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The capacity of the filter-feeding bivalve *Mya arenaria* L. to affect water transport in sandy beds

Received: 14 July 2003 / Accepted: 25 November 2003 / Published online: 16 January 2004
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Abstract Benthic filter feeding macrofauna organisms may be an important factor linking sediment and water column. Transport of water and concomitantly of suspended matter is directly related to the size of the benthic filter feeding population. This paper aims to determine the potential for water transport by the bivalve *Mya arenaria* along a coastal stretch of roughly 100 km length in the southern Baltic Sea. Quantification of population filtration rates specific to the area is based on distribution, abundance and biomass of *M. arenaria* and calculated according to previously published filtration rate–biomass relations. Calculated rates range up to $> 8 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ (at 5–20 m water depth in sandy sediment) with the potential to locally process a volume of water equivalent to the water column within < 1 day. Data from 1991–2002 at one site suggest that the area-specific potential population filtration rate remains remarkably constant in time despite changes in population structure of *M. arenaria*. The related impact on pore water exchange within the permeable sediment associated with the leakage of water from the gape of *M. arenaria* valves is discussed.

Introduction

Benthic organisms modify the sediment structure in many ways (Aller 1977; Brenchley 1981; Rhoads and Boyer 1982; Hansen et al. 1996). They couple processes in the sediment to the overlying water through particle deposition and resuspension and solute transport (Aller 1982;

Forster 1991; Kristensen 2001). Bivalves are particularly effective in transporting particulate matter from the overlying water because of the high filtration capacities invoked by their feeding mode. In some species, deposition of feces within or on the sediment leads to increase of organic supply to the sediment (Amouroux et al. 1990; Newell et al. 2002) whereas others eject particulate matter to the benthic boundary layer (BBL) in the process of bioentrainment (Amouroux et al. 1990, 1991). *Mya arenaria*, for instance, has been shown capable of controlling pelagic chlorophyll standing stock in San Francisco Bay at shallow water depths (Nichols 1985).

The soft shell clam *M. arenaria*, which originates from the Northwest Atlantic, has spread into the North Pacific region as well as Northeast Atlantic and Baltic Sea (Franz and Merrill 1980; Scapati 1984; Kube et al. 1996; Zaklan and Ydenberg 1997; Thorin et al. 1998; Strasser 1999). It inhabits most of the Baltic including parts of the Gulf of Finland and Bothnian Bay.

While most epibenthic bivalves pump water into and out of their body cavity without contact to the surrounding sediment, some endobenthic bivalve species provide an unusual contact to the pore water through a gape in their valves. In this case animal–sediment interactions may exist similar to those found for polychaete burrows. Oxidized sediment around the bivalve's retractable siphon has been identified as a site of nitrification (Henriksen et al. 1983; Pelegri and Blackburn 1995) and intensified sulfur reduction (Hansen et al. 1996). The underlying mechanisms for the halo of oxidized sediment, which may be observed along *M. arenaria* shells as an indication of oxygen transport from the body into the sediment has apparently not been investigated so far.

In this study we quantify the area-specific filtration rate of the *M. arenaria* population living in a shallow water area of the southwestern Baltic Sea. Based on an extended data set on distribution, abundance and biomass of *M. arenaria* we calculate filtration rates using a published filtration rate–biomass relation and assess sources of variability and the uncertainty in the numbers calculated.

Communicated by L. Hagerman, Helsingør

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We discuss the impact that *M. arenaria* has on pore water exchange in permeable shallow water sediments.

Materials and methods

The area investigated is located at 0–45 m water depth along the German coast of the southern Baltic between the Islands of Fehmarn and Rügen (Fig. 2). This is a transition area between saline North Sea water [practical salinity units (PSU > 33)] and low-salinity Baltic conditions (PSU ~ 12), as based on direct measurements and a comparison with grain size parameters (Forster et al. 2004).

