the quadrats, over 90% of the mussels had moved position within the quadrats.

Differences in mean values of shell length among quadrats were statistically assessed using one-way ANOVA ($P = 0.05$). There were no significant differences in the length of mussel shells between replicates.

To measure concentration of benthic matter in these quadrats at later times, we measured suspendable mass in two 26-cm diameter columns per quadrat, as outlined above for the *in situ* comparison. We used 'blind sampling': the operator did not know the number of mussels in the quadrat, although the presence of mussels could be observed. These masses were scaled using known water volumes to determine first the total amount of fine matter in the water and then total for the quadrat (0.5-m^2 area relative to 0.11-m^2 combined area of the two corers). Quadrats were sampled 7, 30, 60 and 90 days after mussels were added to the quadrats.

To evaluate the statistical significance of relationships between amount of benthic material in the quadrats and treatments (0, 10, 20 and 40 mussels), we used two methods. First, significance of the measured correlation between mussel density and fine benthic matter was tested using Spearman's rank correlation on the pooled data set of all 16 quadrats. This is the most informative test to use here because we are asking whether increasing mussel abundance also increases benthic matter; the correlation depends on the value of the independent variable (the number of mussels) for each treatment and the larger sample size of the pooled data set increases the experiments' discerning power. Second, for completeness, we also used a single-factor ANOVA to ask whether any of the treatments are distinct with respect to benthic matter. Given that each treatment has four replicates, this effectively reduces the sample size by half for each statistical comparison. A posteriori comparisons between treatments were made with the Tukey test ($P = 0.05$).

Seasonal variation. The standing crop of benthic organic matter may be increased by mussel biodeposition, but this contribution must be viewed relative to both the temporal contribution from passive deposition and temporal removal by both biological and physical processes (suspension in the water column and mixing to depth).

Using our estimates of mussel biodeposition rates, we compared passive deposition rates to mussel deposition rates from the quadrat experiment using the following framework. The change in benthic material concentration (C) over time (t) is governed by the imbalance of input and output fluxes (F):

$$\frac{dC}{dt} = F_{in} - F_{out} \quad (1)$$

Quadrats with and without mussels in each time period evolve according to

$$\frac{dC_m}{dt} = f_{mb} + f_{ob} - \lambda C_m \quad (2)$$

$$\frac{dC_x}{dt} = f_{ob} - \lambda C_x$$

where f_{mb} = flux of mussel inputs to bed, f_{ob} = flux of other inputs to bed, λ = loss efficiency of removal processes, C_m = concentration of matter in mussel quadrats and C_x = concentration of matter in non-mussel quadrats.

With our measurements, we can calculate λ per time period as a numerical solution to:

$$C_m - C_x - (C_{om} - C_{ox})[\exp(-\lambda t)] - \frac{f_{mb}}{\lambda}[1 - \exp(-\lambda t)] = 0 \quad (3)$$

and then f_{ob} as:

$$f_{ob} = \frac{\lambda}{1 - \exp(-\lambda t)}[C_x - C_{ox}\exp(-\lambda t)] \quad (4)$$

where C_{om} is the concentration of matter in mussel quadrats specified at $t = 0$ and C_{ox} is the concentration of matter in non-mussel quadrats specified at $t = 0$.

In addition, we demonstrated the sensitivity of the calculations for each time period to the assumed biodeposition rates (f_{mb}) by doubling and halving f_{mb} and solving eqns 3 and 4 with these values.

Assessing macroinvertebrate community structure

Macroinvertebrate sampling and identification. To evaluate whether changes in benthic material also induces correlated changes in the macroinvertebrate community structure, we assessed abundance and biomass of benthic invertebrates in the quadrats. After sampling for fine benthic matter in the quadrat experiment, two circular cores (22-cm diameter) were haphazardly placed within each quadrat and forced 10 cm into the substrate. All material within the core was collected and placed in a bucket. The removed contents were elutriated to dislodge invertebrates and poured through 250-μm mesh nylon filters. Materials collected on the filters were placed in whirlpak bags and stored in 70% ethanol (EtOH). We sampled the quadrats 30, 60 and 90 days after mussels were stocked in quadrats.

All macroinvertebrates collected from quadrats with 0 or 40 mussels were identified to family (Merritt & Cummins, 1996) and measured to the nearest 0.5 mm under 10× magnification. Individual biomass was estimated from length-mass regressions (Eckblad, 1971; Boerger, 1975; Meyer, 1989; Smit, Van Heel & Wiersma, 1993; Benke *et al.*, 1999; Johnston & Cunjak, 1999; C. McNeely, unpublished data). Macroinvertebrates were categorised into the following four functional groups (Merritt & Cummins, 1996): predators – Ceratopogonidae, Chloroperlidae, Coenagrionidae, Gomphidae, Perlidae, Sialidae; collectors – Baetidae, Chironomidae, Heptageniidae, Leptophlebiidae, Trichorythidae; shredders – *Gumaga* sp., Tipulidae; scrapers – Elmidae, *Helicopsyche sp.*, Psphenidae.

