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# The functional role of burrowing bivalves in freshwater ecosystems

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## SUMMARY

1. Freshwater systems are losing biodiversity at a rapid rate, yet we know little about the functional role of most of this biodiversity. The ecosystem roles of freshwater burrowing bivalves have been particularly understudied. Here we summarize what is known about the functional role of burrowing bivalves in the orders Unionoida and Veneroida in lakes and streams globally.
2. Bivalves filter phytoplankton, bacteria and particulate organic matter from the water column. *Corbicula* and sphaeriids also remove organic matter from the sediment by deposit feeding, as may some unionids. Filtration rate varies with bivalve species and size, temperature, particle size and concentration, and flow regime.
3. Bivalves affect nutrient dynamics in freshwater systems, through excretion as well as biodeposition of faeces and pseudofaeces. Excretion rates are both size and species dependent, are influenced by reproductive stage, and vary greatly with temperature and food availability.
4. Bioturbation of sediments through bivalve movements increases sediment water and oxygen content and releases nutrients from the sediment to the water column. The physical presence of bivalve shells creates habitat for epiphytic and epizoic organisms, and stabilizes sediment and provides refugia for benthic fauna. Biodeposition of faeces and pseudofaeces can alter the composition of benthic communities.
5. There is conflicting evidence concerning the role of resource limitation in structuring bivalve communities. Control by bivalves of primary production is most likely when their biomass is large relative to the water volume and where hydrologic residence time is long. Future studies should consider exactly what bivalves feed upon, whether feeding varies seasonally and with habitat, and whether significant overlap in diet occurs. In particular, we need a clearer picture of the importance of suspension versus deposit feeding and the potential advantages and tradeoffs between these two feeding modes.
6. In North America, native burrowing bivalves (Unionidae) are declining at a catastrophic rate. This significant loss of benthic biomass, coupled with the invasion of an exotic burrowing bivalve (*Corbicula*), may result in large alterations of ecosystem processes and functions.

*Keywords:* biodeposition, bioturbation, Bivalvia, filtration rates, nutrient cycling

## Introduction

One or more functional groups often play central roles in ecosystem processes (Tilman *et al.*, 1997). In some marine and freshwater systems, bivalve molluscs are dominant filter-feeders that make up most of the biomass and exert control over ecosystem structure and function (Dame, 1996; Strayer *et al.*, 1999). Recently, a large body of research has focused on the functional effects of epifaunal zebra mussels (*Dreissena polymorpha*; Pallas, 1771) in freshwater systems (e.g. Mellina, Rasmussen & Mills, 1995; MacIsaac, 1996; Caraco *et al.*, 1997; Strayer *et al.*, 1999). Zebra mussels impact lakes and streams via the effects of high rates of filter feeding. We contend that freshwater burrowing bivalves [orders Unionoida (families Unionidae, Margaritiferidae and Hyriidae) and Veneroida (families Corbiculidae and Sphaeriidae)] also have the potential to strongly influence ecosystem processes in freshwater systems. These bivalves also can be important filter feeders and in addition can directly impact benthic processes as they burrow through sediments. In this paper we summarize what is known about the functional role of freshwater burrowing bivalves and suggest areas where further research is needed. We conclude with a discussion of how ongoing changes in freshwater systems, such as the loss of native species and invasion of non-native bivalves, may alter rates of ecological processes.

## Ecosystem processes performed by burrowing bivalves

One reason to predict that freshwater bivalves influence ecosystem processes is that in marine and estuarine systems, both epifaunal and burrowing bivalves have been shown to have large ecosystem impacts. Marine bivalves can dominate benthic biomass and couple benthic and pelagic energy and material cycling (Dame & Patten, 1981; Dame & Dankers, 1988; Asmus, Asmus & Reise, 1990; Prins & Smaal, 1994). Water filtration by bivalves can reduce phytoplankton biomass (Ulanowicz & Tuttle, 1992; Alpine & Cloern, 1992; Kimmerer, Gartside & Orsi, 1994). Bivalve production rates in marine mussel beds rival other highly productive systems (e.g. tropical rainforests and kelp beds; Leigh *et al.*, 1987). Sediment mixing by deposit feeding marine bivalves increases oxygen penetration into the sediments

(Levinton, 1995) and stimulates microbial metabolism (Dame, 1996). Aggregations of marine bivalves (e.g. mussel beds, oyster reefs) alter light, temperature, sediment loading and deposition, and water circulation patterns (Dame, 1996; Seed, 1996; Wildish & Kristmanson, 1997) and provide refuge and suitable habitat for a broad suite of associated organisms (Vance, 1978; Suchanek, 1979; Iwasaki, 1995; Tokeshi, 1995; Jaramillo & Pino, 1996; Seed, 1996; Svane & Setyobudiandi, 1996). Based on this extensive knowledge of the functional role of marine bivalves, burrowing bivalves in freshwater systems should perform a similar range of ecological functions (Fig. 1).