Sampling took place on 184 occasions at stations indicated in the subsequent figures. Data on abundance and biomass of the benthic filter feeding bivalve *M. arenaria* were collected between 1998 and 2002. Three van Veen grab samples were analyzed per sampling event. This equipment penetrates to 30 cm in soft bottoms, but only to about 10 cm sediment depth in sands depending on the resistance of the sediment. Occasionally siphons were cut off by the closing grab while the shells of *M. arenaria* were not retrieved. We included those large individuals in our abundance and biomass numbers by using a biomass–siphon diameter relation based on measurements of several hundred large individuals from our samples. We cannot, however, judge the percentage of clams not collected. Shallow water sites at < 5 m water depth were not accessible by ship and therefore are under sampled. Only one site at 0.5 m sampled by hand coring was included (10 cm core diameter; $n = 5$).

Samples were sieved through 1 mm mesh and preserved in 4% formaldehyde solution. Ash free dry weight (AFDW) was determined as the difference between dry weight of all *M. arenaria* (60°C for > 10 h; whole animals dried) and ash weight determined after ignition for 4 h at 550°C. AFDW is closely comparable to dry weight of soft tissue because very little ash is retained from soft parts. Maps based on this information were drawn using the software Surfer.

Calculation of the area-specific population filtration rate is based on the abundance, N (ind m^{-2}), and total biomass per m^2 , M (g AFDW m^{-2}). For each sample we calculated a mean individual biomass, M_i (g AFDW), of a hypothetical average individual of *M. arenaria*.

Based on a relation of individual filtration rate, F_i (l ind $^{-1}$ h $^{-1}$), to individual biomass determined at 11°C (Riisgård and Seerup 2004):

$$F_i = 4.76 \times M_i^{0.71} \quad (1)$$

the area-specific population filtration rate, F_{pop} ($m^3 m^{-2} day^{-1}$) was obtained as:

$$F_{pop} = F_i \times N \times 24 \times 10^{-3} \quad (2)$$

Figure 1 shows the relation given by Riisgård and Seerup (2004) along with the regression lines for two groups of clams, buried and fully opened, reported by Lambert-Jensen (1997) and cited by Riisgård and Seerup (2004).

Based on our sampling scheme we cannot differentiate among size classes in our samples, each of which has their biomass-specific filtration rate decreasing with animal size (Jørgensen 1975; Riisgård and Seerup 2004). This fact has little bearing on our conclusions though, since our calculation of F_{pop} is based on average biomass (M_i), which traces the changing biomass-specific rates (compare Eq. 1). We cannot exclude, however, that erroneous F_{pop} could potentially arise from extremely skewed size-class distributions.

Results

Biomass and abundance essentially follow the same pattern (Fig. 2). Highest abundance and biomass is

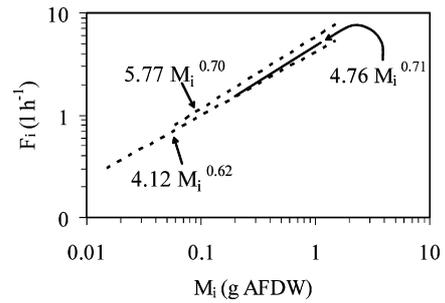


Fig. 1 Relationship of individual filtration rate, F_i , and mean individual biomass as ash free dry weight (M_i g AFDW) used in our calculations (Riisgård and Seerup 2004) ($F_i = 4.76 \times M_i^{0.71}$; Eq. 1). Dashed lines represent similar equations reported by Lambert-Jensen (1997) for buried individuals with partially closed gape (lower; $n = 49$) and fully opened clams (upper; $n = 73$) and cited by Riisgård and Seerup (2004). The length of the lines on the abscissa corresponds to the biomass range give by the corresponding authors

found in the eastern part of the investigation area. Here *M. arenaria* primarily occurs on sandy littoral areas of the Rügen–Falster Plate and off Darss. Here biomass of *M. arenaria* populations reaches between 1 and 30 g m^{-2} throughout the area. Similarly high biomass is found in near-shore sandy areas along a narrow zone off Holstein in the west.