The Monte Carlo bootstrap resampling method (Manly, 1997) was used to test the statistical significance of differences in mean macroinvertebrate biomass (pooled as functional groups) between treatments. This method was used because of apparent pronounced non-normality. First, *P*-values were calculated for each sample time (30, 60 and 90 days) to show how the significance varied over time. Second, those differences found to be significant at $P = 0.1$ were further evaluated using a Monte Carlo method (pooled *P*-value) to account for the triplicate sampling. Biomass measurements for a given functional group from all three times were pooled. This distribution was randomly sampled three times in pairs of four (corresponding to the four replicates of each treatment) and the difference of means calculated for each pair. The maximum of these three was selected and the process repeated 1000 times to compile a distribution for comparison with the measured difference of means. Finally, difference of means of size of individuals from quadrats with and without mussels were evaluated using standard *t*-tests, for families with the largest total biomass differences.

Results

Assessing mussel contribution to the benthic environment

Biodeposition rates. On average, *M. falcata* deposited approximately 12.6 mg h^{-1} in October 2002 and

approximately 13.8 mg h^{-1} in October 2003 (Fig. 1). The biodeposition rate did not show any relationship to size of the organism. Of the total biodeposit approximately 25% is organic matter (3.0 mg h^{-1}). The similarity of these numbers taken a year apart, using different mussels, demonstrates this is a valid estimate for daytime deposition rates in early fall at the study site. Rates earlier in summer are likely to be even larger, because seston concentrations are likely to be higher then.

In situ *comparison.* In the river channel, the amount of fine benthic matter (organic and inorganic) was significantly greater in mussel areas than non-mussel areas, especially in August to October (Fig. 2). The difference in means is statistically significant at $P = 0.05$ in each month (Student's *t*-test). As with the measured biodeposits, 25% of the fine benthic matter was organic.

Isolation experiment. In general, mussel biodeposition (organic and inorganic particulates) was significantly greater than passive deposition in late summer and autumn (Fig. 3). The greatest fractional increases occurred in September and October when mussel biodeposits were nearly twice the sedimentation from

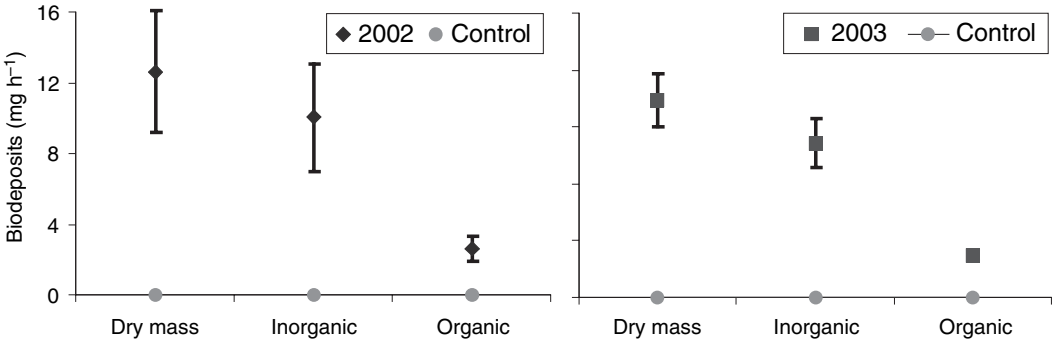

Fig. 1 Mean biodeposition rates (faeces and pseudofaeces) of *Margaritifera falcata* in October 2002 and October 2003. Diamonds and squares represent biodeposits measured in 2002 and 2003, respectively. Gray circles in each time period denote passive deposits measured in control buckets (those without mussels). Note that organic matter is approximately 25% of the total biodeposition. Error bars are ±SE.