### Water column processes

Removing particles from the water column (suspension or filter feeding), excreting nutrients and biodepositing faeces and pseudofaeces (discussed in the next section) are the main water column processes completed by burrowing bivalves in freshwater systems (Fig. 1). Filtration by bivalves can lead to a large decrease in phytoplankton and other particles in the water column (Kasprzak, 1986; Kryger & Riisgård, 1988; Welker & Walz, 1998; Strayer *et al.*, 1999). Filter feeding by burrowing bivalves has the greatest effects on ecological processes when their biomass is large. Welker & Walz (1998) and C.C. Vaughn, K.B. Gido & D.E. Spooner (unpublished data) have found that the volume of water filtered by unionids within dense beds can equal or exceed daily stream discharge. In

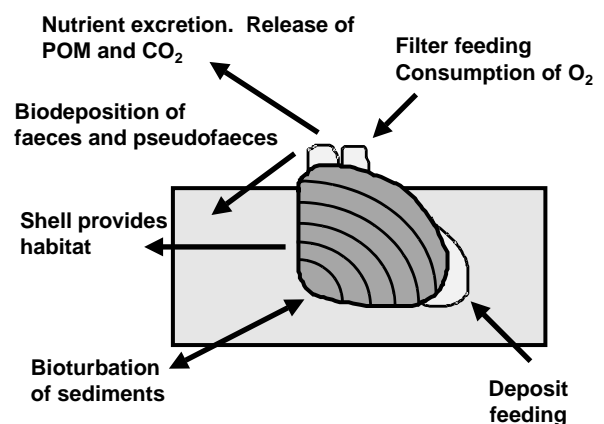


Fig. 1 Potential ecosystem functions performed by burrowing bivalves in freshwater systems.

the River Spree, Germany, filtration by unionids occurring at a density of up to 350 m<sup>-2</sup>, caused 'biological oligotrophication' by decreasing phytoplankton biomass and total phosphorus, and increasing water clarity (Welker & Walz, 1998). When occurring at high biomass, *Corbicula fluminea* (Müller, 1774) also has the ability to influence phytoplankton abundances and water clarity (Cohen *et al.*, 1984; Phelps, 1994). In fact, Strayer *et al.* (1999) and Dame (1996) have suggested that any assemblage of bivalves may significantly influence phytoplankton concentrations when filtration rates are large relative to food supply. However, our ability to estimate these rates is hindered by the fact that filtration rates of freshwater bivalves have often been underestimated as a result of experiments performed under unnatural conditions (i.e. where bivalves were not allowed to burrow in the substratum, where there was mechanical or chemical disturbance, and/or where artificially high algal concentrations potentially clogged gills) (Kryger & Riisgård, 1988). Undisturbed bivalves have been found to have measured filtration rates as much as four times higher than previously reported (Kryger & Riisgård, 1988).

Given that the rate of filter feeding is important in determining when bivalves affect water column processes, the multiple, interacting factors influencing filtration rate are of interest. In freshwater systems water temperature, particle size and concentration, flow regime, and bivalve size and gill morphology all have been found to influence the filtration rate (Table 1). Filtration rate increases with temperature, as bivalve metabolic rate increases (Lauritsen, 1986; Jorgensen, 1990; Vanderploeg, Liebig & Nalepa, 1995). Particle concentration also affects filtration rate, the latter generally increasing with increasing particle concentration up to a threshold, after which the rate may decline (Winter, 1978; Hornbach *et al.*, 1984a; Paterson, 1984; Burky *et al.*, 1985; Way *et al.*, 1990; Englund & Heino, 1996), probably to control ingestion rate (Hornbach *et al.*, 1984a; Burky *et al.*, 1985), as well as in response to gill clogging (Kryger & Riisgård, 1988). *Corbicula* can physiologically adjust its filter-feeding rate in response to food availability, to reach an optimal rate across a range of particle concentrations (Way *et al.*, 1990). Some unionids (*Elliptio complanata* (Lightfoot, 1786)) are more selective in terms of the size of particles consumed when particle concentrations are low (Paterson, 1984).

Filtration rate should also be influenced by current velocity. Englund & Heino (1996) performed a reciprocal transplant experiment between river and lake populations of *Anodonta anatina* (Linnaeus, 1758), then monitored valve movement as an indicator of filtering activity. In the lake this species showed a diurnal pattern of valve movement, but in the river valve movements were more variable, indicating that either variable flow and/or food availability in lotic systems may be influencing filtration more than in lentic systems. Englund & Heino (1996) speculated that in flowing water mussels may save energy and reduce pumping costs by orienting towards the flow.