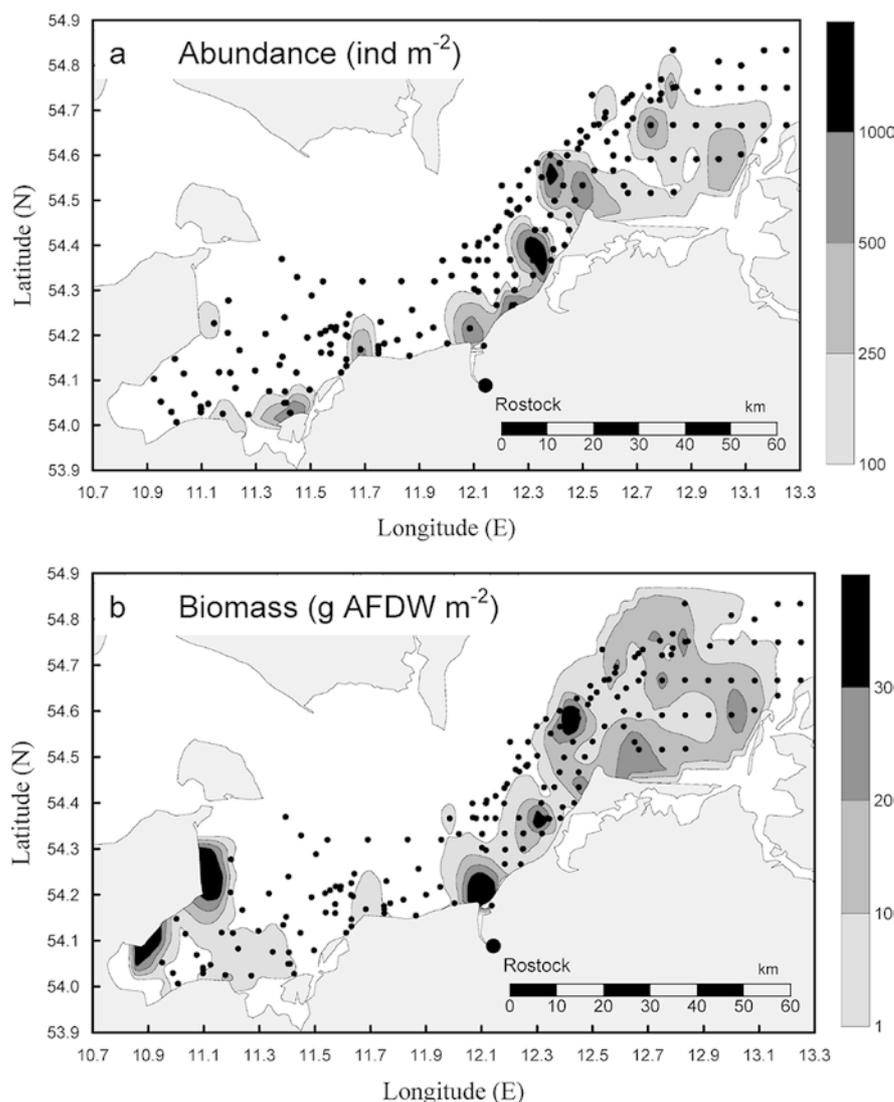
M. arenaria prefers fine to median sand, which dominates the extended shallow grounds in the eastern part of the investigation area. Comparison with the surface sediment grain size characteristics (data not shown) shows a tendency for reduced biomass in areas covered by fine sediment (median diameter < 125 μm). Fine and median coarse sands (125–500 μm) have a tendency to harbor more *M. arenaria* biomass.

Area-specific population filtration rates, calculated from data in Fig. 2, reach up to $\sim 8 m^3 m^{-2} day^{-1}$, with occasional maxima reaching $17 m^3 m^{-2} day^{-1}$ (Fig. 3). The differences in biomass between areas west and east of Rostock result in markedly higher F_{pop} calculated east of 12°E. Here an area with rates $\sim 1 m^3 m^{-2} day^{-1}$ extends halfway across the Danish–German strait.