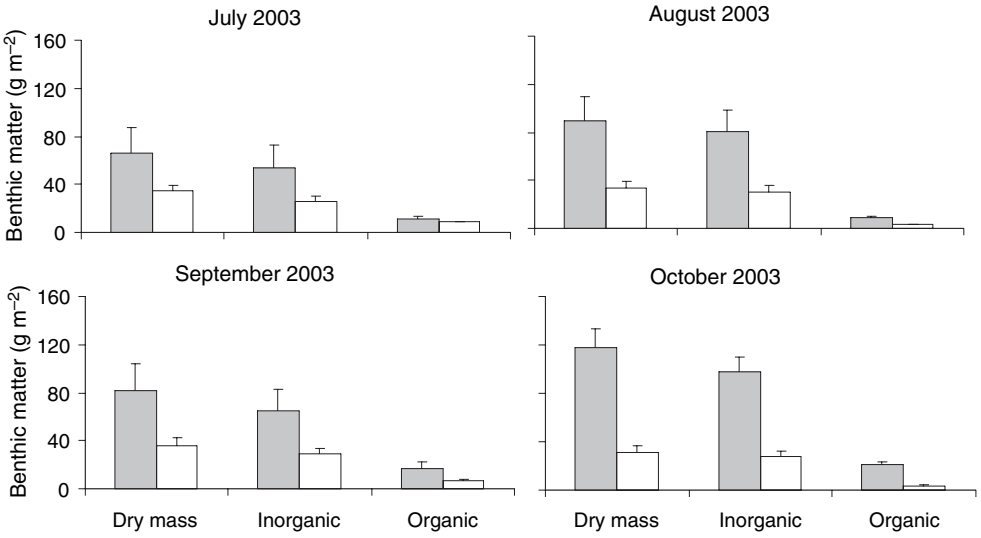

Fig. 2 Comparison of mean fine benthic matter (±SE; total, inorganic and organic) collected monthly from July to October 2003 at eight sites with (shaded bars) and eight sites without (open bars) *Margaritifera falcata*. The total amount in mussel areas in all time periods is significantly greater than the amount in non-mussel areas at $P = 0.05$ (Student's *t*-test).

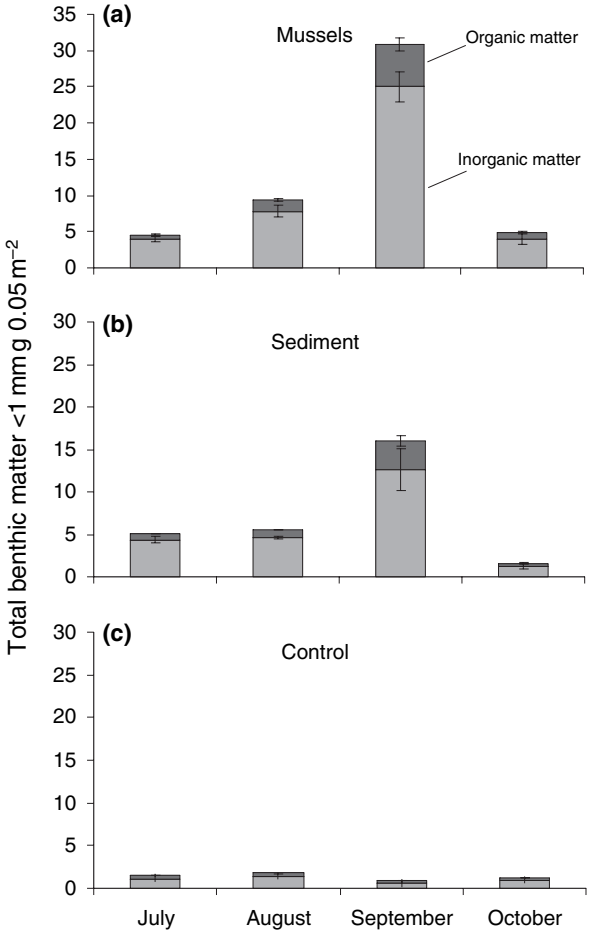

Fig. 3 Mean fine benthic matter (organic and inorganic) collected from the bucket isolation experiment for the mussel (a), sediment (b) and control (c) treatments. In all time periods except July, the amount of material in buckets with mussels was significantly greater than the other two treatments ($P = 0.05$, Tukey test). Note the increase in material in September. Error bars are ±SE.

other sources. FBOM was significantly different (ANOVA, $P = 0.05$) in treatments with mussels than the other two treatments in all time periods except in July (Fig. 3). In August, September and October sedimentation rates were approximately 50% greater in mussel treatments than in the sediment only treatments. In September, FBOM was substantially greater than at other time periods, in both the mussel and sediment treatments. Inorganic matter showed a similar pattern of change over time (Fig. 3).

Quadrat experiment. Under more natural channel conditions, FBOM also significantly increased with greater density of mussels in September (Spearman $r_s = 0.84$, $P = 0.0001$) and October (Spearman $r_s = 0.63$, $P = 0.001$; Fig. 4). In July and August there was no consistent relationship between density of mussels and FBOM, although total organic matter was about 20% greater in quadrats with 40 mussels than in the other three treatments. Similarly, the ANOVA for FBOM concentrations showed significant differences in treatments in September ($P = 0.005$) and October ($P = 0.02$). The Tukey test ($P = 0.05$) identified quadrats with 40 mussels as significantly different from quadrats with 0 and 10 mussels in September and October. No such significance was found for July and August.