Both the size of the gill (Payne *et al.*, 1995; Lei, Payne & Wang, 1996) and the number and structural complexity of cirri on the gill (Silverman *et al.*, 1995, 1997) influence filtering abilities. Silverman *et al.* (1997) compared rates of filtering *E. coli* (a large, laboratory cultured bacteria), for three pond-dwelling versus three stream-dwelling unionid species, and for *Corbicula*. When normalized on the basis of gill surface area, bacterial clearance rates were similar within the group of riverine species and within the group of pond species, but quite different between the unionids from different habitats. Riverine unionids filtered more bacteria than pond species. Examination of their gill structure revealed that the riverine species had more complex and larger cirri than pond species (25 or more cilia per cirral plate in riverine species compared with 16 or fewer cilia per cirral plate in lentic species). *Corbicula*, which occur in both rivers and streams, filtered bacteria at a much higher rate than either group of unionids and had a more complex cirral structure (32–42 cilia per cirral plate; Silverman *et al.*, 1995). These results have several implications. First, we should not assume that all bivalve species have similar feeding mechanisms and behaviour. Second, bivalves may use different food sources in different habitats, and our studies have been very biased towards lentic systems. Finally, bacteria may be an important food source in habitats where plankton is scarce, such as in unproductive, shaded or turbid rivers, and not as important for lakes and ponds where phytoplankton is typically abundant.

Compared with filter feeding studies, much less is known about how burrowing bivalves influence nutrient concentrations in the water column (Fig. 1), but both unionids and *Corbicula* can be important sources of dissolved nutrients (Table 1). Marine

Table 1 Summary of ecosystem processes performed by burrowing bivalves

	Group	Finding	Sources		
<b>Water column processes</b>					
	Filter-feeding	Unionidae, Sphaeriidae	Filtering rates vary with bivalve size	Hinz & Scheil (1972); Hornbach <i>et al.</i> (1984a); Kryger & Risgård (1988); Vanderploeg <i>et al.</i> (1995); Silverman <i>et al.</i> (1997)	
		Unionidae, Sphaeriidae	Filtering rates vary with water temperature	Gale & Lowe (1971); Hinz & Scheil (1972); Benjamin & Burky (1978); Hornbach <i>et al.</i> (1984a); Paterson (1984); Burky <i>et al.</i> (1985); Vanderploeg <i>et al.</i> (1995)	
		Unionidae, Sphaeriidae, Corbiculidae	Filtering rates vary with particle concentration	Winter (1978); Hornbach <i>et al.</i> (1984a); Lauritsen (1985), (1986); Way (1989); Way <i>et al.</i> (1990); Tankersley & Dimock (1993); Englund & Heino (1996)	
		Unionidae	Bivalves are size selective in the particles they retain	Paterson (1984); Jorgensen <i>et al.</i> (1984); Way (1989); Tankersley & Dimock (1993); Vanderploeg <i>et al.</i> (1995)	
		Unionidae, Corbiculidae	Bivalves select particles by type	Bisbee (1984); Leff <i>et al.</i> (1990)	
		Unionidae, Corbiculidae	Bivalves do not select particles by type	Gale & Lowe (1971); Paterson (1984); Lauritsen (1986); Way <i>et al.</i> (1990); Boltovskoy <i>et al.</i> (1995); Parker <i>et al.</i> (1998)	
		Unionidae, Corbiculidae	Variation in gill size and cirral structure is related to filtering ability	Way (1989); Tankersley & Dimock (1993); Silverman <i>et al.</i> (1995), (1997)	
		Filter-feeding: evidence for resource limitation	Unionidae, Corbiculidae	Filter-feeding controlled phytoplankton abundance	Cohen <i>et al.</i> (1984); Phelps (1994); Welker & Walz (1998)
			Unionidae	Competition between unionid species occurred when phytoplankton abundance was limited	DiDonato (1998)
Hyriidae			Bivalve biomass positively correlated with phytoplankton abundance	James (1985), (1987)	
Unionidae	Different unionid species select different particle sizes and/or types		Jorgensen <i>et al.</i> (1984); Bisbee (1984); Parker <i>et al.</i> (1998)		
Filter-feeding: evidence that resources are not limiting	Sphaeriidae	Exploitative competition for food controls the distribution of two <i>Pisidium</i> species	Holopainen & Hanski (1979)		
	Unionidae	Unionids are non-selective, with high diet overlap in the size, type and rates of particles filtered	Bronmark & Malmquist (1982); Paterson (1984); Silverman <i>et al.</i> (1997)		
	Unionidae	Filter-feeding did not control phytoplankton abundance	Cahoon & Owen (1996)		
Nutrient cycling	Unionidae	Filter-feeding controlled phosphorus concentration	Welker & Walz (1998)		
	Unionidae	Phosphorus excretion rates varied among species and seasonally	Lauritsen & Mozley (1989); Davis <i>et al.</i> (2000)		
	Unionidae	Stable nitrogen isotopes indicated that bivalves were turning over FPOM	Raikow & Hamilton (2000)		