The occurrence of *M. arenaria* in the study area is limited to water depth < 25 m, which is also the maximum depth to which F_{pop} by *M. arenaria* is effective (Fig. 4). At depths shallower than 20 m values > 1 $m^3 m^{-2} day^{-1}$ are reached. In accordance with the biomass distribution highest F_{pop} are calculated for the 10–15 m depth interval, for instance in the area between 54.55°N/12.4°E and 54.7°N/12.8°E in Fig. 3. Of all the calculated values with $F_{pop} > 0$ day, the majority (62%) were < 2 $m^3 m^{-2} day^{-1}$ (compare Fig. 4, insert). Eighteen percent of $F_{pop} > 0$ lay between 2 and 4 $m^3 m^{-2} day^{-1}$, 9% reached a maximum of 6 $m^3 m^{-2} day^{-1}$, and the highest population filtration rates, ranging from 6 to 17 $m^3 m^{-2} day^{-1}$, represented 11% of all $F_{pop} > 0$.

Except for one single site at 0.5 m water depth, there is no information on the 0–5 m depth interval.

Fig. 2 a Abundance (ind m^{-2}) and **b** biomass distribution (g AFDW m^{-2}) of *M. arenaria* in the investigation area. Dots indicate sampling locations



The scarce data available suggest though that filtration capacity of several $\text{m}^3 \text{m}^{-2} \text{day}^{-1}$ may occur here, too.

In order to evaluate the variation with time we analyzed a long-term data set from a location at 23 m water depth. Figure 5a shows considerable variation of individual biomass, biomass and number of individuals. The observed population dynamics are typical for growth of a single cohort, though we cannot exclude minor recruitment events. Recruitment success in 1992 was followed by continuous decline in abundance and a simultaneous increase of individual biomass. As depicted in Fig. 5b, this development results in maximum F_{pop} calculated from 1993 onwards. Throughout the years 1993–1999 the combined effect of decreasing abundance and increasing biomass results in a filtration rate of $4\text{--}5 \text{m}^3 \text{m}^{-2} \text{day}^{-1}$ (4.6 ± 0.6 ; $n=6$ years). This indicates that the ecological performance may remain stable in this case despite the changing age structure of the population. Since 2001 biomass is small and filtration capacity remains $< 1 \text{m}^3 \text{m}^{-2} \text{day}^{-1}$.

Discussion

Areal filtration in the southern Baltic

M. arenaria is a common endobenthic organism of many sandy shallow water environments. In the Baltic the euryhaline clam (lower limit 3–5 PSU) is distributed to the Bothnian Bay and the Gulf of Finland with the exception of only the innermost parts of these waters (Jagnow and Gosselck 1987; Warzocha 1994; Olenin 1997). Average abundances are 100–1,000 ind m^{-2} and reach maxima just above 10,000 ind m^{-2} in some coastal localities of the southwestern Baltic (Muus 1967; Kube 1996; Kube et al. 1996; Zettler et al. 2000).

Owing to its wide distribution and dominance in biomass in many assemblages of sandy areas, the areal filtration rate of *M. arenaria* is substantial. The majority of calculated rates ($2\text{--}6 \text{m}^3 \text{m}^{-2} \text{day}^{-1}$) indicate that the population of *M. arenaria* could potentially process a volume of water equivalent to the water column within

Fig. 3 Calculated filtration capacity ($\text{m}^3 \text{m}^{-2} \text{d}^{-1}$) of the *Mya arenaria* population. Numbers are based on abundance and total biomass determined at each sampling site (dot). Mean individual biomass, M_i , was calculated from total biomass, M , and abundance, N , and converted to an individual filtration rates, F_i , using the relation given by Riisgård and Seerup (2004). These numbers were then multiplied by the abundance to yield area-specific population filtration rates, F_{pop}