In quadrats with the highest densities (40 mussels), measured fine benthic matter (both inorganic and organic material) exceeded passive deposits by at least 40% in all time periods except August and also significantly increased with greater density of mussels in September (Spearman $r_s = 0.74$, $P = 0.001$) and nearly significant in October (Spearman $r_s = 0.45$, $P = 0.08$; Fig. 5). Similarly, the inorganic portion of the fine benthic matter significantly increased with greater mussel densities in September (Spearman $r_s = 0.72$, $P = 0.002$) and nearly significantly in October (Spearman $r_s = 0.43$, $P = 0.09$). In quadrats with 20 and 40 mussels, the concentration of material on the substrate in September and October was around two times greater than that in July or August.

Seasonal variation. In July and August the mean flux of organic material from mussels was approximately 30% of the flux from other sources (Fig. 6). But in early autumn (September to October) the mean flux from mussels was a factor of two greater than that from other sources (Fig. 6). The estimated flux from other sources decreased from about 17 g m^{-2} day^{-1} in July to 3 g m^{-2} day^{-1} in October.

Our measured organic matter biodeposition rates (3 mg h^{-1} mussel^{-1}) imply that, in the absence of removal processes, a quadrat with 40 mussels should accumulate approximately 86 g FBOM in 30 days. Yet the largest measured value for standing crops in the 40 mussel quadrats relative to control quadrats was approximately 15 g (September) and only 5 g in mid-summer (July). This strongly suggests that removal processes are significant, especially in mid-summer.

Our calculated turnover times ($1/\lambda$) confirm this; early in the season the estimated turnover time of fine benthic matter in July and August is 11 and 24 h,

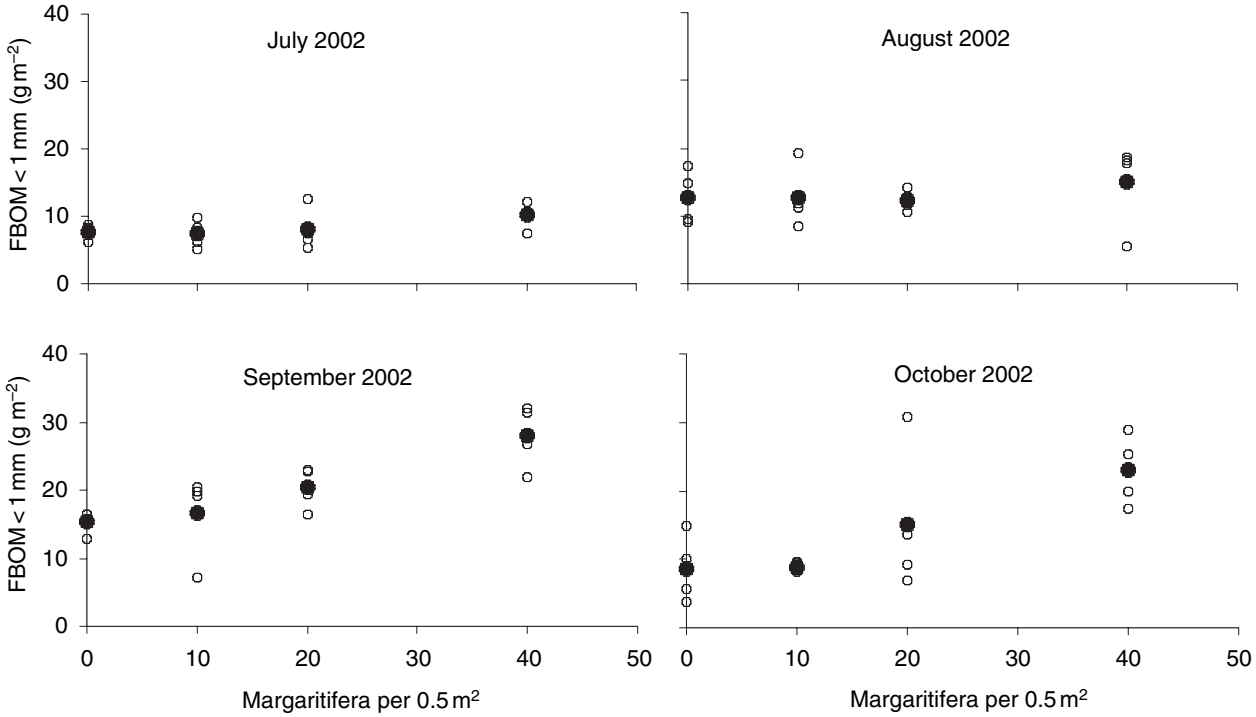

Fig. 4 The relationship of fine benthic organic matter (FBOM; <1 mm) and mussel density from July to October 2002. The Spearman rank correlation coefficient between the number of mussels and FBOM is highly significant in September ($r_s = 0.84$, $P = 0.0001$) and October ($r_s = 0.63$, $P = 0.001$). The darker circles in each graph represent the mean of the four replicates, while the open circles represent individual samples.