Sediment processes	Deposit feeding	Unionidae	Unionid population filtered 13.5% of the total phosphorus and 63% of this was biodeposited	Nalepa <i>et al.</i> (1991)
		Unionidae, Corbiculidae	Bivalves decreased sediment organic matter	Cleland (1988); Reid <i>et al.</i> (1992); Hakenkamp & Palmer (1999); Hakenkamp, unpublished data
		Sphaeriidae	Bivalves remove suspended micro-organisms from interstitial water	Mackie (1986); Lopez & Holopainen (1987)
		Sphaeriidae	Particle collection by ciliary tracts on the foot	Mitropolskij (1966), (1970); Way (1989)
Biodeposition	Unionidae, Sphaeriidae	Filterfeeding rates on phytoplankton too low to support bivalve biomass	Benjamin & Burky (1978); Mackie & Qadir (1978); Hornbach <i>et al.</i> (1984a); Cahoon & Owen (1996)	
	Unionidae, Corbiculidae	Unionids deposited faeces and pseudofaeces on the bottom	Prokopovich (1969); Lewandowski & Stanczykowska (1975); Sephton <i>et al.</i> (1980); Nalepa <i>et al.</i> (1991); Hakenkamp & Palmer (1999); Vaughn <i>et al.</i> , unpublished data	
Bioturbation	Unionidae, Sphaeriidae	Mixed sediments through burrowing activities	McCall <i>et al.</i> (1979), (1995)	
Habitat	Unionidae	Epizoic invertebrates colonize unionid shells	Beckett <i>et al.</i> (1996); Vaughn <i>et al.</i> , unpublished data	
	Unionidae	Epiphytic algae colonize unionid shells	Vaughn <i>et al.</i> , unpublished data	
	Unionidae	Benthic invertebrates occurred in higher densities adjacent to unionids	Sephton <i>et al.</i> (1980)	

bivalves both translocate (feed and pump back out) and transform (change the chemical form of) nutrients (Kuenzler, 1961), and this is undoubtedly also the case for freshwater bivalves. Freshwater bivalves produce a hypo-osmotic urine consisting primarily of ammonia (Burton, 1983). Excretion rate varies between species of bivalves, as well as with individual size, temperature, stage in reproductive cycle and food availability (Potts, 1954; Dietz, 1985; James, 1987; Lauritsen & Mozley, 1989; Williams & McMahon, 1989; Nalepa, Gardner & Malczyk, 1991; Davis, Christian & Berg, 2000). Seasonal variation with spawning may be especially important, given that *Corbicula* showed a 20–40 fold increase in excretion with spawning (Williams & McMahon, 1989). In marine bivalves, excretion rate increases with individual biomass; however, the rate of excretion per unit biomass decreases as an individual grows larger (Burton, 1983; Dame, 1996). Davis *et al.* (2000) found an inverse relationship between unionid size and phosphorus excretion rates.

Bivalves are important cyclers of nitrogen in coastal marine systems, releasing ammonium and dissolved organic nitrogen that can be taken up directly by phytoplankton (Dame, 1996). Several recent freshwater studies have concluded that excretory products from bivalves should be an important and readily useable resource for phytoplankton (James, 1987; Lauritsen & Mozley, 1989) and presumably the benthic algal community. Christian & Berg (2000) and Davis *et al.* (2000) compared seasonal nitrogen and phosphorus cycling by three unionid species in two headwater streams. Prior studies indicated that nutrients were limiting in both systems, so any nutrients contributed by the bivalves should be useful biologically. They found that, while excretion rates varied seasonally, the direction and magnitude of these changes were species specific. In addition, Matisoff, Fisher & Matis (1985) found that unionid activities indirectly influenced nutrient cycling by enhancing the rate of nitrate release in sediments.

We know little regarding how burrowing bivalves influence phosphorus cycling. In contrast, epifaunal bivalves (*Dreissena*) have long been known to be important for nutrient cycling in unproductive European lakes (Stańczykowska, 1984) as well as in Lake Erie (Arnott & Vanni, 1996). On a basin-wide scale, phosphorus recycling by zebra mussels may be sufficient to shift the phytoplankton community

structure towards nitrogen-limited cyanobacteria. Whether excretion by burrowing bivalves can cause similar shifts is unknown.

Bivalves are capacitors with long time constants; i.e. they store materials for long periods of time (Strayer, pers. com.). Turnover time for unionids ranges from 1790 to 2849 days, while that of other burrowing bivalves is much shorter (Sphaeriids 27–1972 days, *Corbicula* 73–91 days) (Lewandowski & Stanczykowska, 1975; Avolizi, 1976; McMahon, 1991). Under steady-state conditions, release of nutrients from dead bivalves should balance the accumulation of nutrients by living bivalves (Strayer, pers. com.), and for unionids both processes are relatively slow. For example, Raikow & Hamilton (2000) traced labelled ammonium in a small Michigan stream with high unionid biomass and diversity. Nitrogen assimilation, based on the appearance of labelled isotopes in unionid tissue, was very slow (turnover rate for muscle tissue was estimated at 357 days). Under non steady-state conditions, bivalves may serve as a nutrient source if bivalve biomass is declining and populations release more nutrients than they absorb. Bivalves may serve as a nutrient sink while a population is growing (i.e. accumulating biomass) or if biomass is being lost from the ecosystem by export or permanent burial (Strayer, pers. com.).