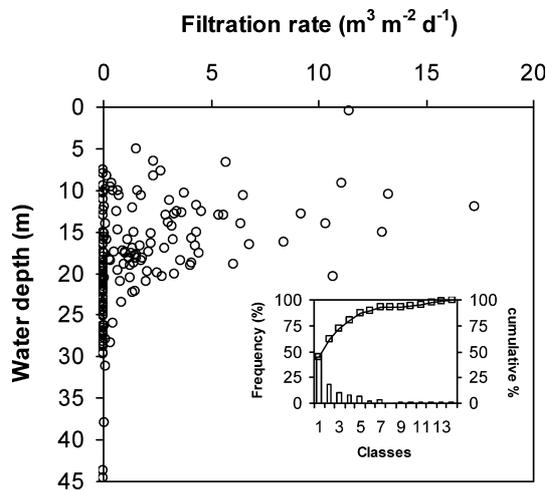
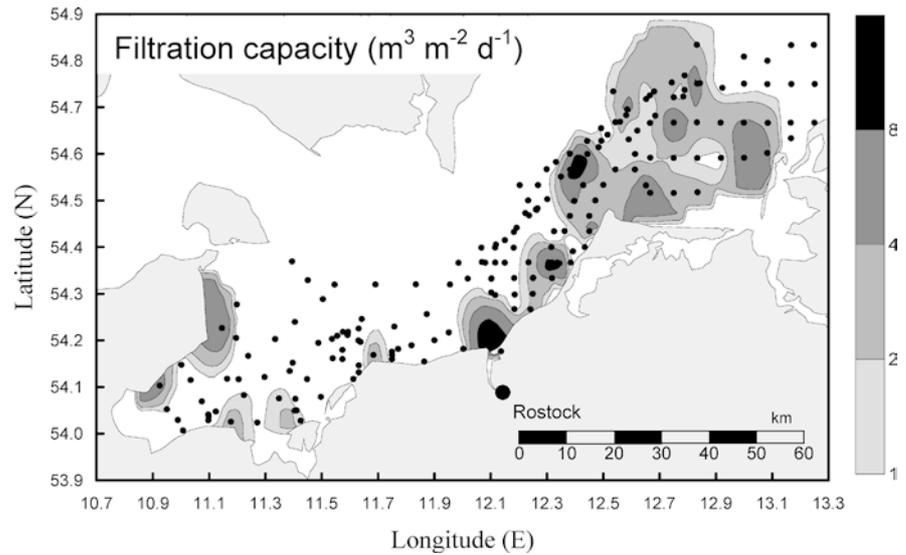


Fig. 4 Depth distribution of area-specific population filtration rates. Depths shallower than about 5 m are under sampled owing to limitations by ship draught. *Insert* shows absolute (*bars*) and cumulative (*squares*) distribution of the calculated values of filtration capacity in classes of $1 \text{ m}^3 \text{m}^{-2} \text{day}^{-1}$. About 62% of all *Mya* populations show a capacity of up to $2 \text{ m}^3 \text{m}^{-2} \text{day}^{-1}$

1–10 days, depending on water depth. At some shallow locations $< 10 \text{ m}$ (e.g. at 9 m water depth, $11 \text{ m}^3 \text{m}^{-2} \text{day}^{-1}$) this water column of equivalent volume may be filtered in less than a day. Assuming a vertically well-mixed water column, which is the case for part of the year at the shallower sites, the half-life of suspended matter may be determined as low as half a day. At a site of 0.5 m water depth in the Baltic and a filtration rate of $\sim 11 \text{ m}^3 \text{m}^{-2} \text{day}^{-1}$, the populations of *M. arenaria* effectively turn over a volume of water equivalent to the water column several times per day. This filtration capacity corresponds to that of other benthic filter feeders (Riisgård et al. 1996). At water depth $< 5 \text{ m}$ *M. arenaria* is likely to affect the water even more by filtration. Nichols (1985) found that a *M. arenaria* population in San Francisco Bay, Calif. filtered up to 4 m of the water column daily, though these authors