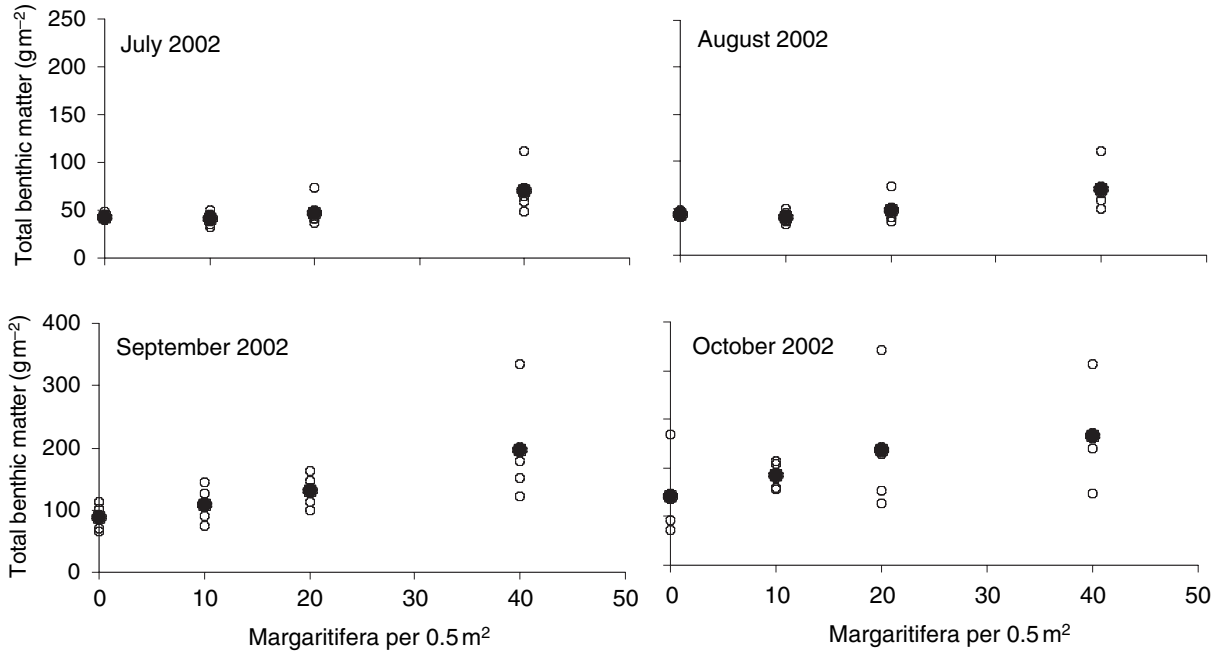

Fig. 5 The relationship of total fine benthic matter (both organic and inorganic, <1 mm) and mussel density from July to October 2002. The Spearman rank correlation coefficient between the number of mussels and benthic matter is highly significant in September ($r_s = 0.74$, $P = 0.001$). In October the correlation coefficient is 0.45 and $P = 0.08$). The darker circles in each graph represent the mean of the four replicates, while the open circles represent individual samples.

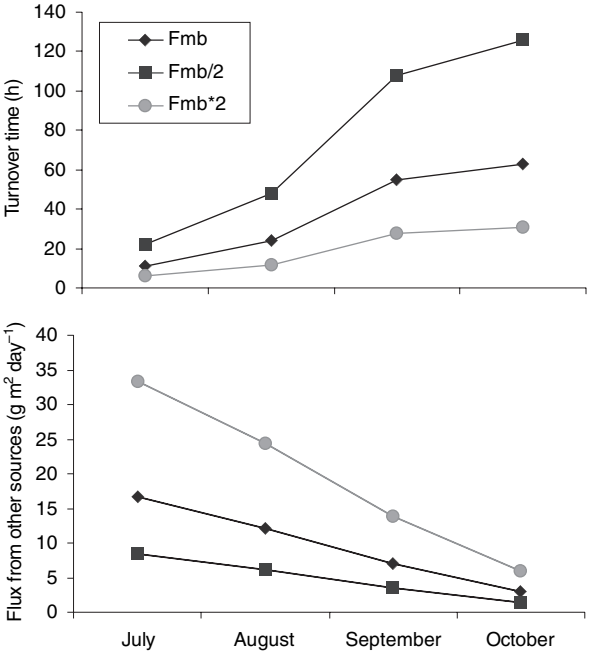

Fig. 6 Estimated turnover time and flux rates of organic matter in the South Fork Eel River, calculated from eqns 3 and 4 using measured biodeposition rates, f_{mb} (triangle), f_{mb} reduced by half (squares) and f_{mb} doubled (circles). See Table 1 for the measured organic matter in quadrats with (C_m) and without (C_x) mussels and measured (f_{mb}), half ($0.5 \times f_{mb}$) and doubled ($2 \times f_{mb}$) biodeposition rates.

respectively. Later in the season the turnover slows to 2.5 days in September and October (Fig. 6). Table 1 lists the values used to calculate loss efficiency of removal processes and turnover times.