Most studies of water column processes have focused on lentic species and habitats. We need a better understanding of suspension feeding in riverine species, particularly unionoids. Specific questions that should be addressed include determining differences in diet between species, and how such differences may be governed by food availability, season and differences in gill size and cirral structure. Are filtered food materials coming primarily from the water column or are they resuspended from material that has been deposited to the sediment? How does flow regime influence filtering ability and capacity? What is the importance of nutrient excretion by bivalves to algal and bacterial growth? Finally, we need much more information on the roles burrowing bivalves play in nutrient cycling and storage in both lentic and lotic habitats.

#### *Sediment processes*

Some freshwater bivalve species supplement suspension feeding in the water column by feeding on organic

detritus and bacteria in the sediments, either through filtering interstitial water or by deposit feeding (McMahon, 1991). Filtering interstitial water has been shown for sphaeriid species including many species of *Pisidium* that filter and consume interstitial bacteria (Mitropolskij, 1966; Lopez & Holopainen, 1987), and *Musculium transversum* (Say, 1829) which utilizes an elongated inhalant siphon to vacuum detrital particles from the streambed surface (Way, 1989).

Pedal feeding, a form of deposit feeding using cilia on the foot to collect buried organic matter, may be more common than previously thought in freshwater bivalves. Reid *et al.* (1992) argued that pedal feeding is a primitive bivalve function that is almost universal in juvenile bivalves and common in the adult forms of small species such as sphaeriids (Way, 1989; Way *et al.*, 1990). Pedal feeding has been observed for juvenile unionids, which have been shown to grow faster when able to feed in sediment as compared with filter feeding alone (Hudson & Isom, 1984; Yeager, Cherry & Neves, 1994; Gatenby, Neves & Parker, 1996). *Corbicula* can both pedal and filter feed as adults (Reid *et al.*, 1992), decreasing sediment organic matter concentrations when little planktonic food is available (Cleland, 1988; Hakenkamp & Palmer, 1999).

Deposit feeding may provide a significant proportion of total food energy. For many groups of burrowing bivalves, filter-feeding alone has been calculated to provide < 50% of the total energy needs of a population (Hornbach, Wissing & Burky, 1984b; McMahon, 1991; Boltovskoy, Izaguirre & Correa, 1995; Cahoon & Owen, 1996). In a field experiment in which a Michigan headwater stream was enriched with <sup>15</sup>N, Raikow & Hamilton (2000) showed that unionids were consuming 80% deposited and 20% suspended material. It is unknown whether deposit-feeding bivalves feed primarily on benthic organic matter or strip bacteria from sediment surfaces. Gut content analyses can be misleading because they do not distinguish ingested material from assimilated material (Raikow & Hamilton, 2000). Although initial studies for some species have not supported selective feeding of bacteria in pedal-feeding bivalves (Gatenby, Parker & Neves, 1997; Leff & Leff, 2000), determining whether bivalves are ingesting bacteria is difficult.

Biodeposition of faeces and pseudofaeces by bivalves is an important sedimentation process in

marine systems (Bayne & Scullard, 1977; Tsuchiya, 1980; Smith & Frey, 1985; Navarro & Thompson, 1997) that influences adjacent benthic communities (Reusch, Chapman & Gröger, 1994). In freshwater, biodeposition by epifaunal zebra mussels conveys high-quality pelagic resources to the sediment, resulting in changes in benthic species composition and abundance (Izvekova & Lovova-Katchanova, 1972; Roditi, Strayer, & Findlay, 1997; Strayer *et al.*, 1999). Biodeposition by zebra mussels can increase the local abundance of macroinvertebrates, especially detritivores (Stewart & Haynes, 1994; Ricciardi, Whoriskey & Rasmussen, 1997; Stewart, Minor & Lowe, 1998). Similar impacts have also been shown for the introduced, burrowing *Potamocorbula* in San Francisco Bay (Carlton *et al.*, 1990; Nichols, Thompson & Schemel, 1990).

We know much less about how biodeposits produced by freshwater burrowing bivalves influence lakes or streams (Table 1). Unionids in Lake St Clair (Nalepa *et al.*, 1991) and a Polish lake (Lewandowski & Stanczykowska, 1975) filtered large quantities of seston much of which was which in turn biodeposited to the sediments. In streams, the presence of *Corbicula* is associated with significant increases in nearby sediment organic matter concentrations (Hakenkamp & Palmer, 1999), increasing sediment concentrations as much as 25–30% in the Delta-Mendota canal, California (Prokopovich, 1969).