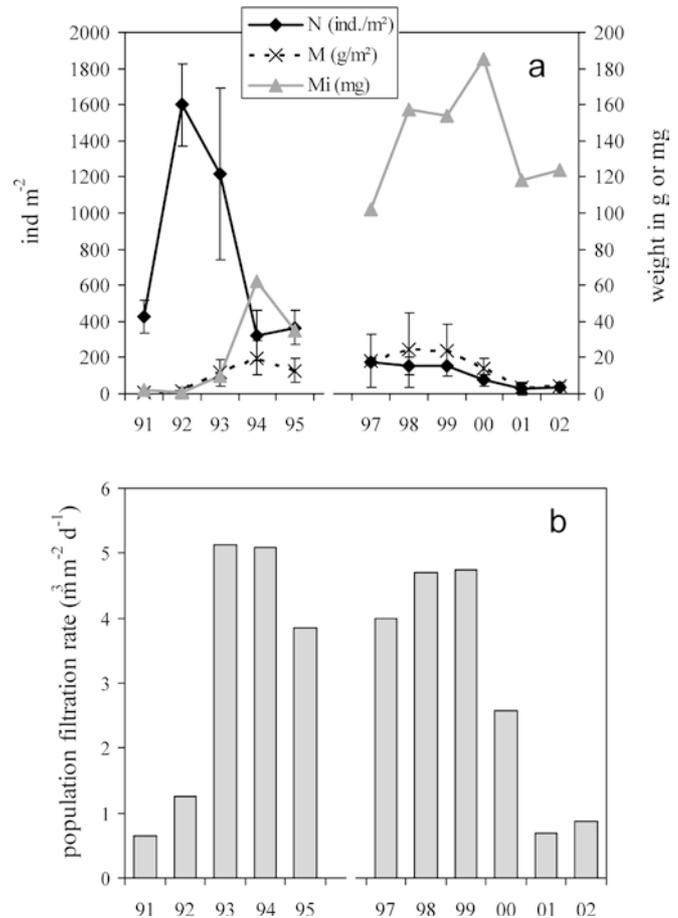


Fig. 5 **a** Time course from 1991–2002 (1996: no data) of abundance, N , mass (M), and individual mass (M_i) at location $54.72^\circ\text{N}/12.75^\circ\text{E}$. Means and standard deviation are given for three grab samples taken per sampling event. **b** Calculated area-specific population filtration rates, F_{pop} , for the same site. During the years 1993 through 1999 and excluding 1996, an average value of $4.6 \pm 0.6 \text{ m}^3 \text{m}^{-2} \text{day}^{-1}$ is obtained

calculated with a different filtration rate–biomass relation (McDowell Capuzzo and Sasner 1977) yielding comparatively low filtration rates.

Wave conditions and substrate do not seem to restrict *M. arenaria* growth at these depths. Predation and patchiness owing to cohort settlement are more likely to affect abundance and biomass in the shallow areas (Emerson and Grant 1991; Strasser 1999). At the location sampled between 1991 and 2002 (Fig. 5) growth of the *M. arenaria* population seems to be dominated by one cohort. Average individual weight almost continuously increases while abundance declines dramatically. Kühl (1981) reports a similar reduction in abundance from 1,500 to ~ 100 ind m^{-2} from the Wadden Sea as the animals grow from age 3 to 7 years. The interesting aspect in the present context is that the calculated filtration capacity remains comparatively constant at $4.6 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ from 1992 to 1999. This indicates that the ‘population filtration rate of *M. arenaria*’, an ecosystem function, may vary little within a wide range of abundances ($200\text{--}1,600$ ind m^{-2}) and biomass values ($2\text{--}23$ g AFDW m^{-2}).

Benthic filter feeders access water close to the sea floor for their carbon supply and are not likely to filter the entire water column above them. The amount of carbon present in the BBL needed to sustain the bivalve population can be roughly constrained and used for a check on the filtration volumes calculated.

We use a P/B ratio for *M. arenaria* between 0.4 and 2.5 (Gray 1981), a respiratory quotient of 1.0 and 50% of the AFDW to be organic carbon. The median of the standing stock biomass, 0.86 g m^{-2} , requires $6\text{--}9 \text{ g C m}^{-2} \text{ year}^{-1}$ of food. The corresponding population filtration rate amounts to $0.3 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$. Bottom water typically contains $1\text{--}3 \text{ mg dm}^{-3}$ of total particulate matter combining roughly 30 weight-% organic carbon (Turnewitsch and Graf 2003). This is equivalent to $30\text{--}90 \text{ g C m}^{-2} \text{ year}^{-1}$ available from the filtered water volume and below $150\text{--}200 \text{ g C m}^{-2} \text{ year}^{-1}$ available from primary production in the area.