Testing the sensitivity of the calculations by doubling and halving the specified biodeposition rate (Fig. 6) shows that the inferred seasonal variation and rapid turnover are not likely because of variations over time in the biodeposition rate or because of errors in its estimated magnitude. Note that although biodeposition rates may change with seston concentrations, our biodeposition rates were calculated in October when seston levels were lowest, i.e. clear water and no algal blooms. Therefore our biodeposition rates are conservative estimates.

Macroinvertebrate community structure

In the quadrat experiment we see an increase of some functional groups' biomass, but no alteration in species composition. Collector/gatherers constituted the greatest number of invertebrates in all time periods in both treatments, averaging over 80% of the total invertebrates (Table 2). Chironomids (primarily tuft weavers) made up at least approximately 40% of invertebrates in all time periods. Predators constituted the greatest biomass in all time periods, although their abundance was low compared with collectors (Table 2). Scrapers and shredders constituted the lowest biomass in all time periods. There was no significant difference in the number of invertebrates collected in mussel and non-mussel quadrats at any time period.

Table 1 Values used to calculate loss efficiency of removal processes and turnover times. Results are shown in Fig. 6.

	July	August	September	October
C_m (g m^{-2})	10.67	17.91	29.06	22.66
C_x (g m^{-2})	7.94	12.16	15.93	7.78
F_{mb} (g m^{-2} day^{-1})	5.76	5.76	5.76	5.76
$F_{mb}/2$ (g m^{-2} day^{-1})	2.88	2.88	2.88	2.88
$F_{mb} \times 2$ (g m^{-2} day^{-1})	11.52	11.52	11.52	11.52

Gomphidae was omitted from the analysis because only 13 individuals were found over the course of the study. All families were found in the four time periods with the exception of the following: in August, Ceratopogonidae were not present; in October, Tipulidae were absent; and in October in quadrats without mussels, Psephenidae and Heptageniidae were absent.

Invertebrate biomass in quadrats with and without mussels did not differ significantly in August and October, but in September there was significantly more biomass of both collectors and predators in quadrats with mussels (Table 2). For predators the difference in means in September was statistically significant ($P = 0.03$; pooled $P = 0.02$) and quantitatively significant (a factor of 2.4). For collectors the difference in mean total mass was weak statistically ($P = 0.08$; pooled $P = 0.12$) and quantitatively modest (a factor of 1.4). This statistical result is too weak to be convincing, however, stronger tests can be made by examining family level data and comparing mean mass of all individuals pooled from quadrats with mussels and without. Leptophlebidae accounts for the majority of collector biomass in September (64.07 g in mussel quadrats versus 41.24 g in non-mussel quadrats). The mean mass of individual Leptophlebidae from quadrats with mussels is 0.454 g, whereas it is 0.389 g from quadrats with no mussels. This difference is significant at $P = 0.03$ (Student's t-test, $n =$

Table 2 Mean ± SE invertebrate biomass [g $(0.5\ m^2)^{-1}$] and abundance [No./g $(0.5\ m^2)^{-1}$] in quadrats with 40 and 0 *Margaritifera falcata*. Significant differences between mussel and non-mussel treatments are bolded. See text for functional feeding group breakdown. The Monte Carlo bootstrap resampling method (Manly, 1997) was used to test the statistical significance of differences in mean macroinvertebrate biomass (pooled as functional groups) between treatments.