Burrowing bivalves also bioturbate the sediment as they move about and feed. In marine systems, bioturbation by deposit feeding bivalves can increase oxygen penetration into the sediments (Levinton, 1995) and stimulate microbial metabolism (Dame, 1996). In lakes, burrowing by unionids has been shown to increase sediment water content, sediment homogenization and the depth of oxygen penetration (McCall, Tevesz & Schwelgien, 1979), with larger bivalves mixing sediments at greater rates (McCall *et al.*, 1995). Bivalve activity also affects flux rates of solutes across the sediment–water interface, with unionids enhancing the release of nitrate and chloride, and inhibiting the release of calcium carbonate from the sediments (Matisoff *et al.*, 1985).

In addition to effects associated with biological processes by bivalves, the physical presence of bivalves in streambed sediments may also influence the distribution of other stream organisms in several ways (Table 1). In marine systems, shells can provide a

suitable substratum for the settlement of benthic algae and invertebrates (Wootton, 1992; Navarrette, 1996). Similarly, in lakes and streams unionid shells may provide a clean substratum for both epiphytic and epizoic colonization (Beckett *et al.*, 1996). Interstices between shells may provide refugia from predators and spates, help stabilize fine-grained sediments and increase habitat suitability for other organisms (McCall *et al.*, 1979; Strayer *et al.*, 1994). Organic matter accumulating in spaces between shells may provide both food and shelter (Gosselin & Chia, 1995) that, along with biodeposition of faeces and pseudo-faeces, may increase the abundance of chironomids and other detritivores (Sephton, Paterson & Fernando, 1980).

Uncertainty over the extent and importance of sediment-related ecological processes performed by bivalves represents the most significant gap in our understanding of the role of burrowing bivalves in freshwater ecosystems. Research should focus on the extent to which both adult and juvenile bivalves obtain food from the sediment, specifically what is being consumed (i.e. sediment bacteria, detritus, benthic versus resuspended planktonic algae), and how it is obtained (i.e. actual pedal feeding versus filtering resuspended material). In addition, future studies should investigate the importance of biodeposition, bioturbation and the physical presence of bivalves to both water column and sediment nutrient cycling and to the distribution and abundance of other benthic organisms.

### Resource use and limitation

Evidence of resource limitation in burrowing bivalves is primarily correlative (Table 1). Numerous studies have reported high abundances of bivalves where food concentrations are greatest. For example, high bivalve densities often occur immediately below dam spillways where nutrient levels and thus algal densities are usually high (McMahon, 1991), and in some impacted rivers such areas harbour the only surviving unionid populations (Vaughn, 1997a). *Corbicula* total benthic biomass and individual growth rates are generally positively correlated with phytoplankton abundance or system trophic status (Foe & Knight, 1985; James, 1987; Beaver, Crisman & Brock, 1991). The implication from these studies is that food can limit bivalve distributions.

A factor influencing resource availability is the degree to which bivalves are selective feeders. Some studies have concluded that bivalves feed selectively (Table 1). For instance, Green (1971) examined the distribution of four unionids and two sphaeriids in Canadian lakes and found that species could be separated primarily by diet. Bisbee (1984) and Parker, Patterson & Neves (1998) found differences in the types and percentage of algal species in the guts of riverine unionids. However, it is important to remember that gut analyses may be misleading because they do not distinguish between ingested and assimilated material (Raikow & Hamilton, 2000). Other studies (largely correlative and focusing on pond species) have found that unionids are generally non-selective with a high dietary overlap, ingesting phytoplankton, bacteria and organic material in proportion to their availability (Table 1; Bronmark & Malmqvist, 1982; Paterson, 1984; Silverman *et al.*, 1997; Nichols & Garling, 1999; Raikow, 1999). Further, the use of stable isotopes has also supported high dietary overlap for unionids in a small Michigan stream (Raikow & Hamilton, 2000). *Corbicula* is usually assumed to be a non-selective feeder (Lauritsen, 1986; Way *et al.*, 1990) primarily based on examination of gut contents relative to phytoplankton availability (Boltovskoy *et al.*, 1995; but see Leff, Burch & McArthur, 1990) suggesting that *Corbicula* would be less impacted when any one type of resource might be limiting.

Resource limitation and competitive interactions between suspension-feeding marine bivalves occur at small spatial scales (generally < 1 m<sup>2</sup>) (Buss & Jackson, 1981; Peterson, 1982). Similar interactions would be predicted between different species of freshwater, burrowing bivalves, given that they are all suspension feeders, and often overlap in spatial and temporal distribution as well as in diet. For example, Holopainen & Hanski (1979) proposed exploitative competition as an explanation for the spatial distribution of two *Pisidium* species. DiDonato (1998) used growth measurements to demonstrate competition between two unionids in a food-limited lake, and linked this to differences in filtering abilities between the two species. Thoughtful consideration has been given to the conditions necessary for competition between bivalves (Strayer, 1999).