In the field, stratification, refiltration of water (O’Riordan et al. 1995), resuspension of benthic material, and the degree of coupling between benthic filter-feeders and fresh phytoplankton modify the actual uptake of POC by *M. arenaria*. The calculation demonstrates, that nutritional requirement of the benthic *M. arenaria* population are easily met.

Critical assessment of the calculated values

Our calculations are based on the formula reported by Riisgard and Seerup (2004), which does not extend to very small individuals. Using the unpublished results by Lambert-Jensen (Fig. 1), F_i values 6% higher for a 600 mg individual and 13% higher for a 50 mg individual are calculated. Thus, with either regression applied, the calculated F_{pop} vary within a very narrow, negligible range.

Temperature has an influence on filtration rates, and the rates calculated here for 11°C . Riisgard and Seerup (2004) published a temperature dependence of individual filtration rates for *M. arenaria*. This can be used to recalculate F_{pop} for 2°C and 20°C , the typical annual temperature interval in the region. For either deviation from 11°C , F_{pop} decreases and increases by 50%, respectively.

Acknowledging that the calculated F_{pop} are derived from maximum individual filtration rates, we will proceed to discuss other factors that can influence F_{pop} in order to assess the robustness of the estimate.

The soft clam *M. arenaria* may not exploit the filtration capacity in the field because of time intervals with reduced filtration activity. Our application of laboratory derived filtration rates applied here neglects a response to food quality and abundance. Mechanisms and controls of the filtration performance in the field are poorly known (Cranford 2001). Riisgård et al. (2003) assume that mussels reduce pumping below a level of $\sim 0.5 \mu\text{g Chl a dm}^{-3}$ in response to nutrition limitations. Typical chlorophyll a (Chl a) concentrations within 40 cm above the sea floor are $1\text{--}5 \mu\text{g dm}^{-3}$ during summer (Jaehmlich et al. 1999). During winter conditions the soft shell clam may frequently experience below threshold levels of chlorophyll. When conditions are lean *M. arenaria* reduces the shell gape (Jørgensen and Riisgård 1988), thus reducing pumping rates to 1/4 of the values determined in wide open clam, and eventually closes and retracts the siphon. Thorin et al. (1998) used siphon aperture to infer activity of *M. arenaria*. They report activity intervals of 12 h per day from field observations, which were confirmed by Betke (2002) in laboratory experiments. Unfortunately, the reduction of pumping rate and siphon aperture are not linearly correlated (Riisgård et al. 2003). Assessment of the activity status in the field remains speculative without either continuous chlorophyll records close to the bed or video observations combined with an experimentally derived siphon aperture to pumping rate relation.

In situ filtration is further influenced by a patchy distribution of *M. arenaria* as indicated by the error bars in Fig. 5. This may locally increase or decrease in situ filtration rates compared to F_{pop} calculated. Different life stages affect calculated F_{pop} , since filtration rates are generally a function of body size and biomass. When biomass changes at constant body size (e.g. spawning, starvation) the filtration rate–biomass relation may be affected accordingly and the estimated filtration capacity of a population would be erroneous.

In summary in situ filtration may deviate towards larger as well as smaller values compared to population filtration capacity calculated here. Intervals of reduced activity will tend to reduce in situ area-specific population filtration rates.

Irrigation of sediment through leakage

M. arenaria has been shown to affect sulfate reduction, nitrification and total oxygen uptake of sediments

(Henriksen et al. 1983; Pelegri and Blackburn 1995; Hansen et al. 1996). All these investigations focus on the effect that the siphon exerts on the sediment as it extends and retracts. A pronounced halo of oxidized sediment visible along the body of the clam in reduced organic rich sediments (Betke 2002), however, indicates that oxygenated water leaks from the clam at the gape where valves do not entirely enclose the soft body. Below we combine several observations to estimate the magnitude of this sediment irrigation.