	Mean biomass [g $(0.5\ m^2)^{-1}$] quadrats with mussels	Mean biomass [g $(0.5\ m^2)^{-1}$] quadrats without mussels	*P*-value	Mean abundance [no. $(0.5\ m^2)^{-1}$] quadrats with mussels	Mean abundance [no. $(0.5\ m^2)^{-1}$] quadrats without mussels	*P*-value
August 2002						
Predators	0.57 ± 0.1	0.58 ± .25	0.49	23 ± 5.2	39 ± 19.5	0.75
Collectors	0.2 ± 0.03	0.22 ± 0.02	0.82	214 ± 20.5	226 ± 22.4	0.63
Shredders	0.12 ± 0.04	0.22 ± 0.1	0.78	18 ± 5.9	43 ± 12.9	0.93
Scrapers	0.15 ± 0.03	0.15 ± 0.04	0.43	45 ± 22.3	54 ± 17.9	0.64
September 2002						
Predators	**1.38 ± 0.22**	**0.64 ± 0.24**	**0.03**	34 ± 7.4	19 ± 15.9	0.12
Collectors	**0.43 ± 0.05**	**0.3 ± 0.07**	**0.08**	223 ± 37.2	204 ± 28.4	0.34
Shredders	0.25 ± 0.08	0.25 ± 0.1	0.52	16 ± 3.4	15 ± 2.5	0.47
Scrapers	0.03 ± 0.01	0.05 ± 0.03	0.69	11 ± 5.1	20 ± 12.9	0.72
October 2002						
Predators	0.26 ± 0.11	0.37 ± 0.14	0.78	11 ± 2.8	17 ± 6.7	0.83
Collectors	0.11 ± 0.06	0.05 ± 0.02	0.11	69 ± 8.9	98 ± 17.6	0.92
Shredders	0.21 ± 0.08	0.35 ± 0.11	0.81	6 ± 1.3	9 ± 2.4	0.87
Scrapers	0.04 ± 0.02	0.01 ± 0.01	0.1	7 ± 3.0	7 ± 2.9	0.58

247). There is no significant difference in individual size in August or October.

Chironomids show the opposite difference with smaller individuals in mussel quadrats (0.012 g in mussel quadrats versus 0.016 g in non-mussel quadrats; $P = 0.03$). Note that the total biomass of chironomids is much smaller (7.64 g in mussel quadrats and 8.77 g in non-mussel quadrats) than for the Leptophlebidae so we expect the latter to be controlling impacts on higher trophic levels.

Discussion

Our investigations in the South Fork Eel constitute a case study of the functional role of mussels in a natural river bed environment, motivated by the potential for these organisms to act as benthic-pelagic couplers transferring resources from the water column to the substrate and stimulating benthic productivity. At our study site, this potential is only partially realised; *M. falcata* does increase both organic and inorganic fine benthic matter, but this increase is significant only during late summer/early fall, with passive deposits overwhelming mussel deposits earlier in the growing season. Response of the macroinvertebrates during the late season is demonstrable but muted. It is instructive to consider these observations in a general context.

Mussel biodeposition in lotic systems can have three direct impacts that may be important: increased flux of resources to the channel bed, increased concentration of such resources on the bed and reduced seston concentration in the water column.

The first of these (increased flux) is quantitatively important only if it exceeds, or is comparable to, the flux from other sources like passive settling of seston and disintegration of benthic algae. At the South Fork Eel, where there is a strong algal bloom in early midsummer (Power, 1990), the mussel fluxes become important only in late summer/early fall (see Results). For the studied 8-km reach of this river, the magnitude of the total flux by mussels can be roughly estimated using the average biodeposition rate of 14 mg h^{-1} per mussel, which amounts to removal of suspended material at approximately 336 mg day^{-1} per mussel. Collectively, the approximately 12 000 *M. falcata* in this reach transfer approximately 4 kg day^{-1} to the riverbed. This is a small number as an average for the reach, but the strong spatial clustering of mussels (Howard & Cuffey, 2003) means that most of this flux is directed to a small fraction of the channel bed. This is probably the reason for the higher concentration of FBOM in channel sections with abundant mussels compared with sections devoid of mussels (Fig. 2) and for its seasonal pattern. For example, the largest *M. falcata* aggregation contains about 1100 individuals in a 75 m^2 area of

channel. Using the calculated biodeposition rate for 2003, this aggregation is therefore capable of depositing 365 g of benthic matter per day, or nearly 5 g m^{-2} day^{-1}, 25% of which is organic. Six per cent of the substrate in the study reach is potentially impacted by biodeposits (total channel area is 47 400 m^2, of which 3000 m^2 contains mussel aggregations; Howard & Cuffey, 2003; Howard, 2004).

Other studies have demonstrated that bivalve deposition rates vary temporally as filtration rates change throughout the year (MacIsaac *et al*., 1992; Prins, Dankers & Smaal, 1994; MacIsaac, Lonnee & Leach, 1995). During high flows, when turbidity is pronounced, bivalves may reduce their filtration rate in response to increased particulate matter in the water column. For example, Way *et al.* (1990) found that the filtration rate of *Corbicula fluminea* were inversely correlated with suspended particle concentration. Jorgensen (1990) also reported declining filtration rates for *Mytilus edulis* in response to increasing concentrations of suspended algae. Filtration rate in *M. edulis* has been shown to increase with increasing temperatures, which Jorgensen, Larsen & Riisgård (1990) attributed to the change in water viscosity. The decrease in viscosity with higher temperatures lessens the resistance to water flow in the mussel pump (Jorgensen *et al*., 1990). In our study system, winter flows are characterised by high discharge and turbidity and we therefore expect the filtration rate and subsequent biodeposition rate of *M. falcata* to be greatly reduced at that time.