There are many factors that influence whether food in the water column is under bivalve control (Strayer *et al.*, 1999). As described previously, the rate at which

an individual bivalve filter feeds is a function of bivalve size, water temperature, food concentration and particle size (Table 1). Whether a bivalve assemblage significantly changes availability of resources in the water column depends on bivalve biomass, food replacement rate, and water volume and movement across the bivalve aggregation (Dame, 1996; Strayer, 1999; Strayer *et al.*, 1999). Thus, control of food resources by bivalves is most likely when the biomass of bivalves is large relative to water volume and where hydrologic residence time is long (Lewandowski & Stanczykowska, 1975; Welker & Walz, 1998; Strayer *et al.*, 1999). When these conditions are not met, freshwater systems are usually not found to be under obvious bivalve control (Cahoon & Owen, 1996). Studies to date have primarily focused on water-column suspension feeding. If bivalves are feeding to a large extent on material in the sediment or re-suspended from layers near the bottom, then models limited to water-column suspension feeding may not apply (Raikow & Hamilton 2000).

There are many issues with respect to resource use and potential competition between burrowing bivalves that need to be addressed. Once again our understanding is limited by our incomplete knowledge of bivalve diets. In addition, we need information on whether feeding varies seasonally and with habitat, and whether significant overlap in diet occurs. We also need a clearer picture of the importance of suspension and deposit feeding and the potential tradeoffs between these two feeding modes. Does the availability of various types of food limit the number and diversity of bivalves? Recent developments utilizing identification of stable isotopes in natural food sources and in bivalve populations, as well as experiments tracing added, labelled foods through bivalve populations, have the potential to make a large contribution to answering these questions (Christian & Berg, 2000; Eggers & Jones, 2000; Lajtha & Michener, 2000; Pinnegar & Polunin, 2000; Raikow & Hamilton, 2000).

### **Bivalve decline, invasive species, and ecosystem function**

Freshwater bivalves are threatened and declining globally (Bogan, 1993). This phenomenon has been best documented for rivers in North America. While North American freshwater bivalves are a highly



speciose group (299 species and subspecies of unionids, five species of margaritiferids and 39 species of sphaeriids; Turgeon *et al.*, 1998), more than 70% of these species are considered threatened (Williams *et al.*, 1993; Neves *et al.*, 1997). The largest family, the unionids, historically occurred as dense, multispecies assemblages (Vaughn, 1997b; Vaughn & Taylor, 2000) that dominated the benthic biomass of eastern rivers (Parmalee & Bogan, 1998), especially in undisturbed systems. The biomass of such bivalve assemblages can exceed the biomass of all other benthic organisms by an order of magnitude (Negus, 1966; Layzer, Gordon & Anderson, 1993), and production by these bivalves (range from 1–20 g dry mass m<sup>-2</sup> year<sup>-1</sup>) can equal that by all other macrobenthos in many streams (Strayer *et al.*, 1994). In recent years, many North American unionid and sphaeriid populations have undergone a drastic decline (Eckblad & Lehtinen, 1991; Neves, 1993; Wilson *et al.*, 1995; Neves *et al.*, 1997; Vaughn & Taylor, 1999), and many of these are predicted to go extinct in the next few decades (Shannon, Biggins & Hylton, 1993).

How will this catastrophic loss of bivalve species affect ecosystem processes in North American rivers? If bivalves perform similar ecological processes at similar rates (i.e. they are 'functionally redundant' *sensu* Walker, 1992), these mass extinctions may make little difference in an ecosystem context, as long as the overall bivalve biomass is maintained (see below). If species play distinct roles, however, this loss of biodiversity may permanently alter ecosystem functioning in many rivers. Regardless, it seems reasonable to assume that large numbers of bivalve species (i.e. high biodiversity) may give an ecosystem higher resilience and/or resistance to future disturbance and environmental fluctuations (Walker, 1992; Johnson *et al.*, 1996).

In most cases, both rare and common bivalve species are in decline (Wilson *et al.*, 1995; Vaughn, 1997a; Vaughn & Taylor, 1999). For example, 42% of North Carolina's historically abundant unionid populations are in poor condition and only 31% may remain viable over the next 30 years (Neves *et al.*, 1997). Such a decline represents a significant loss of bivalve biomass. Recent work indicates that the rates of ecological processes performed by bivalves are linearly related to biomass (Strayer *et al.*, 1999; Vaughn, Gido & Spooner, unpublished data). Thus, a significant decline in unionid biomass, regardless of species,

where they historically made up a large proportion of the benthos should result in an alteration of ecological processes and ecosystem function. The degree and significance of such alterations will be context-dependent and vary with bivalve biomass, system size and system stability.