Investigating individual *M. arenaria* in laboratory experiments, Betke (2002) detected transport of oxygen and bromide tracer ions at the gape of *M. arenaria* in a permeable sediment (permeability, $k = 3\text{--}6 \times 10^{-12} \text{ m}^2$). O_2 concentration monitored continuously in the laboratory revealed that oxygen transport into the adjacent sediment is coupled to filtration activity and concentrations reached $\sim 50\%$ O_2 saturation. Reduced NH_4^+ concentrations in the pore water surrounding the clam and results of tracer experiments further indicated transport higher than diffusive flux from the gape into the sediment (Betke 2002).

An estimate of leakage rates from the gape may be obtained from Darcy's Law (Darcy 1856),

$$Q = k_i \times A \times p \times l^{-1} \quad (3)$$

which relates mass flux of interstitial water (Q , in ml) to an external pressure (p) and hydraulic conductivity (k_i) of the permeable sediment. For *M. arenaria* we assume a geometry where horizontal plug flow into the sediment occurs from a vertically orientated gape area.

We assume $k_i = 0.006 \text{ cm s}^{-1}$ (equivalent to permeability $\sim 5 \times 10^{-12} \text{ m}^2$). The area of the gap between the valves, $A = 2.5 \text{ cm}^2$, across which leakage is assumed to occur corresponds to a large individual with $M_i = 750 \text{ mg AFDW}$. Pressure driving the flow is produced by the gill pump of the bivalve. We assume the range of 1–3.5 mm H_2O given by Jørgensen and Riisgård (1988). The length of the path along which the water flows, $l = 4 \text{ cm}$, equals the horizontal distance across which Betke (2002) observed effects on pore water composition.

The leakage rate thus calculated amounts to 2–5 ml h^{-1} for a sizable individual under the given circumstances. This corresponds to 0.1% of the water filtered by the same size bivalve according to Eq. 2 (3,881 ml h^{-1}). The result agrees with the notion that most of the water filtered by *M. arenaria* actually leaves the exhalant siphon. The relatively small volume leaking from the clam, however, is by no means negligible for sediment geochemistry.

The simplified geometry of flow assumed may differ considerably under natural conditions. Also the volume leakage probably varies with body size and is a function of the pressure generated by the clam. Provided that the leakage expressed as a percentage of the filtration remains constant, our data suggest that 1 $\text{l m}^{-2} \text{ day}^{-1}$ pore water may be displaced by water leaking from *M. arenaria* for every 1 m^3 filtered $\text{m}^{-2} \text{ day}^{-1}$. This

volume is equivalent to a sediment layer of 0.25 cm thickness in which the pore water is exchanged (porosity: 0.4). Sediments with abundances of *M. arenaria* $> 250 \text{ ind m}^{-2}$ are generally at least as permeable as assumed in the above calculation (Forster et al. 2004). In some areas shown in Figs. 3 and 4 F_{pop} exceed $1 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$. Here the irrigation flux would strongly dilute concentrations of solutes in sediment layers of $> 2 \text{ cm}$ thickness and stimulate microbial processes requiring oxygen. This suggests sediment irrigation by *M. arenaria* as an important process and ecosystem function to be noticed.

M. arenaria has profound influence on the sediment via its suspension feeding lifestyle. The clearance of particulate matter from the water column has the capacity to turn over suspended matter within a few days in much of the coastal areas of the southern Baltic. In addition, leakage of water from the shell gape as a mechanism of sediment irrigation has potential impact on sediment biogeochemistry. The combined activities by *M. arenaria* of particle and solute transfer from the water to the sediment in coarse permeable sediments are likely to cause considerable variability in pore water solute concentration, as often observed in sandy sediments.

Acknowledgements We wish to thank Doreen Betke for discussions about the leaking soft shell clam and for sharing observations. Ines Glockzin and Christine Peters helped sorting many benthos samples including those with *M. arenaria*. H.-U. Riisgård made us aware of new results on filtration rates of *M. arenaria* and his constructive criticism on an earlier version improved this manuscript. We appreciate the help of two anonymous reviewers.

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