The second impact (increased concentration) depends not only on the enhanced fluxes to the bed but also on the lag time for removal from the bed, either by physical processes of suspension and downward mixing, or by biological processing. For example, Jorgensen (1990) described how in the marine environment the turnover rate varies with the degree of turbulence characteristic for a habitat. At the South Fork Eel, it appears that rapid turnover of bed material is strongly limiting the impact of mussels on benthic concentrations, relative to their potential (Fig. 6). During the summer months, the measured biodeposits constitute just 5% of the nominal cumulative flux in July and approximately 20% in September (See Seasonal variation results above). Similar results have been reported in the marine environment, where measured biodeposits constituted between 10% and 16% of the cumulative total (Riisgård, 1988).

The third impact (reduction of seston concentration) depends on the magnitude of the mussel flux relative to the throughput flux of seston in the river. As others have found in large-scale studies (Caraco *et al*., 1997; Strayer *et al*., 2004), seston concentrations may be locally reduced over high-density mussel aggregations along a river's course. We did not measure removal of suspended material directly in the South Fork Eel river channel, but a rough estimate may be made, as above, using the average biodeposition rate of 14 mg h^{-1} per mussel. Average seston concentrations in early fall are approximately 1.2 mg L^{-1} (J. Howard, unpublished data). Total discharge during this time of year is approximately 400 L s^{-1}. Therefore, we estimate that 42 000 g of material is passing through this section of channel each day. Collectively, the approximately 12 000 *M. falcata* in this 8-km reach of river are capable of removing approximately 10% of total seston per day. The largest aggregation of mussels, totalling approximately 1100 mussels, is capable of filtering 1% of the seston flux.

In general these three direct impacts of biodeposits are dependent on the abundance and population density of active mussels, the presence of conditions favourable for mussel activity (temperature, turbidity, substrate stability) and the presence of seston in the water column. At the South Fork Eel, the seasonal cycle of winter flood and summer drought coupled with the dominance of in-channel carbon sources for seston mean there is a distinct summer growing season for mussels; winter flows are cold and turbid, whereas summer flows are seston-rich and relatively free of suspended sediment. As a result, mussel shells here have distinct seasonal bands (Howard, 2004). It is therefore unlikely that mussel transfers of resources to the bed have any significant impacts in winter here.

Whether the impact of mussel biodeposition on the benthic food web is important or not also depends on the increased resource flux and/or concentration, plus additional constraints. As shown by Beckett *et al*. (1996), there can be a direct link between native freshwater mussels and increased epibenthic invertebrates. In this study we examined the potential for mussels to impact food webs indirectly, by converting and re-directing food resources to other branches of the trophic web. Although mussels are rarely consumed in stream systems (van Tets, 1994; Tyrrell & Hornbach, 1998),

they should not necessarily be viewed as carbon sinks and dismissed as having little relevance in the trophic web (Leff *et al*., 1990). At the South Fork Eel there does appear to be a link between mussel-derived resources and other macroinvertebrates (benthic insects), with modest impacts on two trophic levels. Similar results were reported following zebra mussel invasions, where deposit-feeding macroinvertebrates increased in abundance (Sephton, Patterson & Fernando, 1980; Stewart & Haynes, 1994; Greenwood *et al*., 2001). For these links to be important, the mussel's impact on benthic resources must coincide with the life cycle of the affected macroinvertebrates. In addition, there will only be a response to enhanced resources if the primary consumers are already resource-limited (rather than being limited by predation or reproduction). There are also spatial considerations; if mussel resources are strongly concentrated spatially, as at the South Fork Eel, then there will not be a broad impact on the benthic food web unless primary consumers are highly mobile.

Ecological significance

Freshwater mussels have rapidly declined throughout North America and continue to do so (Williams *et al*., 1992; Vaughn *et al*., 2004). An understanding of their role in the ecosystem may provide insight into changes of benthic resource availability and possibly water quality. Although often the dominant consumer biomass within stream reaches, the functional role of these organisms in the river food web has been poorly studied (Strayer *et al*., 1999; Raikow & Hamilton, 2001).

As long-lived organisms, freshwater mussels are often considered resource sinks rather than sources. Yet this study provides evidence that native mussels are a vital component of the stream ecosystem, recycling and translocating nutrients within and between habitats. This shift in resources, in turn, may increase the abundance and biomass of other benthic community members during late summer resource bottlenecks.

We identified two effects mussels have on the benthic community. First, they increase the inorganic and organic component of the sediment. Second, macroinvertebrates respond to these increases when fluxes from mussels dominate other depositional processes. Hence, mussel patches may at times serve as nutrient and productivity hotspots within the stream environment.

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