In North America, significant interest has focused on the relationship between native unionids and the introduced *Corbicula*. Like unionids, *Corbicula* burrows in the substratum and filter feeds, however, this species differs from unionids in many important ways. *Corbicula* is less sedentary, shorter-lived (1–5 year), grows rapidly, matures earlier, reproduces two-three times per year, and disperses both actively and passively throughout its life cycle (Prezant & Chalermwat, 1984; McMahon, 1991). Like unionids, *Corbicula* often occurs in dense aggregations (c. 9000 m<sup>-2</sup>; Isom, 1986), that can consist solely of *Corbicula* or be intermixed with native assemblages. *Corbicula* biomass can exceed that of all other benthic metazoans in sandy streams (Poff *et al.*, 1993). While *Corbicula* is typically smaller than unionid bivalves, its markedly greater mass-specific filtration rate (Kraemer, 1979; Mattice, 1979; McMahon, 1983) and typically higher abundance (Kraemer, 1979; McMahon, 1991) result in community filtration rates that often exceed those of native bivalve assemblages (Strayer *et al.*, 1999).

The invasion of *Corbicula* has been speculated to have negatively impacted native bivalve abundance and diversity in North America (Gardner *et al.*, 1976; Taylor & Hughart, 1981; Clarke, 1988). *Corbicula* has the potential to affect unionids in several ways. First, at very high density the burrowing activity of *Corbicula* may uproot unionids in sandy sediments (Fuller & Richardson, 1977). Second, suspension and deposit feeding on juvenile unionids by *Corbicula* may negatively impact juvenile recruitment by unionids (Yeager *et al.*, 1994). Strayer (1999) suggests that *Corbicula* may compete for benthic food resources with sphaeriids and juvenile unionids, and that bioturbation by *Corbicula* could reduce available habitat for sphaeriids. Finally, *Corbicula* have much greater filtration rates (on a per biomass basis) than sphaeriids or unionids (McMahon, 1991) and thus have the potential to limit availability of planktonic food to native bivalves. A recent literature review concludes that experimental evidence for a negative impact of *Corbicula* on native bivalves

is weak and the relationship remains unresolved (Strayer, 1999).

Strayer (1999) reminds us that, if resources are limiting, the winner of exploitative competition is not necessarily the bivalve that feeds at the greatest rate, but the one that can survive and reproduce at the lowest food concentration (e.g. Tilman, 1982). *Corbicula* has a number of life history traits that could favour food acquisition and rapid recovery from gametogenesis. These include high filtration rate, multiple reproductive events per year and a rapid growth rate (McMahon, 1991). *Corbicula* allocates a higher percentage of non-respired energy to somatic growth than unionids (McMahon, 1991). Further, *Corbicula* has the ability to deposit feed, giving it a broader diet breadth when there is little food available in the water column or when flow conditions make suspension feeding difficult (e.g. during floods) than is known for unionids. Deposit feeding by *Corbicula* is likely to have been a mechanism contributing to their invasion success in North America, especially in streams with smaller sediment sizes (e.g. sandy streams) that would allow easy burrowing and feeding.

Bivalves store energy in the form of glycogen (Hemelraad *et al.*, 1990; Naimo *et al.*, 1998). Glycogen stores fluctuate seasonally, typically ebbing during periods of gametogenesis, and decrease rapidly in response to reduced food availability and environmental stress (Williams & McMahon, 1989; Haag *et al.*, 1993; Patterson, Parker & Neves, 1997; Naimo & Monroe, 1999; Patterson, Parker & Neves, 1999). Examining seasonal fluctuations in the glycogen content of bivalves may provide an additional explanation for the decline in North American unionid species diversity (see also Strayer, 1999). If low glycogen stores coincide with periods of low food availability in a stream, bivalves may have reduced tolerance for additional stressors such as competition with exotic species or reduced food availability. In a different stream where food is not limiting, however, the same type of bivalve community would appear to be much more tolerant of species invasions or human interventions. The interplay between energy storage, food availability and environmental stress may help explain the variability in unionid response to the invasion of *Corbicula* (Gardner *et al.*, 1976; McMahon, 1991; Miller & Payne, 1998; Strayer, 1999).

In North American rivers where *Corbicula* has become established, *Corbicula* biomass may replace, or compensate for, lost unionid biomass. If *Corbicula* functions in a manner similar to unionids, then the decline in bivalve biodiversity may have little impact on the functional roles of molluscs in these systems. If species play distinct roles, however, then multispecies assemblages must be maintained to protect ecosystem health and functioning. While unionids and *Corbicula* share many functional roles, differences in the range of processes and the rates at which these processes are performed may be leading to a dramatic shift in the current functional role of burrowing bivalves in some freshwater ecosystems.

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